

## Spatial Patterns of Seed Dispersal by White-Faced Capuchins in Costa Rica: Evaluating Distant-Dependent Seed Mortality

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### ABSTRACT

Spatial patterns of seed dispersal are the focus of numerous theoretical examinations of endozoochory. Here, we examine the spatial pattern of seed dispersal by white-faced capuchin monkeys *Cebus capucinus* in Santa Rosa National Park, Costa Rica, and the neighborhood characteristics and distance variables most closely associated with seed survival and germination, and seedling survival and growth in various locations. Overall, distance to the nearest fruiting conspecific tree has the most positive, consistent effect on growth and survival variables, which supports a variation of the Janzen–Connell seed escape hypothesis.

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*Key words:* *Cebus capucinus*; Santa Rosa National Park; seed escape hypotheses.

THERE ARE NUMEROUS WAYS OF MEASURING the effect of animals on the seeds of the fruit they disperse (Schupp 1993). These include disperser selection for seed and fruit traits (Russo 2003), variation in seed-handling strategies (Chapman & Russo 2007), variation in postdispersal seed fate (Forget & Wenny 2004) and effects of behavior and ranging on postdispersal seed mortality (Zhang & Wang 1995). Another important aspect of seed dispersal is the impact of distance and seed distribution patterns on germination, growth, and seedling survival (Lambert & Chapman 2005). The spatial dimension of dispersal is particularly important as it is central to understanding the survival, recruitment and population dynamics of tropical forest trees (Link & Di Fiore 2006), as well as being the focus of most theoretical attempts to understand the process of endozoochory (Janzen 1970, Connell 1971, Howe & Smallwood 1982, Chapman & Chapman 1996). Most hypotheses rely on distance and density as the critical variables not only in seed survival (Chapman & Chapman 1996), but in the resultant structure of forests (Clark & Clark 1984), the maintenance of species diversity (Harms *et al.* 2000), and the very existence of angiosperms (Sussman & Raven 1978).

All current models used to explain the consequences of seed dispersal by animals posit that the reproductive benefit to the plant is affected by the distance and density that seeds are deposited, and the location of deposition (Howe & Smallwood 1982, Chapman & Chapman 1996, Nathan & Casagrandi 2004). Empirical support for density-dependent mortality at some life stages for some plant species has been documented (Clark & Clark 1984, Howe 1990, Condit *et al.* 1992, Harms *et al.* 2000). The oft-cited Janzen–Connell model predicts higher seed mortality beneath parent trees due to an increased incidence of distance- and density-responsive seed predators, pathogens, and herbivores (Janzen 1970, Connell 1971). Seeds that are dispersed away from the parent plant should

escape this local concentration of predators and pathogens, resulting in increased survivorship (Janzen 1970, Connell 1971). Seed survival and seedling recruitment will thus be higher at some distance away from the parent plant, and density-dependent and distance-responsive recruitment will limit the ability of abundant species to reproduce, resulting in the maintenance of species diversity in tropical forests.

The aim of this study is to evaluate the Janzen–Connell model in the context of seed dispersal patterns produced by white-faced capuchins. We do so by evaluating the effect of distance variables and neighborhood characteristics at actual seed dispersal locations on seed survival and germination, and seedling establishment and growth.

### METHODS

**STUDY SPECIES AND SITE.**—The study took place in the Santa Rosa sector of the *Area de Conservacion Guanacaste* (ACG), in north-western Costa Rica (10°50' N Latitude, 85°38' W Longitude). Much of the forest of the Santa Rosa sector is deciduous, tropical dry forest, with fragments of semievergreen and riparian forest at various stages of growth, as well as regenerating pasture land (Janzen 1983). Santa Rosa is home to three species of nonhuman primate, including several habituated groups of white-faced capuchins, *Cebus capucinus* L. 1758. Two of these groups were the focus of this study: Cerco de Piedra (CP) group composed of 19 individuals, and Los Valles (LV) group, composed of 17 individuals. All monkeys were individually identifiable based on size, sex, facial markings and scars.

**BEHAVIORAL DATA COLLECTION.**—During 8 months of study (May–July 2005, January–May 2006), two observers collected behavioral data and fecal samples from all adults in both groups ( $N = 16$ ) during focal follows. We conducted 50 follows for a total of 393.5 h. Each day two observers continuously observed one adult monkey all day or for as long as possible. The mean duration of

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follows was 7 h 43 min with a range of 2 h 12 min–12 h 53 min. We discarded focal follows where the focal animal was not fully visible for > 10 percent of follow time. We recorded behavioral and defecation data using a hand-held data logger (Psion Workabout MX, Psion Teklogix Inc., Mississauga, ON, Canada) and location data using a Garmin GPS unit.

