

# Disperser limitation and recruitment of an endemic African tree in a fragmented landscape

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**Abstract.** Forest fragmentation may have positive or negative effects on tropical tree populations. Our earlier study of an endemic African tree, *Leptonychia usambarensis* (Sterculiaceae), in the East Usambara Mountains of Tanzania, found poorer recruitment of seedlings and juveniles in small fragments compared to continuous forest, and concomitant reduction of seed-dispersal agents and seed dispersal. However, the possibility that other biotic or abiotic consequences of the fragmentation process contribute to diminished recruitment in fragments was left open. Here we test whether excessive seed predation, diminished fecundity, low seed quality, or adverse abiotic effects acted independently or in concert with reduced seed dispersal to limit seedling and juvenile recruitment in fragments. Extended observations of disperser activity, a seed placement experiment, seed predator censuses, and reciprocal seedling transplants from forest and fragment sources failed to support the alternative hypotheses for poorer seedling and juvenile recruitment in fragments, leaving reduced seed dispersal as the most plausible mechanism. Poorer recruitment of this species in forest fragments, where high edge-to-area ratios admit more light than in continuous forest, is particularly striking because the tree is an early successional species that might be expected to thrive in disturbed microhabitats.

**Key words:** Africa; doves; Eastern Arc Mountains; edge effects; frugivory; habitat fragmentation; inbreeding; mutualism; rodents; seed dispersal; seed predation; tropical forest.

## INTRODUCTION

Fragmentation of extensive forest into discontinuous parcels has profound and varied effects on remnant communities (Laurance 2005). Loss of tree species is one important factor, and is a special concern in diverse tropical forests. Many or even most tree species do not occur in small tropical forest fragments because they exist at such low densities that passive sampling leaves them out of small areas. In hyperdiverse forests of the Amazon, for instance, most tree species occur at densities of <1 individual/ha (Pitman et al. 2001), so samples represented by a small area fail to adequately represent tree diversity. New fragments carved from continuous forest therefore start with a depauperate flora, which can be further depleted by stochastic losses of species represented by few individuals (MacArthur 1972). Finally, fragmentation may adversely affect tree species through the ecological changes imposed on organisms in newly disturbed habitats. Altered ecological interactions in fragments due to modified abiotic conditions, poor representation of mutualists, or in-

creased effects of predators or pathogens, may increase the likelihood of local loss of tree species. Conversely, tree species that are well served by long-distance pollinators or dispersal agents, or by opportunists in the altered habitats, are likely to have a competitive advantage, particularly if they also can gain physiological advantages by making use of modified abiotic environments. Yet other species may be overwhelmed by cascades of interactions, which make the fortunes of rare and uncommon species difficult to predict.

Determining the particular reasons why a given species fails or succeeds during forest fragmentation is instructive in understanding how to prevent, reduce, or mitigate potential extinctions of interdependent species. Here we test multiple factors that could influence the apparent inability of an endemic African tree, *Leptonychia usambarensis* (Sterculiaceae), to prosper in forest fragments in the East Usambara Mountains of Tanzania. Previously, we found 44% fewer seedlings within 20 m of reproductive trees in fragments compared to continuous forest. Of these seedlings, 91% occurred within 10 m from the base of parent trunks (i.e., “under”) and 9% occurred from 10 to 20 m away (i.e., “away”) from parent trees in fragments; in continuous forest, 64% and 36% occurred under and away from parent trees, respectively. We also found 58% fewer

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juveniles within 20 m of reproductive trees in fragments compared to continuous forest. Fewer juveniles recruited away from adults (19%) than under them (81%) in fragments, whereas in continuous forest these percentages were 61% and 39%, respectively (Cordeiro and Howe 2003). Results from that study suggested that in fragments, fewer seeds escaped the vicinity of parents, and that seedlings under parents experienced higher mortality and a lower transition success to juvenile sizes than those 10–20 m away from parent crowns. This ultimately resulted in substantially lower recruitment of juveniles in fragments than in continuous forest.

There are a number of factors other than dispersal limitation that could influence recruitment. Here, in addition to testing differences in dispersal of seeds in continuous and fragmented forests, we test factors that might limit the recruitment of seeds to seedlings and of seedlings to juveniles. We address four sets of questions:

1) Is dispersal reduced in fragments? Reduced seed dispersal may occur if key dispersal agents are absent or too scarce to effectively remove fruits and disperse seeds (see Howe 1977, Schupp 1993). Reduced dispersal can lead to recruitment limitation in the immediate vicinity of parent trees, or dramatically reduced recruitment if, for example, density-dependent mortality of undispersed progeny kills most seeds or seedlings near parents (Janzen 1970, Connell 1971, Harms et al. 2000). Previous data on visitation and seed removal (Cordeiro and Howe 2003) were replicated in 2003 with a different set of trees in continuous forest to test the hypothesis of reduced seed dispersal in a second fruiting season. In addition, we tested seed and seedling fate near and far from fruiting trees to assess variation in recruitment success near vs. far from the crown of fruiting trees, as well as if and how fragmentation influences this variation.

2) Is seed predation higher in fragments? Increased seed predation by rodents or birds could disproportionately affect plant recruitment in small forest patches (Leigh et al. 1993, Terborgh et al. 2006). There are several possible mechanisms underlying such a pattern. Seed predation might be higher in fragments if particularly effective vertebrate seed predators thrive, as when density compensation increases their numbers and effects on plants (Leigh et al. 1993). A given plant species could also be suppressed if seed predators not normally found in deep forest invade fragments, as has been suggested in some fragmented African landscapes (Chapman and Chapman 1996). Finally, even stable populations of vertebrate seed predators may have greater effects in fragments if contingencies of resource availability force heavier use of seeds for immediate consumption rather than storage (Jorge 2007). To test the potential of excessive rodent or dove seed predation in suppressing *Leptonychia* in fragments, we counted these animals, and then used seed placement experiments to examine predation risk in forest fragments vs. continuous forest.

3) Is there evidence of reduced seed quantity or quality in fragments? Pollinator or resource limitation may limit fecundity in fragments, while resource limitation, maternal effects, or inbreeding depression could limit seed quality (Mazer and Gorchoff 1996, Young et al. 1996). Pollinator limitation could occur if key pollinators are absent in fragments, or because generalized pollinator assemblages of insects or vertebrates are not loyal enough to fly long distances to visit conspecific plants (see Knight et al. 2005, Kramer et al. 2008). Inadequate numbers of pollinators can reduce seed set, while insufficient long-distance pollination could result in reduction of seed quality from loss of heterozygosity. A first approximation can address seed quantity by comparing fecundity of trees of comparable size in continuous forest and fragments. Inbreeding with close relatives, selfing, or maternal effects of stressed parents could affect seed quality. It is beyond the scope of this paper to rigorously distinguish all possible causes of inferior seed quality, but controlled and reciprocal transplant experiments can determine if seed quality actually differs between habitats. Here we specifically report on these indirect tests of possible inferior seed quality by comparing growth of seedlings from forest or fragment seed sources. Elsewhere we report genetic findings showing no evidence of increased levels of inbreeding in seedlings from fragments and continuous forest (N. J. Cordeiro, H. J. Ndangalasi, and M. V. Ashley, *unpublished manuscript*).

4) Is seedling quality affected by edge effects? Seedlings or juveniles may not perform as well under the altered abiotic conditions of small fragments, where light availability is greater and humidity lower due to edge effects (e.g., Kapos 1989), as compared to continuous forest. Our seed placement and reciprocal transplant experiments permitted us to test responses of this species to edge and interior growth environments to determine whether this early successional species germinates and/or grows better at forest edges. This is not a direct assessment of effects of abiotic factors, but does indicate whether they are likely to matter.

