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SHORT COMMUNICATION

# Regeneration patterns among bird-dispersed plants in a fragmented Afrotropical forest, south-east Kenya

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Fruit-eating birds play an important role in the seed dispersal of many tropical plants (e.g. Herrera 1984), and the foraging behaviour of avian frugivores may affect their seed-dispersal capabilities (Loiselle & Blake 1999, Schupp 1993, Traveset 1994). For instance, shorter visits tend to produce less clumped seed distributions (Graham *et al.* 1995). Also, avian frugivores often feed on the fruits of several plant species over short periods of time (Herrera 1984, 1988a; Levey *et al.* 1994) in some non-random pattern (Herrera 1998). This potentially produces a predictable spatial pattern of the dispersed seeds (White & Stiles 1990). Forest destruction leads to fragmentation and degradation of the remaining habitats, which may influence patterns of adult tree distribution if the production, predation, dispersal, and/or regeneration of tree seeds is affected (Harrington *et al.* 1997). If dispersal of avian frugivores is disrupted by habitat fragmentation, plant species might face reduced regeneration, or even local extinction if they depend on a single, locally extinct disperser (Kellman *et al.* 1996). Increased predation of seeds and regenerating plants in the edges

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and gaps may also directly reduce regeneration rates (Corlett & Turner 1997, Harrington *et al.* 1997, Schupp 1988).

We studied the distribution patterns of five tree and one climber species, all fleshy-fruited and probably bird-dispersed, in a fragmented tropical forest. Here we examine whether (i) birds shape their habitats by influencing spatial patterns of seed deposition and, hence, the distribution of regenerating individuals; (ii) the spatial distribution of regenerating individuals resembles that of adult plants; and (iii) fragment size and disturbance levels influence tree regeneration rates. We did not control for other potentially important features such as survival and germination of seeds, unpredictability of germination sites, seedling mortality or actual seed rain (Heithaus 1986, Herrera *et al.* 1994, Schupp 1988). However, since for many plants mortality occurs mainly in the seed or seedling stages, enumeration of juvenile plants can be used to describe present patterns and predict future ones (Howe 1993).

Our study sites were the severely fragmented forests of the Taita Hills (south-east Kenya; 3°20′S, 38°15′E). At present, less than 400 ha of original forest remains, in a scatter of three larger fragments (50–220 ha) and nine tiny remnants (2–4 ha, one of 12 ha) (Lens *et al*. 1999). Between May and July 1998, data were collected in seven forest fragments: Ngangao (NG, 92 ha), Chawia (CH, 50 ha), Fururu (FU, *c.* 6 ha), Ndiwenyi (ND, *c.* 2.5 ha), Macha (MA, *c.* 3 ha), Mwachora (MW, *c.* 3 ha), and Yale (YA, *c.* 3 ha). Fragments NG and CH were divided into six and three sections, respectively, while the small fragments were treated as single sections each. For NG and CH, sections were contiguous forest blocks ranging between 10–18 ha in size, with obvious margins such as major paths, cliffs and ridges. Sections varied in their avifaunal composition and habitat structure (Githiru 1999), both of which would potentially influence spatial patterns of adult and juvenile plants. Of 279 individual movements of colour-ringed frugivorous birds of four species (Cabanis's greenbul *Phyllastrepus cabanisi*, stripe-cheeked greenbul *Andropadus milanjensis,* Taita thrush *Turdus (olivaceus) helleri,* and Taita white-eye *Zosterops (poliogaster) silvanus*), 208 (74.6%) were within a block (Lens *et al.* 1999, M. Githiru, unpubl. data). We therefore considered sections as independent units with respect to frugivorous bird movements, and treated them as replicates, nested within forest-fragment size category, in our analyses.