Each time the focal animal fed on fruit, we recorded this observation in the data logger along with the tree species and the number of trees of that species that the focal animal fed on during the follow. A fruit-eating bout began when the focal animal picked or bit the first piece of fruit, and ended when the focal animal left the tree, changed behavioral state, or continued to forage but did not pick or eat fruit for 30 sec. We recorded a waypoint for each tree, with the same name and number as was recorded in the data logger.

Each time the focal animal defecated, we recorded the defecation event and number in the data logger, took a waypoint, and collected feces. We returned fecal samples ( $N = 549$ ) to the lab, where seeds were counted and their species and number recorded.

**SPATIAL DATA COLLECTION.**—We determined the distance a seed traveled from the parent tree by counting back from a defecation event containing a seed to that species of tree within our observed range of capuchin gut passage time (35 min–5 h). We determined the range of gut passage times in our study subjects using the following method: whenever a species of a fruit was consumed only once during one of our focal follows, we calculated the time between its consumption and defecation. The range of gut passage times that we estimated in this way for our study animals is consistent with the range of gut passage times that Wehncke *et al.* (2003) observed for wild white-faced capuchins in Panama when they consumed rarely eaten fruits (mean =  $94 \pm 43$  min) and consistent with the range found for captive white-faced capuchins fed four cultivated fruit species (mean time for > 75% of seeds to appear =  $105 \pm 38$  min). In cases where multiple individual trees of a species were consumed during a single follow, where the exact parent tree was not known, we used Wehncke *et al.*'s (2003) mean of 105 min to 'seed appearance' to identify the parent tree.

We determined the distance between the parent tree and the defecation event by comparing the distance between the waypoint records for the parent tree and defecation event using GPS mapping software (Ozi Explorer). We calculated distances between consecutive defecations using GPS mapping software (Ozi Explorer) for all those cases where the focal animal was continuously in sight at all times from the first defecation to the subsequent one.

**EXPERIMENTAL PLOTS.**—We placed seeds from fecal samples of the five most commonly ingested and passed species (*Acacia collinsii* [AC], *Casearia arguta* [CA], *Sciadodendron excelsum* [SE], *Trichilia martiana* [TM] and *Genipa americana* [GA]) back in the feces in which they had been deposited. Seeds were variable in size (mean  $\pm$  SD): AC:  $6.8 \pm 0.8$  mm,  $N = 99$ ; GA:  $7.7 \pm 1$  mm,  $N = 99$ ; SE: < 2 mm; TM:  $5.7 \pm 0.5$  mm,  $N = 103$ ; CA:  $2.3 \pm 0.3$  mm,  $N = 80$ . Seeds in feces were returned to between five and ten defecation locations (hereafter, experimental plots) within 48 h of col-

lection. A portion of collected seeds remained in the lab and were planted in soil and raised to seedlings for use in seedling plots.

Plot locations were determined in the following manner: For each species, we compiled a list of distances of defecations from parent trees. We then chose the defecation event that was closest to the parent tree for each species, the defecation event that was furthest from the parent tree for each species, and three to eight intermediate defecation events (Table S1). Once several defecation locations and parent trees were identified for a species, feces were collected and placed at experimental plot locations within 48 h of feces collection.

At each experimental plot, we placed four piles of ten seeds of a single species on the forest floor a minimum of 1 m away from each other. Exclosures were not used to avoid positively skewing survival rates, since terrestrial seed predators are found at the study site (Chapman 1989). At each experimental plot, we also planted between four and six lab-raised seedlings a minimum of 1 m away from each other. We tagged each seedling with a numbered aluminum tree tag. We recorded data on neighborhood characteristics at the time of planting, as well as the following information about each seedling: height of the stem (hereafter height), number of leaves, length of the longest leaf, and leaf state. We recorded leaf state as undamaged (all leaves), some damage (one or more leaves) or completely destroyed/gone. We took measurements using vernier calipers.