The particular suite of factors that limits distribution and abundance of tree species is contingent on each species' ecological requirements and the conditions it faces in different environments (e.g., Lawton 1999). Here we address those ecological aspects likely to be important for *L. usambarensis* recruitment in the fragmented forest of the East Usambara Mountains. Signals might indicate that one or more of these effects influence recruitment of *Leptonychia* in fragments as compared with continuous rain forest.

#### STUDY SITE AND TREE

The East Usambara Mountains of the Eastern Arc Range (4° S, 38° E) of northeastern Tanzania (Appendix: Fig. A1), are recognized for their exceptional biodiversity and high levels of endemism (Burgess et al. 2007). The East Usambaras rise from the coast to

1506 m, with an extensive submontane plateau between 800 and 1100 m; ~4000 ha of lowland forest is continuous with 3500 ha on the submontane plateau. While pastoral and agricultural humans have lived in and transformed this landscape for at least the last 2000 years, forest fragmentation from human activities has escalated since the late 1800s due to clearing for colonial estates, tea and sisal plantations, commercial logging and, more recently, intensive subsistence cultivation (e.g., Hamilton and Bensted-Smith 1989, Newmark 2002). The five fragments used in this study were 2, 9, 16, 21, and 31 ha, all surrounded by tea plantations and located at 900–1100 m in elevation (Appendix: Fig. A1). As representative of continuous forest we used the more extensive 3500-ha forest tract and a 520-ha extension that is separated by 300 m from the larger continuous submontane forest (Appendix: Fig. A1).

Our study tree, *Leptonychia usambarensis*, is endemic to the Eastern Arc Mountains of eastern Africa (see Appendix), an area of ancient rain forests >30 million years old that is believed to have once spanned central Africa (Griffith 1993). The fruit of this 2–20 m tall tree is a capsule that dehisces during the day, revealing 1–5 but generally 2–3 black seeds, enveloped by scarlet-red arils, which are fleshy fruit-like structures partially covering the seeds (Appendix: Fig. A2). Mean seed length ( $\pm$ SD) is  $1.18 \pm 0.11$  cm, width  $0.69 \pm 0.08$  cm and fresh mass  $0.40 \pm 0.11$  g. Experimental removal of arils improves seed germination (see Appendix).

Most dispersal studies in tropical forests select trees because of their conspicuously high levels of activity. *Leptonychia* experiences low rates of bird visitation and seed removal with a high proportion of untouched seeds falling below parents, a little-studied natural history phenomenon in rain forests (H. F. Howe, *personal observation*). Crop sizes average ( $\pm$ SE; hereafter all error terms are standard errors)  $768 \pm 75$  fruits. Fruiting occurs for up to six weeks (peak of 1–2 weeks) from May to October, with most trees fruiting between July and September. A large proportion of trees begin reproduction at  $\geq 8$  cm dbh in the study area, but fruiting in trees as small as 5–8 cm is not rare. Seed germination occurs within one week under wet conditions, but can take up to nine weeks in drier weather.

## METHODS

### *Seed dispersal and seed/seedling fate*

To identify the seed dispersers and quantify dispersal and visitation, focal watches were conducted on 13 trees in four widely spaced continuous forest sites and 11 trees in four fragments that harbored *Leptonychia* (2, 9, 16, and 31 ha) in 2003. Each tree was watched once for 12 hours between 06:00 and 18:30 hours, from the end of August to the beginning of October, yielding a total of 288 hours of observation. All vertebrate visitors were identified, counted, and classified as dispersers (removed seeds from trees), predators (destroyed seeds), or non-dispersers (did not feed on seeds, or dropped all seeds

under parent crowns). An estimate of the removal effectiveness of the different species was achieved through visitation and seed removal rates (Schupp 1993). For focal watch observations in 2003, a different continuous forest patch was used. Because nearly all trees in the continuous forest sites used for sampling in 2002 failed to fruit successfully in 2003 (fruits were aborted prior to full development), we chose trees in the 520-ha forest adjacent to the more extensive continuous forest; we term this 520-ha forest patch “continuous forest” for purposes of this specific study. Similar to results in 2002 (Cordeiro and Howe 2003), crop sizes of all 24 focal trees did not differ significantly between fragments ( $720 \pm 204$  fruits) and continuous forest ( $711 \pm 126$  fruits;  $t = -0.04$ ,  $df = 17$  for unequal variances,  $P = 0.49$ ).

To experimentally test if seed and seedling fate was affected by proximity to a parent tree, we placed seeds at 2 and 18 m away from 32 trees (e.g., see Howe et al. 1985, Howe 1993), including each of 16 “parent” trees in the 3500 ha of continuous forest and 16 trees in fragments. Fifteen seeds (with arils manually removed) were placed at 2 and 18 m distance at each of four trees in four widely spaced sites in the continuous forest and four trees in each of the small fragments (2, 9, 16, and 31 ha;  $n = 960$  seeds). The experiment began in August 2002, using seeds sourced from 20 continuous forest trees. This experiment indirectly tests for effects of removal or seed/seedling predation, and allows overall assessments of habitat suitability for emerging seedlings in continuous forest and fragments. Seed fate (removal, germination, and postgermination survival) was monitored weekly from week 3 to week 10, whereas seedling survival was monitored weekly up to the third month, every two weeks thereafter up to the sixth month, and monthly thereafter up to 15 months from planting.

### *Seed predator abundance*

Rodents and doves could be disproportionately important seed and/or seedling predators in fragments if they are more abundant than in continuous forest, or change their diet. Censuses of rodents were conducted in January–February 2001 (baited with *Allanblackia stuhlmanni* seeds and coconut), in June–July 2002 and July–August 2005 (baited with *Leptonychia* fruits and coconut). The trapping intensity, using line transects of 11 traps, was positively correlated with fragment area ( $r = 0.92$ ,  $P < 0.05$ ; see Appendix). Each transect was sampled for three days and consisted of five Tomahawks and six Sherman box traps; each trap type was used alternately every 8 m. A sampling season comprised 1056 trap-nights, where a trap-night is defined as a single 24-hour period per trap. Rodents were identified to species, measured, and marked before release.

Tambourine Doves *Turtur tympanistria* and Lemon Doves *Aplopelia larvata* were counted as part of an overall investigation of forest birds in the fragmented landscape (Cordeiro and Howe 2001, 2003; N. J.

Cordeiro, unpublished data). Relative abundance was estimated using the unlimited distance point count method (Blondel et al. 1981). Point counts were conducted for 15 minutes per station where all birds heard or seen were recorded, resulting in a total of 136 point count censuses spread over four sampling periods (February, June, October 2000, and February 2001). Point count stations were fixed, each of which was 150 m apart from another. The number of counts was positively correlated with fragment area ( $r_s = 0.93$ ,  $P < 0.01$ ; see Appendix).

#### *Seed set*

Smaller fruit crop sizes in fragments as compared with continuous forest could have several possible mechanisms: pollinator limitation (Aizen and Feinsinger 1994); inbreeding resulting from reduced pollinator activity and/or small population sizes (Young et al. 1996); or mothers that are stressed by challenging abiotic environments (Mazer and Gorchov 1996). We tested this prediction by comparing fruit crop sizes of trees in fragments and continuous forest specifically standardized by tree size (dbh) in both years. This was a test of fragmentation effects on tree fecundity, independent of "quality" of the resulting seeds.