We selected five fleshy-fruited tree species, *Allophylus abyssinicus, Canthium oligocarpum, Maesa lanceolata, Rapanea melanophloeos* and *Xymalos monospora* (see Table 2 for details), the fruits of which show characteristics of the 'bird-dispersal syndrome' (*sensu* Gautier-Hion *et al.* 1985, Dowsett-Lemaire 1988, Levey *et al.* 1994). Apart from *Maesa*, all these trees are regarded as non-pioneer, moist forest species (Beentje 1994). 'Seedlings' were defined as individuals less than 1 m in height, while 'saplings' were those 1–8 m (1–4 m for the small tree *Maesa*). We did not investigate the influence of other dispersal agents, e.g. bats and other mammals, on their regeneration patterns. During

178 h of diurnal observation of frugivory on 48 focal trees (mean observation session = 3.7 h), only six trees were fed on by other vertebrates, specifically Sykes's monkeys *Cercopithecus mitis*. As birds were the main diurnal feeders and were 'legitimate dispersers' (*sensu* Traveset 1994), they were probably the main dispersal agents of these trees. We further studied one climber species, *Cissus oliveri* (Engl.) Gilg. (Vitaceae) that bore purplish-black, odourless fruits. The species occurred in all but one (YA) of the study fragments. During scan-samples of individual climbers with ripe fruits in different fragments (Githiru 1999), only birds were observed feeding.

We established between two and five 20-m-wide transects in each section (42 in total). Transects were 200 m long in NG and CH and 100 m long in the smaller fragments. Data were collected at 5-m intervals from alternate sides along the transects. At each point we established a 10 m sampling line perpendicular to the transect line. We identified all adult trees, fleshy-fruited or otherwise, occurring directly on this sampling line. We indicated, for each individual, whether a climber was present, and whether there were any seedlings and saplings of any of the five focal tree species within the span of its canopy on the ground. Additionally, we enumerated all adults, seedlings and saplings of the focal tree species. Except for very tight seedling clumps, distributions were mapped individually by indicating distance along transects and perpendicular distance from the transect line.

All tree species identified were classified as fleshy-fruited or non-fleshy-fruited. We used a multinomial logistic regression model to test the null hypothesis that, given their relative densities, the two tree types did not differ in the frequency of their association with the climber or juvenile individuals of the focal trees. To investigate the spatial patterning of the adult plants, their seedlings and saplings, we used Hill's two-term local quadrat variance (TTLQV) method (see Ludwig & Reynolds 1988 and references therein). This method uses changes in block size, through combining abutting quadrats, to identify both the intensity and grain of the distribution pattern. It is appropriate when individuals of species occur continuously across the community (Ludwig & Reynolds 1988). The 20-m-wide transects were divided into 5 m blocks along their lengths, giving a base quadrat size of 100 $m^2$. Numbers of adult and juvenile plants were counted within each quadrat, and the variance of these counts plotted against a series of increasing block sizes. Three main patterns (and their intermediates) can occur: random (variances fluctuate randomly with different block sizes); uniform (variances low and tend not to fluctuate at different block sizes); or clumped (variances tend to peak at a block size equivalent to the radius of the mean clump area). For a clumped distribution, the average distance between the clump centres will be twice the block size or spacing where the variance peaks (Ludwig & Reynolds 1988). Variance estimates at larger block sizes lack reliability because of diminishing degrees of freedom; we thus only calculated variances up to a maximum block size of

20% of N (the total number of quadrats) (Ludwig & Reynolds 1988). Maximum block size differed when transect lengths were different. This did not affect results when congruence was examined for sections or plant stages in the same fragment, but could potentially influence comparisons between the larger fragments and small ones. These analyses were performed by section, and data for all the focal trees were lumped: a separate analysis found that the effect of tree species on avian frugivore assemblages disappeared when trees were in the same section (Githiru *et al*., in press). To examine the variation in juvenile to adult ratios across different sizes of fragment (where ratios were calculated per section from the respective density estimates), we used a nested one-way analysis of variance (sections nested within fragment size). These data were square-root transformed to reduce kurtosis and skewness in the counts. Newman–Keul's test was used for *post-hoc* comparison of means.