Neighborhood characteristics recorded for each pile and seedling were percentage of canopy openness (hereafter canopy cover), distance of piles from the nearest fruiting conspecific tree (Table S1), diameter at breast height (dbh) of the nearest fruiting conspecific tree, and distance to the parent tree (Table S1). We determined canopy cover using a spherical concave densiometer. We determined the distance of the nearest fruiting conspecific by walking in ever-increasing rings around the plot and recording a waypoint for each adjacent fruiting conspecific tree, up until the distance of the parent tree. We checked all piles and seedlings for disappearance, germination, seed establishment and seedling growth and damage 3 d after deposition/planting, and every 7 d thereafter until the end of the study period, and recorded all cases of disappearance, germination, seedling establishment, seedling damage and seedling growth.

**ANALYSIS.**—We conducted separate backward stepwise logistic regressions to determine the effects of neighborhood characteristics and distance variables on categorical measures of seed survival and germination, and seedling survival. Neighborhood characteristics and distance variables used in this analysis are: distance from the parent tree, percentage of canopy openness, distance to nearest fruiting conspecific tree, and dbh of nearest fruiting conspecific tree on four different dependent variables. The dependent variables are: (1) whether there were seeds/germinated seeds/seedlings present at the end of the study period for the three species for which any seeds survived to the end of the study period (GA, CA and SE); (2) whether seeds germinated, given that there were seeds remaining in the piles at least 10 d after deposition; (3) whether seedlings established in those piles where one or more seeds had germinated;

(4) whether seedlings survived in experimental plots to the end of the study period for the four species where seedlings survived to the end of the study period (GA, AC, CA and TM). The pile, and not the individual seed, is the unit of analysis.

We conducted separate backward stepwise regressions to determine effects of neighborhood characteristics and distance variables on continuous measures of seed survival and germination, and seedling survival. Neighborhood and distance variables used in this analysis are distance from the parent tree, percentage of canopy openness, distance to nearest fruiting conspecific tree and dbh of nearest fruiting conspecific tree. The three dependent variables used in this analysis are (1) the number of days since seed deposition prior to seed disappearance; (2) seedling growth, measured as the change in seedling height, length of longest leaf, number of leaves; and (3) seedling damage. We calculated change in the first three variables as the percentage increase between values at planting and at last measurement. We measured damage as the percentage of records where each plant was recorded as damaged vs. undamaged.

Unless stated otherwise, we conducted all analyses in SPSS for Windows 14.0.

## RESULTS

Capuchins dispersed seeds an average of 235.6 m away from the parent tree (range 4–757 m,  $N = 333$ ; Fig. 1), and defecated seeds an average of 136 min after ingestion (37–355 min,  $N = 373$ ). The average distance between two consecutive defecation events was 81 m (0–677 m,  $N = 434$ ). The average time between two consecutive defecations was 28.3 min (12 sec–292 min,  $N = 434$ ).

Of the three species for which seeds survived until the end of the study period (GA, CA and SE), dependent variables of two species were significantly affected by the neighborhood characteristics and distance variables measured here (Table S2). Of the four species whose seeds germinated in experimental plots (GA, CA, AC and SE) dependent variables of one species were significantly affected by the distance and neighborhood variables measured here (Table S2). Of the two species whose germinated seeds also established as seedlings (GA and CA), neither had dependent variables that were sig-

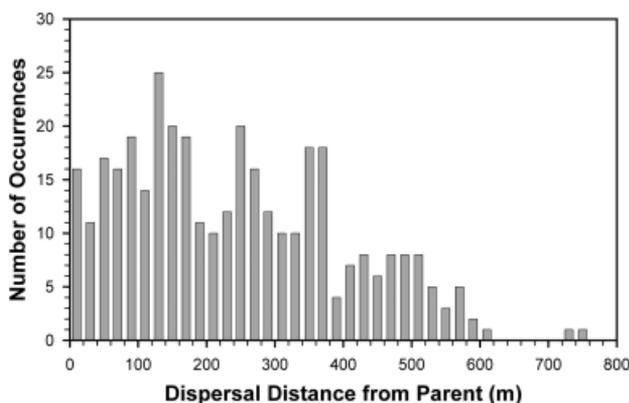


FIGURE 1. Frequency distribution of the distance seeds deposited from parent trees.

nificantly affected by the distance and neighborhood variables measured here. Of the four species for which seedlings survived until the end of the study period, the dependent variables of two were significantly affected by the distance and neighborhood variables measured here (Table S2).