#### *Seedling performance*

We tested whether seed quality was reduced in fragments compared to continuous forest. Local pollination could result in selfing, or inbreeding among close relatives, with the possibility of inbreeding depression. In July and August 2002, we planted 1090 seeds sourced from 15 trees in three small fragments (2, 16, and 31 ha;  $n = 416$  seeds) and 32 trees from three sites in continuous forest ( $n = 674$  seeds) by random arrangement in a screenhouse in the study area. The screenhouse is a 12 × 24 m structure enclosed in wire and mosquito mesh, and covered on the top and sides by shade cloth. Heights of seedlings were measured at two and nine months of age from 115 fragment seedlings sourced from 13 trees, and 211 continuous forest seedlings sourced from 14 trees (average of 12 seedlings per tree), all of which had germinated at the same time.

During the wet season of April 2004, we initiated the second *Leptonychia* transplant experiment in four fragments and four continuous forest sites using 288 fragment and 288 continuous forest nine-month-old seedlings to test the prediction that potentially inbred recruits from fragments experience greater mortality and reduced growth under competitive natural conditions. Husband and Schemske (1996) found that these effects were a stronger indication of inbreeding depression than seed set or germination. Fragments chosen for this transplant experiment were 9, 16, 21, and 31 ha, compared with trees from four widely spaced continuous forest sites (two in a 520-ha tract and two in a 3500-ha forest). Equal numbers of nine fragment and nine continuous forest-sourced seedlings were randomly

drawn and placed in two dispersed arrays at 3 and 30 m from the forest edge in all eight sites. This design was chosen to allow this early successional species to respond to high light conditions, as well as to test it in interior forest conditions. All remaining individuals were carefully harvested, separated as roots and shoots, oven-dried, and weighed at the University of Dar es Salaam, Tanzania, in August 2005.

#### *Edge and altered abiotic effects*

The seed and seedling fate experiment offered an indirect gauge of how seed germination and subsequent seedling growth respond to altered abiotic effects in fragments with a higher edge-to-area ratio than continuous forest. In the *Leptonychia* seedling transplant experiment, biomass of shoots and roots at distances of 3 and 30 m from the edge provided an avenue to more directly examine edge effects, particularly in this fragmented system where edges are abrupt (Hanson et al. 2007).

#### *Analyses*

We use Mann-Whitney  $U$  tests to examine differences in the number of visits per tree and in the number of seeds removed per tree in fragments vs. continuous forest. In the seed and seedling fate experiment, a Kolmogorov-Smirnov distribution test was used to detect differences in germination time between continuous forest and fragments, whereas nested ANOVA was used to test for effects of habitat and distance. In this nested ANOVA, habitat (continuous forest vs. fragments) and distance were fully crossed, site was nested in habitat, and tree was nested in site. The dependent variables were arcsine-transformed proportions of germinated seeds, seeds and sprouts removed at 9 weeks, seedling survival at 15 months, and log-transformed heights at 13 months.

Analysis of rodent abundances per trap-night against fragment size (small fragments  $\leq 31$  ha vs. continuous forest of 520 and 3500 ha) was completed using a generalized linear mixed model with a binomial error term, with fragment size class as a fixed effect and year and site as random effects. Analysis of dove abundances against fragment size used a similar generalized linear mixed model and a Poisson distributed model for count data on dove abundance (number of individuals per point count). Fragment size class was considered a fixed effect and census period and site considered random effects. The importance of the random effects was evaluated by inspection of  $t$  values of coefficient estimates and respective standard errors (see also Moore and Swihart 2007). For analyses of both rodents and doves, Satterthwaite's formula was used to correct for degrees of freedom due to random effects (Satterthwaite 1946). We also systematically included a scale parameter for overdispersion (McCullagh and Nelder 1989, Littell et al. 2006). Preference for bait by rodents was assessed with a chi-square test.

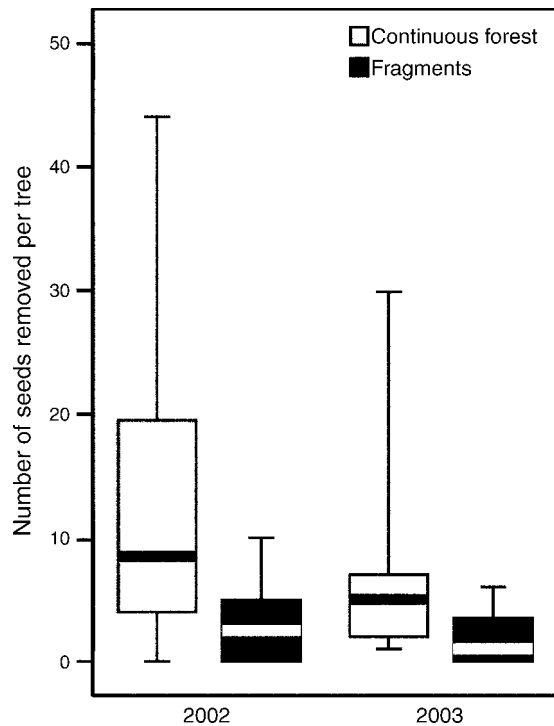


FIG. 1. Box plot showing median (line of contrasting color across the box) number of seeds removed per *Leptonychia usambarensis* tree, plus 25% and 75% quartiles (lower and upper end of box), in fragments and continuous forest during 12-hour watches in 2002 and 2003. The vertical bars represent the minima and maxima of the data. A total of 10 trees were sampled in fragments and 16 trees in continuous forest in 2002 (data from Cordeiro and Howe [2003]), whereas 11 trees were sampled in fragments and 13 trees in continuous forest in 2003.

In the greenhouse experiment that tested for differences in seed quality, a repeated-measures ANOVA with time and habitat sources (fragment or continuous forest) as factors and log-transformed measures of height as the dependent variable was used. A univariate ANOVA tested for the effects of source habitat on growth. A nested ANOVA was employed in the transplant experiment, where habitat type and seedling source were fully crossed, site was nested in habitat, distance (3 and 30 m from the edge) was nested in site, and transect was nested in distance. Shoot and root mass were log-transformed. A univariate ANOVA tested for habitat, distance from edge, and the interaction of these two factors on root and shoot biomass. For the same transplant experiment, a nested ANOVA tested for the effects of habitat and seed source on seedling to juvenile survival (arcsine-transformed proportions); both factors were fully crossed.

Analyses were performed using SYSTAT version 11.0 (SYSTAT 2004), SAS version 9.0 (SAS 2007), and SPSS version 8.0 (SPSS 1997).

## RESULTS

### *Seed dispersal and seed/seedling fate*

As in 2002 (Cordeiro and Howe 2003), reduced dispersal in 2003 was again evident in small fragments. Compared with trees selected from continuous forest, trees in fragments had much lower overall bird visitation, were visited much less by three key dispersal agents (two species of *Andropadus* greenbuls and a thrush, *Turdus roehli*), lost several dispersal agents, had fewer seeds removed, and had fewer juveniles >10 m from under fruiting trees in 2002 (Cordeiro and Howe 2003). In 2003, with trees from an additional small fragment and a 520-ha patch that is a "broken" extension of the continuous forest, the general results for visitation and seed removal were similar to those of 2002 (Figs. 1–3). The median number of bird visits per tree was 75% less than that in continuous forest (median of 1 vs. 4, respectively: Mann-Whitney *U* test,  $Z = 2.14$ ,  $P < 0.05$ ). Two species (Waller's Starling, *Onychognathus walleri*; Common Bulbul, *Pycnonotus barbatus*) that visited trees in 2002 were not observed in the 2003 focal watches. The Stripe-cheeked Greenbul, *Andropadus milanjanensis*, was not found in fragments, and the Little Greenbul, *Andropadus virens*, and Green Barbet, *Stactolaema olivacea*, had more visits per tree in 2003 than in 2002 (Fig. 2). Differences in visitation were similar across years: there were 56% fewer visits per tree in fragments than continuous forest in 2003, and 65% in 2002.

