Survival without Dispersers: Seedling Recruitment under Parents

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Introduction

The loss of tropical forest is a central conservation issue, and much effort has been invested in understanding the extent of forest conversion, the factors contributing to its loss, and possible solutions to decrease the rate of destruction. Human activities in forests are not limited to the cutting of trees, however, subsistence and commercial hunting have affected large tracks of forest but have left their physical structure relatively unaltered (Redford 1992). For example, subsistence hunting by 230 inhabitants of three Waorani villages in Ecuador kills an estimated 3165 mammals, birds, and reptiles annually (Yost & Kelley 1983). Unfortunately, there is little understanding of how these hunting activities alter the processes governing the maintenance and long-term sustainability of forest ecosystems. For example, large animals are the preferred species for hunters, and it may be that these species play particularly significant roles in the dispersal of large, seeded tropical trees (Terborgh 1988; Wrangham et al. 1994). Wrangham et al. (1994) demonstrated that, although chimpanzees (*Pan troglodytes*) constitute only 1.4% of the primate frugivore populations and 14.2% of the primate frugivore biomass, they are responsible for an estimated 45.3% of the seeds defecated by the frugivorous primates.

Such findings support the idea that seed dispersal by frugivores is vital to the survival of fruiting tree populations because the survival of fallen fruit does not appear to be sufficient to maintain populations of many tropical tree species (Howe 1984; Pannell 1989; Chapman et al. 1992). A number of species-specific studies examining seedling survival under parent trees have found little or no recruitment under parent trees (Augspurger 1984). For example, Howe et al. (1985) found that 99.96% of *Virola surinamensis* fruit that drop under the parent are killed within only 12 weeks. Similarly, Schupp (1988) documented 7% survival of *Faramea occidentalis* seeds under the crown in 30 weeks, in comparison to 24% survival 5 meters away from the parent tree. Other studies, however, reveal relatively small differences in the probability of survival between seeds under parent trees and those dispersed further away (DeSteven & Putz 1984). Such conflicting results make it difficult to predict the consequences of a reduction in frugivore populations on plant biodiversity. Studies such as those by Leigh et al. (1993) and Bierregaard et al. (1992) illustrate the initial loss of tree biodiversity that results when populations are restricted to islands with reduced faunas; but, the time scales over which these studies have been carried out (1913–1980 and 1979 on, respectively) are short relative to the lifespan of the tree species. In addition, a number of factors are involved in the reduction of species numbers on islands.

Based on a sample of 25 tropical fruiting tree species in the Kibale National Park, Uganda, this study identifies the proportion of tree species that have many conspecifics growing under parent trees and the proportion of species that do not. The objective of the analysis is to provide an initial assessment of the extent of loss of biodiversity that might result from a significant reduction in populations of seed dispersers.

Methods

The Kibale National Park (766 km^2), located in western Uganda (0° 13′–0° 41′ N and 30° 19′–30° 32′ E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest, transitional between lowland rain forest and montane forest (Struhsaker 1975; Skorupa 1988). The study site is situated at an elevation of 1500 meters, and mean annual rainfall (1987–1991) is 1832 mm (range = 1607 mm–1952 mm). A system of approximately 166 km of trails provides access to an area of approximately 11 km^2. Fruiting trees such as *Diospy-*

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ros abyssinica (12.3% of 2111 enumerated trees, ≥10 cm diameter at breast height), *Markhamia platycalyx* (11.8%), *Celtis durandii* (10.9%), *Uvariopsis congensis* (9.8%), and *Bosqueia phoberos* (8.7%) are common in the area.