The number of days that elapsed before the disappearance of all seeds from experimental plots was affected by a minimum of one of the distance and neighborhood variables in the case of each of the five species for which seed experimental plots were established (Table S3). At least one aspect of seedling growth or damage, measured here as an increase in seedling height, longest leaf length, number of leaves and percentage of time spent damaged, was significantly affected by one or more neighborhood variables for each of the five species analyzed (Table S4). The dependent variable most commonly affected across all species by neighborhood variables was longest leaf length, though each of the four dependent variables measured here were affected in at least one species by at least three of the independent variables measured here.

The independent variable most responsible for variation in seedling growth and damage across all species was the distance to nearest fruiting conspecific tree. Distance to nearest fruiting conspecific tree significantly affected each of the four dependent variables, in three of the five species.

## DISCUSSION

The independent variable that had the most consistent effect on seed survival to the end of the study as well as on seed germination was distance to the nearest fruiting conspecific tree. Both seed survival and the likelihood of germination increased as a function of the distance of the nearest fruiting conspecific tree for two of the three species for which seeds survived to the end of the study (GA and CA). However, while seeds of the species SE also survived to the end of the study period and germinated, none of the independent variables measured here had any effect.

Distance to the nearest fruiting conspecific tree also consistently affected the duration of seed survival, as well as the number of days that elapsed before the disappearance of all seeds for each of the five species analyzed here. In the case of seeds of the species GA, CA and AC, the duration of seed survival increased as a function of distance to the nearest fruiting conspecific tree. In the case of seeds of the species TM and SE, the number of days that elapsed before the disappearance of all seeds decreased as a function of distance to the nearest fruiting conspecific. While the other variables had an effect on the duration of seed survival in the case of at least one species (canopy cover, two cases; dbh of nearest fruiting conspecific, two cases; distance to parent, one case) these variables were not consistently significant, and were not always consistent in the direction of their effect.

The trend for at least three of the five species analyzed here is that an increase in distance between a defecated seed and the nearest fruiting conspecific tree results in an increase in survival and germination. Interestingly, the two species for which distance to nearest fruiting conspecific tree did not correlate with increased survival and germination are also the only two species in this sample that do

not show increased germination potential with capuchin gut passage (Valenta & Fedigan 2009), and that exhibit signs of a bird dispersal syndrome, having small, unprotected, unhusked, brightly colored fruits (see Janson 1983, Link & Stevenson 2004). The remaining three species—and those for which gut passage increases germination—exhibit signs of a mammal-dispersal syndrome (Janson 1983). This indicates that the importance of dispersal away from the parent crown may be specific to individual trees and be related to that species' strategy of seed dispersal.

Working in Santa Rosa National Park, Costa Rica, Hubbell (1979) found that adult trees exhibiting different dispersal syndromes (wind, bird and bat, mammal) were dispersed in different patterns from one another, in separate clusters along a leptokurtic continuum. Presumably, any forces working toward or against this pattern (*e.g.*, the need for a seed of a given species to escape the crown of the parent tree in order to avoid predation) would be reflected in the factors affecting seed survival and germination (Russo 2003). This is perhaps what we are seeing here.

Three of the five species for which seedling survival and growth were analyzed showed increased survival and growth rates for at least one measure as an effect of distance to the nearest fruiting conspecific tree (CA: number of leaves, leaf length; TM: height, number of leaves, leaf length; GA: leaf length, damage). In only one case (TM: seedling damage) was the effect reversed. With seedlings, as with seed survival and germination, the distance to the nearest fruiting conspecific tree accounts for most of the variation in survival and growth, and, along with dbh of nearest fruiting conspecific, is largely consistent in the direction of its effect. The other independent variables measured here were not consistent in the direction of their effect. Additionally, here, as with seed survival and germination, seedlings of the species SE were not responsive to the distance of the nearest fruiting conspecific.

Overall, across species and survival and growth variables, the distance to the nearest fruiting conspecific tree was the most consistent and frequent predictor of seed and seedling survival, germination, and growth. Of the 24 dependent variables that were affected across all species by the distance to the nearest fruiting conspecific tree, only three showed decreased benefit as a function of distance. All species in this analysis had several dependent variables that were affected by the distance to the nearest fruiting conspecific, except SE. Interestingly, SE seeds were also unusual within this sample in other ways: SE seeds did not show increased germination potential with capuchin gut passage, unlike most of the other seeds sampled during this study (Valenta & Fedigan 2009), and this species' characteristics indicate a bird dispersal syndrome: small, unprotected, unhusked, brightly colored fruits (see Janson 1983, Link & Stevenson 2004). This indicates that the importance of dispersal away from the parent crown may be specific to individual trees and be related to that species' strategy of seed dispersal (Hubbell 1979).