For all sections combined, 24.2% of fleshy-fruited (FF) trees carried the climber *Cissus oliveri*, compared with only 14.3% of the non-FF trees. The overall model with the two main factors (section and tree type) plus their interaction was significant: $\chi^2 = 44.7$, df = 3, $P < 0.0001$. Only tree type exerted an independent significant effect on the presence of the climber ($\chi^2 = 13.4$, df = 1, $P < 0.0001$), while section ($\chi^2 = 0.017$, df = 1, $P < 0.90$) and the interaction between tree type and section ($\chi^2 = 0.38$, df = 1, $P < 0.54$) did not. Next, for all sections combined, 10.2% of all FF trees had a seedling of one of the five focal tree species adjacent to them, compared with only 6.8% of non-FF trees. The overall model was also significant: $\chi^2 = 11.6$, df = 3, $P = 0.009$. Again, tree type ($\chi^2 = 6.83$, df = 1, $P < 0.009$) but not section ($\chi^2 = 1.78$, df = 1, $P < 0.18$) nor the interaction between the two ($\chi^2 = 1.56$, df = 1, $P < 0.21$) had a significant independent effect on the presence of juveniles. Thus, young individuals of the focal tree species and the climber *C. oliveri* occurred more often than expected in association with fleshy-fruited tree species. The spatial patterns of seed deposition may be reflected clearly in seedling recruitment, or may be masked to a variable extent by events acting on seed and seedling survival (Loiselle & Blake 1999). How far such events shape juvenile recruitment in the case of these trees in the Taita Hills is unknown. However, these substantially non-random patterns of regeneration may, at least in part, be a result of the foraging activities, movement patterns and consequent seed deposition by birds (cf. Herrera 1985, 1988a, b).

Within each section, little congruence occurred in the spatial patterns of adults, saplings and seedlings (Table 1). Only in three sections did they show similar patterns (section 2 (clumped), 9 (uniform) and 12 (random)). Within each of the life-history stages (adult, sapling or seedling), there were also no clear patterns across sections (Table 1). In absence of data on survival probability of seeds and the plant stages, which could allow an assessment of the dispersers' 'effectiveness' (*sensu* Schupp 1993), lack of congruence between the three plant life-history stages is difficult to interpret. First, birds may have been feeding on a much larger array of fruits,

Table 1. Results of spatial pattern analyses by section for adults, saplings and seedlings of the five focal trees, using Hill's TTLQV technique (see text for details).

| | | Adult | | | Sapling | | | Seedling | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fragment | Section | Pattern | Dist. | Grain | Pattern | Dist. | Grain | Pattern | Dist. | Grain |
| NG | 1 | R | | | R | | | C | 170 | INT |
| | 2 | C | 230 | LU | C | 270 | INT | C | 270 | INT |
| | 3 | C | 150 | INT | C | 130 | HS | R | | |
| | 4 | R | | | C | 160 | INT | R | | |
| | 5 | R | | | C | 50 | LU | R | | |
| | 6 | R | | | U | | | — | | |
| CH | 7 | C | 150 | LU | R | | | R | | |
| | 8 | U | | | R | | | U | | |
| | 9 | U | | | U | | | U | | |
| FU | 10 | R | | | C | 100 | LU | R | | |
| ND | 11 | R | | | R | | | C | 20 | INT |
| MA | 12 | R | | | R | | | R | | |
| MW | 13 | R | | | C | 30 | HS | C | 20 | HS |
| YA | 14 | C | 50 | INT | C | 70 | LU | U | | |

Pattern refers to the overall spatial pattern, where R = Random, U = Uniform and C = Clumped; dist. refers to the mean distance between centres of clumps (for clumped distributions only); grain indicates the exact nature of the clumped pattern: whether with variance peak high and sharp (HS), with variance peak low and poorly defined (LU) or intermediate (INT).