As in 2002 (Cordeiro and Howe 2003), overall visitation and seed removal was much lower in fragments than in continuous forests. Median seed removal per tree by birds in fragments in 2003 was 80% less than that in continuous forest (Mann-Whitney *U* test,  $Z = -2.23$ ,  $P < 0.05$ ); in 2002 the same comparison of seed removal was >70% less in fragments (Fig. 1). Ten bird species removed seeds in continuous forest in 2002, while eight did so in 2003; two of the eight in 2003 landed in focal trees (Little Greenbul and Tiny Greenbul [*Phyllastrephus debilis*]) but were not observed removing seeds (Fig. 3). Nonetheless, the most effective removal agents remained generally consistent between years, with Shelley's Greenbul, *A. masukuensis*, Green-headed Oriole, *Oriolus chlorocephalus*, and Green Barbet removing 26%, 85%, and 24% fewer seeds in fragments than continuous forest in 2003. Two very effective (Stripe-cheeked Greenbul and Usambara Thrush *Turdus roehli*) and two less effective seed removal agents (Fischer's Turaco, *Tauraco fischeri* and Dark-backed Weaver, *Ploceus bicolor*) were not recorded feeding at *Leptonychia* trees in fragments (Figs. 2 and 3). The net result from the plant perspective is that reduced visitation and fewer effective bird species in fragments compared to continuous forest led to consistently low removal of seeds in both years.

In the seed and seedling fate experiment, neither seed removal from the forest floor nor seedling survival

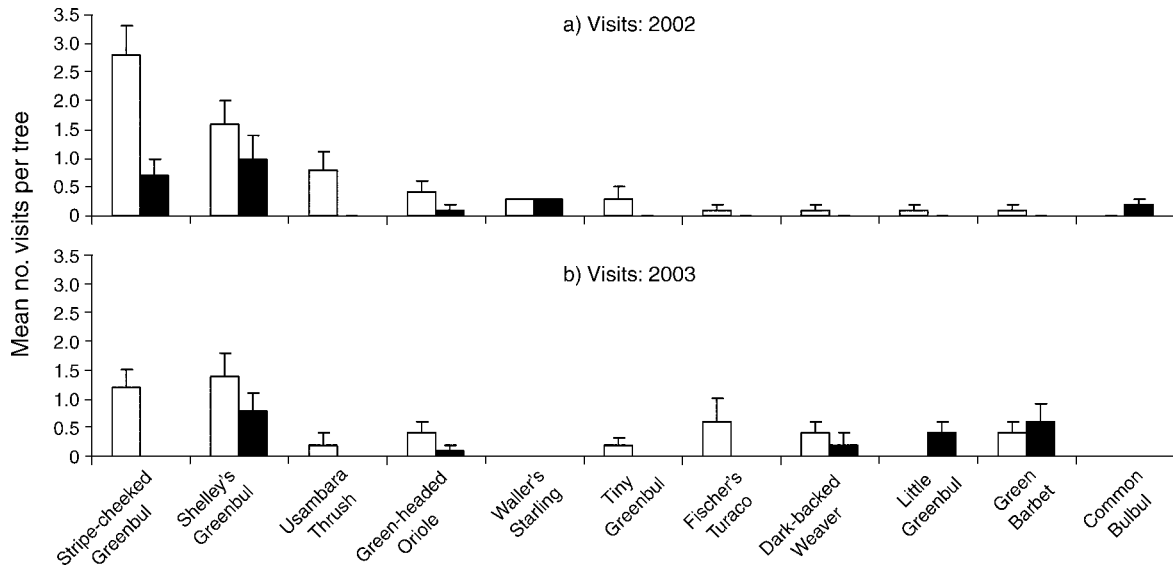


FIG. 2. The number of visits per tree by different bird species at *Leptonychia usambarensis* trees in continuous forest (open bars) and small forest fragments (<31 ha; solid bars) in (a) 2002 and (b) 2003. Data (means + SE) are based on single 12-hour focal watches at each of 10 and 16 trees in fragments and continuous forest, respectively, in 2002 (data from Cordeiro and Howe [2003]); and 11 and 13 trees in fragments and continuous forest, respectively, in 2003. For scientific names of birds see *Results: Seed dispersal and seed/seedling fate*; nomenclature for Usambara thrush *Turdus (abyssinicus) roehli* follows Bowie et al. (2005).

differed under vs. away from trees, or between fragments and continuous forest habitats. Even though germination was high overall, removal of seeds and sprouts (i.e., recently germinated seeds) was high across treatments, resulting in substantial overall removal by nine weeks after placement. Rodents and doves were the likely animals that removed ~45.0% or 432 individuals

by week 9, removing mostly freshly germinated seeds or sprouts after germination. A nested ANOVA showed significant differences among sites ( $F_{6,24} = 6.91, P < 0.001$ ) and individual trees ( $F_{24,31} = 2.24, P < 0.05$ ), but no significant effects of distance from trees ( $F_{1,31} = 0.18, P = 0.67$ ). In addition, removal rates of seeds and sprouts at nine weeks were similar in continuous forest

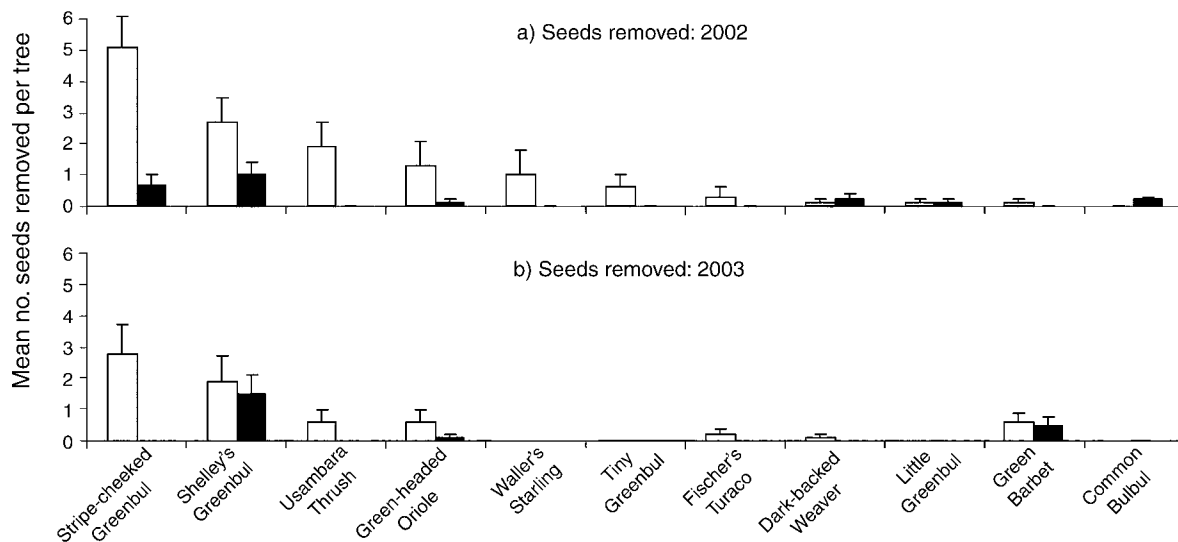


FIG. 3. The number of seeds removed per *Leptonychia usambarensis* tree by different bird species in continuous forest (open bars) and small forest fragments (<31 ha; solid bars) in (a) 2002 and (b) 2003. Data (means + SE) are based on single 12-hour focal watches at each of 10 and 16 trees in fragments and continuous forest, respectively, in 2002 (data from Cordeiro and Howe [2003]); and 11 and 13 trees in fragments and continuous forest, respectively, in 2003. For scientific names of birds see *Results: Seed dispersal and seed/seedling fate*; nomenclature for Usambara thrush *Turdus (abyssinicus) roehli* follows Bowie et al. (2005).