Canopy cover, while affecting 11 dependent variables of four different species, showed an inconsistent directionality of effect. Five of the 11 affected variables showed increased benefit with greater canopy openness, while six showed a decrease. It is interesting to note that four of five cases of increased benefit with canopy

openness occurred for the species AC, which was the only 'pioneer' species in this sample (Janzen 1983).

The dbh of nearest fruiting conspecific tree showed a consistent directionality of effect, with five or six of significant effects across three species showing decreased benefit in relation to the dbh of the nearest fruiting conspecific across three species. The single case of increased benefit occurred for seeds of the species SE. Again, this species was the exception.

Distance to the parent tree had, overall, less of an effect than distance to the nearest fruiting conspecific tree and canopy cover. Additionally, this variable did not consistently affect the dependent variables measured here. Five of the nine affected variables were positively affected as a result of distance to the parent tree, while the remaining four were negatively affected.

Thus while the Janzen–Connell model is not supported, a variation of it is, as seeds that are dispersed a greater distance from any fruiting tree of the same species increase the likelihood of survival and germination. This is a logical extension of the Janzen–Connell model: if distance from the parent tree is the crucial variable in seed survival and seedling growth due to the resultant proximity of host-specific predators, then proximity to any other fruiting tree of that species should be equally crucial to seed and seedling survival as they will also harbor at least some of the same host-specific predators as the parent.

Additional support for a revised version of the Janzen–Connell model comes from the effect of dbh of nearest fruiting conspecific trees on seed survival and germination and seedling growth. Dbh is a measure of fruit production (Chapman *et al.* 1994), and dbh of the nearest fruiting conspecific tree consistently negatively affects seed survival and germination, and seedling growth. A larger fruit crop would likely be coincident with a higher local density of species-specific seed and seedling predators, and thus result in higher rates of secondary predation. That is the trend in our data, lending further credence to a revised version of the seed escape hypothesis.

Elsewhere, results from tests of the Janzen–Connell hypothesis are mixed, suggesting that these processes may be site- or species-specific. One review of 24 datasets found that most showed patterns of distant- and density-dependent mortality (Clark & Clark 1984). Several subsequent field studies have also supported the predictions of the model (Yamada & Suzuki 1997, Harms *et al.* 2000, Packer & Clay 2000, Wehncke *et al.* 2004). However, some studies provide evidence to the contrary (*e.g.*, Burkey 1994). One study involving 80 species found that more species showed a significant increase in recruitment closer to adults than a significant decrease (Condit *et al.* 1992), and a meta-analysis of the hypothesis involving datasets from 40 studies found that on average, distance to parent did not enhance survival (Hyatt *et al.* 2003). Still other studies have resulted in both supporting and conflicting evidence within sites, and between species (Cintra 1997, Gilbert *et al.* 2001, Stevenson *et al.* 2005, Chapman & Russo 2007).

The pattern in our data supports a variation of the Janzen–Connell model of distant-dependent seed mortality. Seeds that are dispersed a greater distance from any fruiting tree of the same species, regardless of whether or not the fruiting tree is the parent, show an increased likelihood of survival and germination.