Seedlings, saplings, and poles growing directly under the canopy of five adult trees of 25 species were identified, and their height was measured (93.7% of the plants could be identified to species level). For exceptionally large parent trees (such as *Parinari excelsa*, and *Balanites wilsoniana*) the sampling area was reduced to an area within a 3-meter radius from the trunk. The species selected were chosen based on their abundance (very rare species in the area were excluded) and on their ecological species group (for example, pioneer, climax [Swaine & Whitmore 1988], inclusion in a ecological species group was based on [Hamilton 1991], and growth trials of seedlings in gaps and understory locations [Chapman & Chapman unpublished data]). To ensure that the individuals of the selected species were distributed throughout the forest, only one individual of a species was sampled on each of 26 sampling transects that were established throughout the trail system (location and direction of the transect were randomly selected). The 200-meter-by-10-meter transects are part of a long-term monthly phenological study. Each tree 10 cm or more in diameter at breast height within 5 meters of each side of the trail had been individually marked with a numbered aluminum tag.

It is difficult to state conclusively whether or not seedlings of a particular species can recruit under adult conspecifics because it is not clear what the number of seedlings or saplings under a parent should be compared to. It is possible that recruitment of a particular species is not occurring in an area or occurs only under specific conditions that arise occasionally over a long period. For example, in the early 1960s it was noted that there was little or no recruitment of *Parinari excelsa* (Langdale-Brown et al. 1964), and this is still the case today (Chapman & Chapman, unpublished data). Thus, if one found no *Parinari excelsa* seedlings growing under adult conspecifics and no seedlings growing away from parent trees, one could not draw conclusions with respect to the ability of seedlings of this species to grow under parents. Further, it is difficult to state conclusively whether or not seedlings can recruit under conspecifics because the growth and survival of saplings may be negatively affected by being under a conspecific adult (Hubbell & Foster 1990). But the presence or absence of seedlings and saplings under adult conspecifics does provide an initial assessment of the extent of loss of biodiversity that might result from a significant reduction in populations of seed dispersers.

Following the premise that seed rain will be higher under the parent tree than away from it, we considered four categories of distributions for the seedling data: (1) If there are no seedlings, saplings, or poles under the parent plant but many under other species of trees, we considered this tree species typically not capable of recruiting under parent trees. (2) If there was a large number of conspecifics of various sizes (including more than 1 meter in height), under a parent tree and few under other species of trees, we assumed that the species could recruit under parent trees. (3) If there was a small number of seedlings under parent trees but they included large individuals (more than 1 meter in height) and a small number away from parent trees, we assumed that recruitment under parents might be possible, but the evidence was not as strong as in the second case. (4) If there was a small number of seedlings under the parent tree (and they were not large) and a small number away from parent trees, then no conclusion could be reached.

Results

The 25 tree species considered ranged in density from 51.5 to 0.10 trees per hectare (Table 1). A total of 3784 seedlings were identified under the parent trees. We were unable to identify 6.3% of the species of tree seedlings under the adults (range between adult trees 0–18.1%)

Only *Mimusops bagshawei* had a large number of seedlings under other species of trees and no seedlings under the five parent trees (category 1, Table 1). Four species (16%) had a large number of conspecifics of various sizes under the parent tree and thus were considered capable of maintaining their populations for some time without dispersers (category 2). The majority of the species fell into categories 3 and 4. Under the parent trees of six species (24%), we found large saplings (>1 m), suggesting that for these species recruitment was possible under the parent. The number of saplings was small, however, so the conclusion is not as strong as with category 2. The majority of the species considered (56%) had few seedlings under their respective parent trees, and few seedlings were found away from the parents (category 4).

Discussion

If one considers only those species that had no seedlings under parent trees but many seedings away from the parent, then removal of frugivore seed dispersers would result in a 4% decrease in species richness of fruiting trees in a single generation. It is likely that tree species that had no (or very few) conspecific seedlings under the adults (none large) and few seedlings away are also unable to recruit individuals into the adult population with the absence of seed dispersers. If we combine category 1 and category 4, then 60% of the trees would be

Table 1. Survey of the seedlings, saplings, and poles growing under 5 individuals of 25 tree species found in Kibale National Park, Uganda.