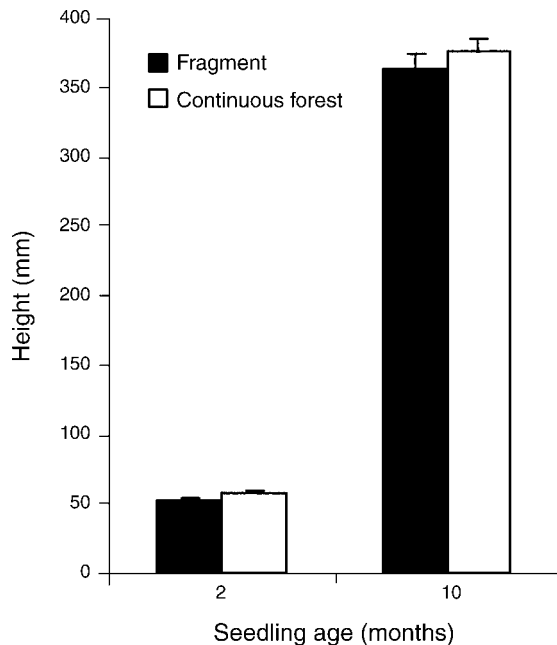


FIG. 4. Seedling heights of *Leptonychia usambarensis* (untransformed means  $\pm$  SE) at 2 and 10 months of age sourced from fragments and continuous forest and grown under controlled conditions in a greenhouse in the study area. Differences are significant at 2 months ( $P < 0.001$ ), but not at 10 months.

(57.3%  $\pm$  4.3%) and fragments (52.7%  $\pm$  3.2%;  $F_{1,6} = 0.23$ ,  $P = 0.65$ ). Consistent with findings on seed removal in the first two months, survival of remaining seedlings did not differ significantly between continuous forest and fragments at 15 months ( $F_{1,6} = 0.09$ ,  $P = 0.77$ : fragments 26.3%  $\pm$  3.5%, continuous forest 24.4%  $\pm$  2.3%). In addition, distance effects were not apparent, as survival of seedlings was similar under and away from parent trees ( $F_{1,31} = 0.26$ ,  $P = 0.61$ ).

#### Seed predator abundance and seed preference

Overall rodent and dove abundances did not differ significantly between years or census periods (Appendix: Table A1), and were not significantly different between fragments and continuous forest (Appendix: Fig. A3). Rodent abundances, expressed as the number of individuals per trap-night, were not significantly different in continuous forest and fragments ( $F_{1,92.06} = 1.72$ ,  $P = 0.19$ ; fragments, 0.04  $\pm$  0.01 rodent per trap-night [mean  $\pm$  SE]; continuous forest, 0.05  $\pm$  0.01 rodent per trap-night). Rodent abundance varied a great deal (fragments, 0–0.12 rodent per trap-night; continuous forest, 0–0.27 rodent per trap-night), with totals of 104 rodents caught in 2001, and only 21 each in 2002 and 2005 for the same effort (Appendix: Table A2). Increased numbers of *Praomys delectorum* (25 g) dominated captures with 95.4%, 85.7%, and 71.4% of the samples in 2001, 2002, and 2005, respectively. Dove abundance, expressed as the number of individuals per

point count, also did not significantly differ between habitats ( $F_{1,130.4} = 0.04$ ,  $P = 0.84$ ; fragments, 0.06  $\pm$  0.02 individuals; continuous forest, 0.05  $\pm$  0.01 individuals). Dove abundances also varied in fragments and continuous forest, with 0–0.14 individuals per point count in fragments and 0.02–0.09 individuals in continuous forest (Appendix: Table A3). Tambourine Doves were the most frequently counted of the two dove species (91.9%). Lemon Doves were not recorded in small fragments.

Not all potential seed predators actually ate *Leptonychia* seeds during the sampling period. Of interest, most rodents did not show a preference for *Leptonychia* seeds as bait in comparison to coconut. In contrast, while the abundant *Praomys delectorum* did not show a significant preference in each year (2002;  $\chi^2$  corrected = 1.7,  $df = 1$ ,  $P = 0.19$ ; 2005;  $\chi^2$  corrected = 3.1,  $df = 1$ ,  $P = 0.08$ ), pooling data from both years showed a preference for this rodent to remove *Leptonychia* seeds over coconut ( $\chi^2$  corrected = 5.3,  $df = 1$ ,  $P < 0.05$ ). Pooling both years, total capture frequencies of this small rodent were 70.3% with *Leptonychia* as bait compared to 29.7% with coconut bait. Focal watches in 2003 revealed no significant differences in dove visitation under *Leptonychia* trees in fragments vs. continuous forest (Mann-Whitney  $U$  test,  $Z = -1.04$ ,  $P = 0.30$ ). There is no evidence that rodents or doves ate more seeds in fragments as compared with continuous forest.

#### Seed quantity

Crop sizes were not significantly different between trees in continuous forest and fragments. For trees of similar dbh, fruit crop sizes of 10 continuous forest trees (501.50  $\pm$  102.76 fruits) were comparable to the 10 in fragments in 2002 (464  $\pm$  96 fruits;  $t = 0.27$ ,  $df = 18$ ,  $P = 0.75$ ), and again in 2003 (continuous forest: 841  $\pm$  353 fruits, fragments: 747  $\pm$  224 fruits;  $t = 0.23$ ,  $df = 15$ ,  $P = 0.82$ ). There is therefore no support for pollination limitation, inbreeding, or any other indirect effects of fragmentation on seed set.

#### Seed and seedling quality

Under controlled conditions of light and water, growth significantly increased with time for continuous forest and fragment seedlings in our greenhouse (repeated measures ANOVA,  $F_{1,324} = 2348.8$ ,  $P < 0.0001$ , a trivial result), but there was no significant interaction of continuous forest and fragment source with time ( $F_{1,324} = 0.39$ ,  $P = 0.53$ ). A univariate ANOVA to test for differences between habitat types showed that continuous forest seedlings (58.1  $\pm$  0.9 mm) had grown 12% larger than those from fragments (52.1  $\pm$  1.1 mm) at 2 months of age ( $F_{1,324} = 17.90$ ,  $P < 0.0001$ ), but by 10 months of age their heights were similar ( $F_{1,324} = 1.19$ ,  $P = 0.27$ ) (Fig. 4). Initial performance differences consistent with inbreeding depression or maternal effects of stressed mother trees in fragments were not sustained in the greenhouse.

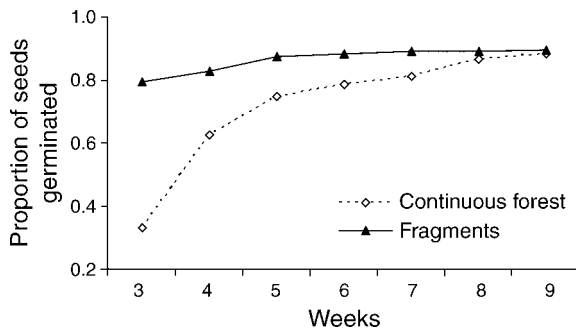


FIG. 5. The proportion of *Leptonychia usambarensis* seeds germinated in fragments and continuous forest in the East Usambara Mountains over 9 weeks after planting in 2002. Seeds in fragments germinated significantly faster than those in continuous forest ( $P < 0.001$ ).