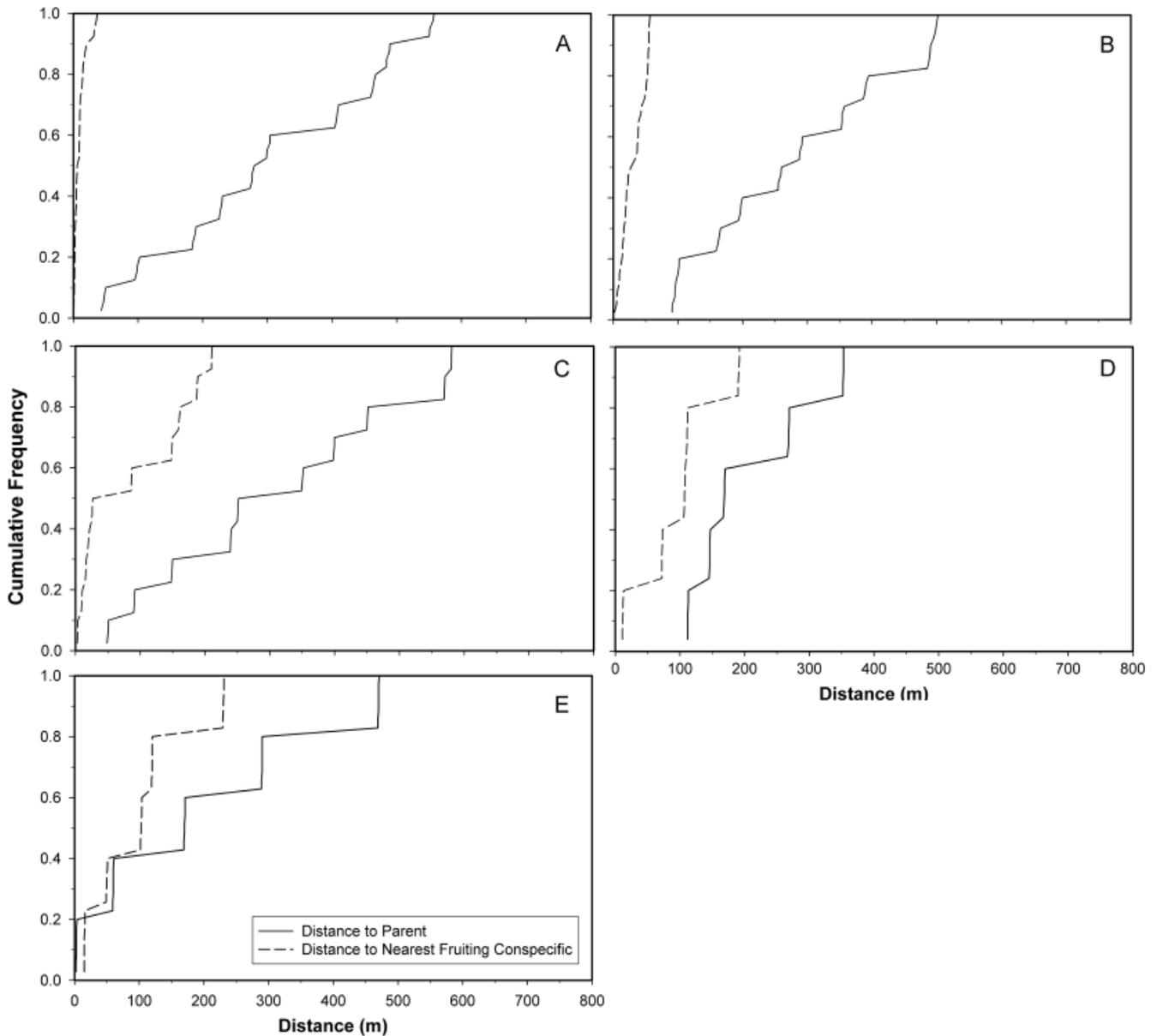


FIGURE 2. Cumulative Frequency Distributions of distance that seeds of five most commonly consumed seeds are dispersed away from parent trees vs. nearest fruiting conspecific trees: (A) *Acacia collinsii*, (B) *Casearia arguta*, (C) *Genipa americana*, (D) *Trichilia martiana*, and (E) *Sciadodendron excelsum*. Solid lines indicate distance to parent trees, while broken lines indicate distance to nearest fruiting conspecific trees.

If deposition away from fruiting conspecifics increases the success of an escaping seed of mammal-dispersed species, then it follows that studies of seed dispersal should take account not only of the straight-line distance that a seed travels from a parent, but also the deposition location in terms of the nearest fruiting individual of that species, as well as the fruit production of that individual tree (Fig. 2). Mapping the locations of trees of a given species would also allow measuring the likelihood of a seed being dispersed toward or away from a nearest fruiting conspecific, here, the most important predictor of seed and seedling survival, germination and growth across species.

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adhered to the national laws of Costa Rica, where the research was conducted.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Distance to parent tree and nearest fruiting conspecific tree of experimental plots.*

TABLE S2. *Significant cases of the effect of distance and neighborhood variables on seed survival, germination, seedling establishment, seedling survival.*

TABLE S3. *Significant cases of the effect of distance and neighborhood variables on the number of days that elapsed prior to the disappearance of all seeds from experimental plots.*

TABLE S4. *Significant cases of the effects of distance and neighborhood variables on seedling growth and damage.*

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