which precluded a strong association between life-history stages among a subset (five) of these fruiting species. Second, these plants may lack 'high quality dispersers' – birds that feed on a large proportion of fruits as legitimate dispersers, and deposit seeds in the most appropriate sites (assuming that the probability of plant survival is highest in habitats with the greatest proportion of adults: Loiselle & Blake 1999). If dispersers were highly effective, we would expect clumped patterns at fairly similar spacing, such as those found in section 2, to be more frequent (Table 1). Third, other factors in the recruitment process, such as spatial variation in seed and seedling survival, might exert a strong effect, thus modifying patterns arising from seed deposition (e.g. Herrera *et al.* 1994, Schupp 1988).

When comparing mean juvenile to adult ratios, there was no significant difference across the three fragment size classes for the five tree species combined (Table 2). However, patterns differed for individual species. Mean ratios for *Allophylus*, *Rapanea* and *Canthium* were always highest in NG; ratios for *Xymalos* differed little with fragment size; and ratios for the pioneer species *Maesa* were highest in small fragments. Disturbance has been associated with increased seed and seedling mortality (e.g. through increased predation: Schupp 1988), leading to the presence of disproportionately few juvenile individuals of tree species in small and/or degraded forests (Harrington *et al.* 1997). Since disturbance-induced mortality is likely not to be density dependent, some species will increase and have a surfeit of juvenile plants while others will have a deficit (Howe 1993). Unsurprisingly, we found that the pioneer species *Maesa* had a higher juvenile:adult ratio in small (relatively degraded) than in large

Table 2. ANOVA results showing variation in seedling to adult ratios for the various tree species and species combinations in the three different fragment size categories, with post-hoc comparison of mean ratios for different fragment size categories.

| Tree species | Large (NG) | Medium (CH) | Small (others) | $F_{2,28}$ value | P-value |
|---|---|---|---|---|---|
| Five species combined | $3.06^{a}$ | $3.25^{a}$ | $3.95^{a}$ | 0.86 | 0.43 |
| *Maesa lanceolata* Forssk. (Myrsinaceae) | $1.21^{ab}$ | $0.89^{a}$ | $1.58^{b}$ | 3.01 | 0.066 |
| *Xymalos monospora* (Harv.) Warb. (Monimiaceae) | $2.89^{a}$ | $3.05^{a}$ | $3.01^{a}$ | 0.01 | 0.99 |
| *Allophylus abyssinicus* (Hochst.) Radlk. (Sapindaceae) | $1.96^{a}$ | $0.78^{b}$ | $0.94^{b}$ | 6.65 | 0.0043 |
| *Canthium oligocarpum* Hiern. (Rubiaceae) | $1.49^{a}$ | $1.46^{a}$ | $0.71^{a}$ | 2.67 | 0.087 |
| *Rapanea melanophloeos* (L.) Mez (Myrsinaceae) | $1.56^{a}$ | $0.71^{b}$ | $0.98^{ab}$ | 3.04 | 0.064 |

Means with similar superscript letters within each row are similar at P = 0.05; Newman–Keuls test.

(relatively intact) fragments, while the reverse was true for three non-pioneer species (see also Charles-Dominique 1986). These results were not completely consistent across the three fragment size classes, perhaps because large tracts of the medium-sized fragment, Chawia, were heavily disturbed. *Xymalos*, however, which is not regarded as a pioneer species (Beentje 1994), did not follow this trend, but showed high juvenile:adult ratios across all fragment sizes.

We conclude that frugivores appear to play an important role in determining the distribution of our focal plants in the Taita Hills. However, factors other than seed dispersal are significant too. To understand how these different influences interact, more information is required on the frugivores (e.g. patterns of movement after feeding) and plants (e.g. predictability of germination sites and actual seed and seedling survival). As habitat disturbance appears to affect the regeneration of several species, a better understanding of these processes is urgently needed for effective conservation of these small, highly threatened forests.

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