Differences in seedling growth and survival consistent with differences in seed quality were not detected under competitive field conditions. The transplant experiment did not reveal significant differences in plant performance for juvenile height, leaf number, or mass for either plants situated 3 m from the edge, those situated 30 m into the forest, or overall. The most stable response variables were log-transformed mass of shoot and root at 16 months after planting. Nested analysis of variance on those data for shoots do not show significant effects of habitat ( $F_{1,6} = 0.29$ ,  $P = 0.61$ ), site ( $F_{6,8} = 1.30$ ,  $P = 0.37$ ), or distance from edge ( $F_{8,2} = 2.25$ ,  $P = 0.34$ ), and no significant effect of seed source ( $F_{1,439} = 2.27$ ,  $P = 0.13$ ) (Appendix: Fig. A4). Results for roots were similar across sites ( $F_{6,8} = 2.50$ ,  $P = 0.12$ ), forest or fragment planting ( $F_{1,6} = 0.25$ ,  $P = 0.63$ ), distance from edge ( $F_{8,2} = 1.63$ ,  $P = 0.44$ ), and seed source (continuous forest or fragments;  $F_{1,439} = 2.14$ ,  $P = 0.14$ ). Although these differences in means were not significant, they were in the direction predicted for lowered seed or seedling quality, with juveniles from fragment sources smaller than those from continuous forest. Comparisons of only edge and only interior plants produced the same results. Similarly, this experiment did not reveal poorer seedling/juvenile survival 16 months after establishment, with no significant effects of habitat ( $F_{1,6} = 1.06$ ,  $P = 0.662$ ) or seed source ( $F_{1,45} = 0.001$ ,  $P = 0.976$ ) (Appendix: Fig. A5).

#### Edge effects

Germination occurred within nine weeks after placement in the seed and seedling fate experiment, with seeds in fragments germinating faster than those in continuous forest (Kolmogorov-Smirnov  $Z = 7.51$ ,  $P < 0.001$ ; Fig. 5). The ultimate proportion of seeds germinating, however, showed no significant differences with respect to habitat (nested ANOVA,  $F_{1,6} = 0.06$ ,  $P = 0.81$ ) or distance ( $F_{1,31} = 0.003$ ,  $P = 0.95$ ) treatments, nor in local effects of either site ( $F_{6,24} = 1.60$ ,  $P = 0.19$ ) or host tree ( $F_{24,31} = 1.00$ ,  $P = 0.49$ ). By nine weeks, 89.0% of seeds germinated in both habitats.

In the seedling transplant experiment where we tested seed quality effects, we found that distance from edge did not significantly affect survival to the juvenile stage ( $F_{8,2} = 1.67$ ,  $P = 0.43$ ), or shoot ( $F_{8,2} = 2.25$ ,  $P = 0.35$ ) or root biomass ( $F_{8,2} = 1.63$ ,  $P = 0.44$ ), a result that was likely due to strong local site effects. We therefore used univariate ANOVAs to test for an effect of habitat (continuous forest vs. fragment) and distance from edge in the same seedling transplant experiment. Edge effects did not significantly affect survival (3 m from edge,  $81.6 \pm 2.6\%$  vs. 30 m from edge,  $78.5\% \pm 2.7\%$ ;  $F_{1,60} = 0.679$ ,  $P = 0.41$ ), but root mass was 30% higher near the edge ( $0.65 \pm 0.04$  g vs.  $0.50 \pm 0.03$  g;  $F_{1,450} = 7.71$ ,  $P < 0.01$ ). Smaller differences in shoot mass at 3 and 30 m from the edge were not statistically significant ( $1.06 \pm 0.06$  g vs.  $0.97 \pm 0.05$  g;  $F_{1,452} = 1.62$ ,  $P = 0.20$ ; Fig. 6). The seed and seedling fate experiment also suggested small (but not quite significant) positive edge effects (heights of seedlings at 13 months were  $104 \pm 3$  cm in fragments,  $92 \pm 2$  cm in continuous forest,  $F_{1,6} = 3.52$ ,  $P = 0.11$ ), probably due to strong site effects ( $F_{6,21} = 2.53$ ,  $P < 0.05$ ), despite earlier germination in fragments (see *Results: Seed dispersal and seed/seedling fate*).

#### DISCUSSION

*Leptonychia usambarensis* appears to be failing to recruit as well in small fragments as it does in continuous forest due to reduced dispersal. We previously found almost 50% fewer seedlings within 20 m of reproductive trees in small fragments vs. continuous forest (Cordeiro and Howe 2003). Of these seedlings, >10 times more occurred under (i.e., <10 m) vs. away from (i.e., 10–20 m) adult crowns in fragments, whereas in continuous forest, almost twice as many seedlings occurred under vs. away from adults. We also found 58% fewer juveniles within 20 m of reproductive trees in small fragments vs. continuous forest. Of these juveniles, almost one-fifth as many occurred away from vs. under adults in fragments, whereas in continuous forest, a little

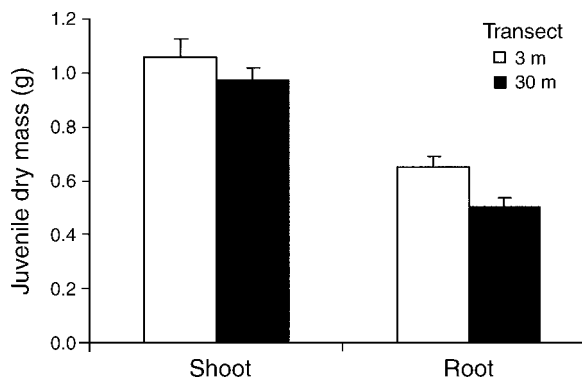


FIG. 6. Biomass (untransformed means of dry mass + SE) of transplanted *Leptonychia usambarensis* juveniles at edge (3 m) vs. interior (30 m) transects pooled in both continuous forest and fragments. Apparent shoot differences are not significant; root differences are ( $P < 0.01$ ).



under two times more juveniles occurred away from vs. under adult trees. More seedlings under and fewer seedlings away from adult trees in fragments, compared to continuous forest, suggested reduced seed dispersal in fragments. These demographic data suggest both density-dependent mortality and a recruitment advantage gained through more efficient dispersal (Cordeiro and Howe 2003).

Poorer recruitment in fragments of a species often successful at edges is puzzling, because such species often benefit from greater light availability. Apart from reduced dispersal, however, other factors that might constrain *Leptonychia* recruitment remained unaddressed in the earlier study. Here, we tested other factors that may reduce seed quantity and quality of progeny in fragments as compared to continuous forest, but our results failed to support these alternative hypotheses. The confirmation of reduced dispersal coupled with high density-dependent mortality in the seedling-to-juvenile transitional stage, leaves this mechanism as the best-supported explanation for poor regeneration of *Leptonychia usambarensis* in fragments.

#### *Disperser limitation*

Consistent with earlier results, we found strong evidence for reduced seed dispersal of *Leptonychia* in small, isolated fragments in 2003. The disperser assemblage was comparable between years, and consistently diminished in fragments, resulting in substantially less seed removal than in continuous forest. Additionally, in both years, dispersal agents that removed most seeds in continuous forest were lost or reduced in abundance in fragments, and not replaced by other dispersers from the surrounding matrix. Comparable visitation and seed removal patterns between habitats in both years suggests that reduced dispersal of *Leptonychia* is a predictable phenomenon in East Usambara fragments.