Species	*Adult Density*	*Mean DBH Transect*	*Mean DBH Sample*	*Number Under*	*Mean Height*	*Number >50 cm High*	*Number >1 m High*	*Mean Number under Other Species*	*Category**
Uvariopsis congensis	51.45	15.78	18.1	58	53	30	4	19	2
Markhamia platycalyx	49.10	25.63	25.7	0	—	—	—	0.75	4
Diospyros abyssinica	45.90	27.23	19.0	1	200	1	1	9.3	3
Celtis durandii	45.30	32.56	25.5	0	—	—	—	0.29	4
Bosqueia phoberos	43.50	14.33	17.5	4	189	4	2	2.4	3
Funtumia latifolia	33.24	24.88	35.2	0	—	—	—	0.35	4
Leptonychia mildraedii	27.40	14.20	16.5	5	45	2	0	0.44	3
Teclea nobilis	20.00	15.77	17.4	19	79	16	9	15	2
Chaetacme aristata	14.40	17.81	15.3	0	—	—	—	0.44	4
Strombosia scheffleri	10.88	42.98	49.9	1	60	1	0	0.65	4
Dombeya mukole	8.35	28.56	25.4	0	—	—	—	0	4
Cassipourea ruwensorensis	7.06	19.98	13.8	1	53	1	0	0.7	4
Celtis africana	6.76	46.93	57.9	2	370	2	2	0.57	3
Tabernaemontana holstii	5.00	14.17	16.8	1	1200	1	1	2.9	3
Millettia dura	4.10	20.55	18.7	0	—	—	—	0.13	4
Olea welwitschii	3.24	50.40	117.8	0	—	—	—	0.08	4
Neoboutonia macrocalyx	2.70	21.83	26.5	0	—	—	—	0.04	4
Myrianthus arboreus	2.65	18.21	20.0	0	—	—	—	0.16	4
Mimusops bagshawei	2.40	75.06	67.6	0	—	—	—	4.7	1
Parinari excelsa	2.06	101.09	113.5	0	—	—	—	0.08	4
Balanites wilsoniana	1.19	43.80	126.6	20	1785	20	19	0	2
Pseudospondias microcarpa	1.18	116.78	137.0	11	116	11	8	0.48	2
Polyscias fulva	0.88	20.73	49.7	0	—	—	—	0	4
Monodora myristica	0.29	53.50	60.2	2	130	2	2	2	3
Trema orientalis	0.10	10.26	21.7	0	—	—	—	0	4

** (1) No seedlings, saplings, or poles under the parent plant but many under other species of trees; (2) a large number of conspecifics of various sizes (including >1 m in height) under a parent tree and few under other species of trees; (3) a small number of seedlings under parent trees but including large individuals (>1 m in height) and a small number away from parent trees; (4) a small number of seedlings under the parent tree (not large) and a small number away from parent trees.*

lost if frugivores were removed. With the species in category 4, it seems likely that some recruitment might be possible on some occasions. Thus, the time to the loss of these species from an area may be longer than for category 1 species. The evidence presented here suggests that in the short term at least 16% of the species would have individuals recruiting into the adult proportion of the population without seed dispersers because seeds that fell from parent's canopy could germinate and survive.

Long-term demographic studies on Barro Colorado Island have shown that the growth and survival of saplings are both commonly negatively affected when they grow under a conspecific adult (Hubbell & Foster 1990). Thus, it seems likely that the percentages that we have presented are conservative and that the loss of seed dispersers will have a stronger deleterious effect on the recruitment of tropical fruiting trees than suggested by our analysis.

In reality, hunting is likely to cause the removal of only a few seed-dispersing species, while the majority of frugivore populations will be reduced in size. However, the most susceptible species to hunting will be the larger-bodied frugivores. It is interesting that *Mimusops bagshawei*, a species that shows no evidence of recruitment under the parent tree, relies heavily on chimpanzees for much of its seed dispersal. From focal-tree observations and counts of the fruits eaten by all diurnal frugivores attending *M. bagshawei* trees, we have estimated that 34.5% of the fruits processed at *M. bagshawei* trees are eaten by chimpanzees. Such species that are highly dependent on large-bodied frugivores may be particularly susceptible to extinction under increased hunting pressure.

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