Dispersal limitation is not uncommon in contiguous plant populations, and can be altered by anthropogenic disturbances. In a Central American study, dispersal limitation best explained poor recruitment over seed availability for 10 of 13 pioneer tree taxa (Dalling et al. 2002). Three animal-dispersed species with abundant seed crops had the lowest sampling probabilities in seed traps relative to nearest adult distances, suggesting that despite high seed availability, animals did not transport seeds effectively (Dalling et al. 2002). Even for pioneers with abundant fruit crops, dispersal limitation can be exacerbated by habitat fragmentation if dispersal agents are negatively affected and not replaced by effective dispersers from the landscape (Wright and Duber 2001, McEuen and Curran 2004, Galetti et al. 2006). Although important elsewhere (e.g., Moore and Swihart 2007), disperser redundancy is not apparent for *Leptonychia* at our site.

In contrast, *Prunus africana* (Rosaceae), a larger and more fecund tree, attracts a larger disperser assemblage, and showed seed removal rates slightly higher in

fragments than in more extensive forest in western Kenya (Farwig et al. 2006). Differences in seed removal rates could be due to much larger fragment sizes (130–1400 ha), a larger suite of forest-dwelling dispersers, relative proximity of fragments to extensive forest, and a heterogeneous intervening matrix that enables frugivore movement across the landscape to increase seed removal rates in fragment-dwelling *Prunus africana*. Usambara fragments were surrounded by a homogenous matrix of tea cultivation, and were smaller (<31 ha) and more isolated (generally from 0.5 to 7 km away from the continuous forest), factors that reduce the pool of potential fruit-eating animals both in and around these fragments (Newmark 1991, Wethered and Lawes 2003, Stouffer et al. 2006). We surmise that *Prunus africana* may be substantially less specialized, may have more substitute dispersers, and in any event occupies some very large fragments.

#### *Seed predators and seed and seedling mortality*

Forest fragmentation can lead to density compensation, where loss or reduced abundance of some species allows increased density of competitors. Density compensation in seed predator communities, such as rodents (Laurance 1994) and birds (Wethered and Lawes 2003) could increase predation rates of undispersed seeds and/or seedlings in fragments. In the temperate zone, granivory by rodents can strongly suppress seedling recruitment of some species, with initial effects that last for years (Howe and Brown 2001), while selective rodent herbivory on seedlings may alter forest succession pathways (Ostfeld et al. 1997). At least one ubiquitous rodent (*Praomys delectorum*) and two birds (*Turtur tympanistria* and *Aplopelia larvata*) ate *Leptonychia* seeds. The generally inconsistent temporal and spatial distribution and abundance patterns of these three species (also see Newmark 1991 and Hanson et al. 2007) suggests local but not consistent or general effects on *Leptonychia* recruitment.

Seed, seedling, and juvenile distributions offer clues to factors affecting recruitment limitation. Seedling carpets near fruiting *Leptonychia* trees suggest that immediate insect- or pathogen-induced mortality is not overwhelming within days or weeks of germination, as it is in some Neotropical legumes (Augsburger 1984, Augspurger and Kitajima 1992). Density-dependent seed and seedling mortality are probably general (Harms et al. 2000), but the particulars that determine success or failure at different growth stages, and in one microhabitat over another, vary among species (Terborgh et al. 1993), even within a genus (e.g., *Viola calophylla*; Russo et al. 2006). Our observations indicate that the species appears to have unusually persistent seedlings (cf. Howe et al. 1985). If consistent nonrandom mortality occurs between juvenile and adult stages, it will probably be from competition among maturing juveniles, saplings, poles, and young adults (Peters 2003), a pattern of recruitment

that may be common in African forests (Teketay 1997) and elsewhere.

#### *Seed quantity and quality*

Seed quantity and quality could decline in fragments because of pollinator limitation (Ghazoul 2005, Knight et al. 2005), inbreeding from diminished pollinator assemblages, and/or small population sizes (Young et al. 1996), or if mothers are stressed from unfavorable abiotic environments (Mazer and Gorchoff 1996). We found no evidence that trees in fragments set fewer seeds for their size than those in continuous forest. Similar *Leptonychia* fruit crops in fragments and continuous forest in either year do not eliminate pollinator limitation as a factor, but there is certainly no evident signal of pollinator limitation. An ongoing genetic study (N. J. Cordeiro et al., unpublished data) also fails to suggest pollinator limitation.

The weak evidence for fragmentation-induced inbreeding depression in *Leptonychia* is somewhat surprising. Forest fragments with very small stands widely separated from conspecifics should promote inbreeding, which in many normally outcrossing species produces inbreeding depression (Husband and Schemske 1996, Young et al. 1996). This species may be unaffected by inbreeding, or long-distance pollination continues to promote outcrossing (Ghazoul 2005, Lowe et al. 2005, Kramer et al. 2008). It is also plausible that more generations would be required to produce a stronger signal.

#### *Edge effects*

Patterns of plant recruitment change in response to biotic agents, but also from edge effects in fragments (Benitez-Malvido 1998). For example, in the Amazonian fragment complex, fragments  $\leq 10$  ha gain more pioneers and light-demanding species after isolation than do continuous forest (Nascimento et al. 2006). In that system, an enormous influx of pioneer species into small fragments and edges of larger fragments occurred over 13–17 years following isolation (Laurance et al. 2006). Consistent with *Leptonychia* as an early successional forest tree species (Cordeiro and Howe 2003), we found faster germination in fragments than in continuous forest and higher belowground biomass at edge vs. interior locations in forest and fragments. Its apparent poor recruitment in fragments is especially interesting given these paradoxical results, underscoring *Leptonychia* as an intriguing case.

#### *Conclusions*

Processes that limit the recruitment of new individuals in populations can be driven by a variety of mechanisms, from low seed output, to reduced availability of effective dispersers, to adverse biotic and abiotic effects (Muller-Landau et al. 2002, Schupp et al. 2002, Orrock et al. 2006, Jordano et al. 2007). Forest fragmentation can alter any of these processes to change the recruitment

dynamics of plant populations. Our earlier study demonstrated poorer seedling recruitment of *Leptonychia usambarensis* in fragments resulting from a reduction of effective dispersal, and concomitantly lower overall recruitment from seedling to juveniles in East Usambara fragments (Cordeiro and Howe 2003). Left open were alternative hypotheses that potentially explain diminished recruitment. The present study indicates that fecundity and seed quality are not different in fragments vs. continuous forest, nor is seed predation consistently different in the two habitats. The clearest signal explaining differences is reduced seed dispersal and subsequent mortality of seedlings or juveniles near *Leptonychia usambarensis* adults in small fragments. This result has important implications for land management throughout the tropics, where forest fragmentation is one of the main threats to biodiversity (Brooks et al. 2002). If *Leptonychia*, which appears to fare well at edges, is so vulnerable to disperser limitation, the situation is likely to be dire for interior forest trees relying on uncommon, specialized dispersers that are highly susceptible to forest fragmentation (Cordeiro and Howe 2001). Dispersal limitation may then be a significant force structuring fragmented tropical forests that harbor a diversity of primary forest species, the majority of which are animal dispersed.

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#### APPENDIX

Information on study area and focal tree species, with supplementary details on methods and results (*Ecological Archives* E090-066-A1).

**Norbert J. Cordeiro, Henry J. Ndangalasi, Jay P. McEntee, and Henry F. Howe. 2009. Dispersal limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90:1030–1041.**

Appendix A. Information on study area and focal tree species, with supplementary details on methods and results.

### **Supplementary information and methods**

#### Study area

The East Usambara Mountains form the northeast extension of the Eastern Arc range, a term coined by Jon Lovett (Lovett 1988) to describe a biogeographical region of Africa characterized by high numbers of endemic species in several taxonomic groups (Lovett and Waser 1993, Burgess et al. 2007). The climate in the East Usambara Mountains follows a bimodal monsoon pattern with heavy rains from March to May and short rains from October to December. Rainfall at an altitude of *c.* 1000 m averages 2000 mm per year and relative humidity is high (Hamilton and Bensted-Smith 1989). The study area is further described at the following website:

[www.fieldmuseum.org/africaforest](http://www.fieldmuseum.org/africaforest)

Humans have lived in the East Usambara Mountains for at least the last 2000 years (Schmidt 1989), and are believed to have shaped parts of the landscape through cultivation. Of the different types of disturbances to forest, habitat fragmentation has been a severe threat in the East Usambara Mountains and its foothill forests, particularly since the colonial period in the late 1800s into the early to mid-1900s (Hamilton and Bensted-Smith 1989, Newmark 2002). In the submontane plateau, at least 60 forest fragments ranging in size from < 1 to > 2000 ha have been separated from the continuous forest of 3,500 ha for > 70–90 years (Newmark 2002). Of these fragments, only four small and very isolated (<40 ha, and isolated from larger tracts of 520 ha and 3500 ha by > 0.5 km) have been found to harbor the focal tree species, *Leptonychia usambarensis* K.Schum (Sterculiaceae). These fragments lie at 900–1100 m in elevation and are surrounded by a matrix of tea plantations (Plate 1 in main text). Other larger fragments (98, 177 ha) also have *Leptonychia*, as do other fragments that are separated from continuous forest by a 6–10 m wide road. The primary fragments and continuous forest sites are depicted in Fig. A1.

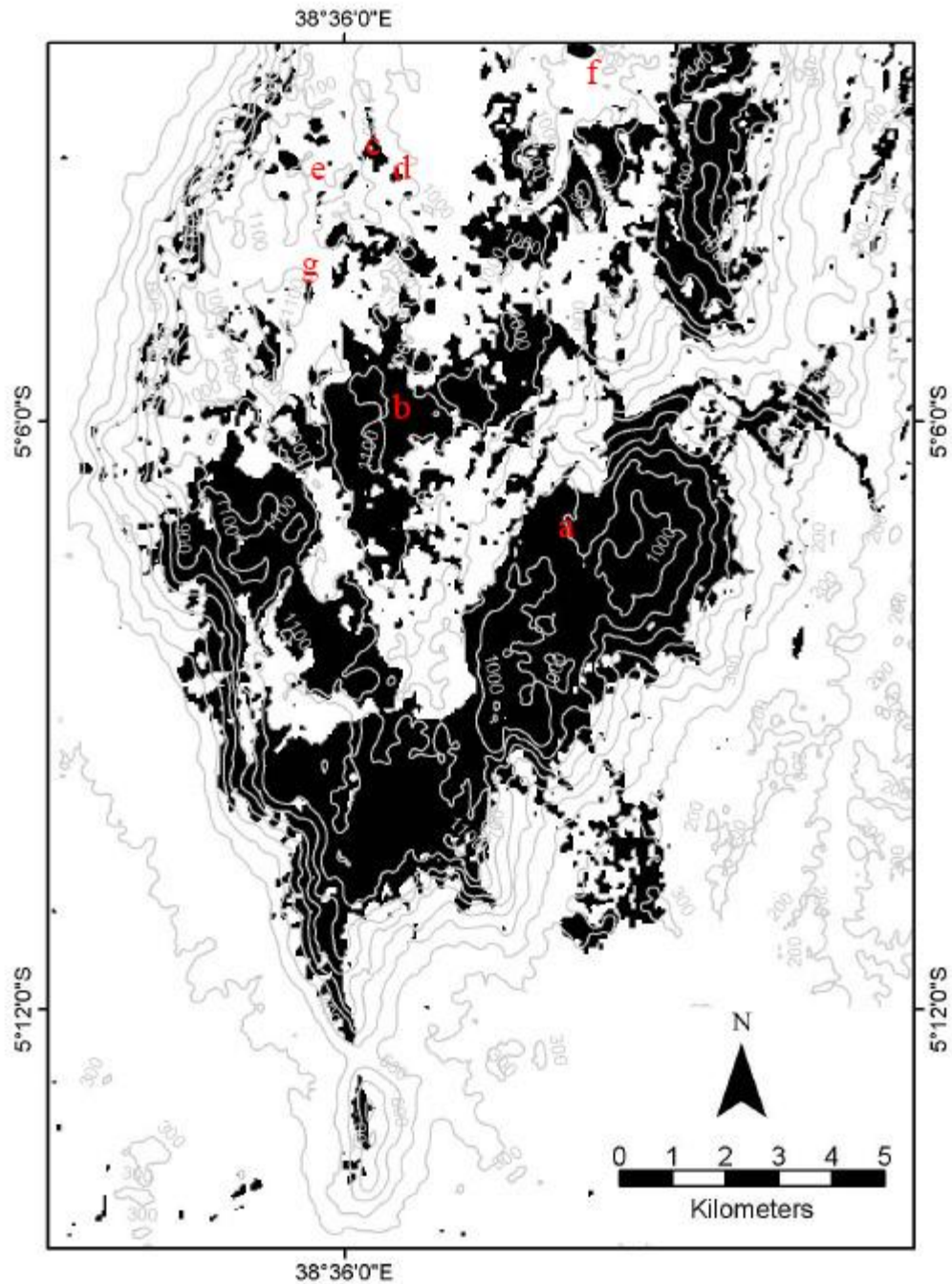


FIG. A1. The fragmented landscape of the southern portion of the East Usambara Mountains, Tanzania. The continuous forest sites used are 3500 ha (a) and 520 ha (b), and fragments include the 31 ha (c), 9 ha (d), 2 ha (e), 16 ha (f) and 21 ha (g), the latter site used only of the reciprocal transplant experiment. Scale limitations prevent an accurate depiction of the smaller fragments.

## Focal tree species

*Leptonychia usambarensis* K.Schum (Sterculiaceae) is endemic to the Eastern Arc Mountains (Burgess et al. 2007), however a new isolated population of this tree has recently been found in the foothills of Mt Kilimanjaro (Hemp 2006), which is a much younger mountain compared to the Eastern Arc mountains. The tree occurs in the under- to midstory, with a height of 2-20 m. Flowers are creamy-white in color whereas seeds are located in capsules that face upwards, advertising to birds in mid- and overstory where seeds may be exposed from 1–4 days (Fig. A1). Fruit crop ranges from 2 to 8412 seeds ( $768 \pm 75$ , 238 trees: 2002 data), and seed length of 63 seeds ranges from 1.0 to 1.5 cm ( $1.2 \pm 0.14$ ; see also Cordeiro and Howe 2003), width from 0.49 to 0.9 cm ( $0.69 \pm 0.10$ ) and fresh weight from 0.2 to 0.7 g ( $0.4 \pm 0.01$ ). Crop sizes were estimated following Laman (1996) and Clark et al. (2004), where fruits were carefully counted on 3 to 5 branches per tree, computing the average fruits per branch, and multiplying this average by the total number of branches in each tree. In July of 2000, a germination trial on moist tissue using 20 seeds with arils and 20 seeds with arils manually removed showed that removal of arils favored germination: 75% of the seeds with arils removed germinated within 13 days compared



FIG. A2. (a) Capsules and arillate seeds and (b) flowers of *Leptonychia usambarensis* (Sterculiaceae), an early successional tree species endemic to the Eastern Arc Mountains. The length of the seed and the flower bud is approximately 1 cm.

to 20% where arils were not removed.

## Rodent and dove censuses

Rodents were sampled over 1056 trap-nights for each year (2001, 2002, 2005); fruiting in several sites had failed in 2004 and so trapping was carried out in the following year. Fresh bait was replaced daily and traps were baited separately with coconut or the seed species through a stratified random scheme for each sampling period where six of the 11 traps in a given transect had native seed bait and the other five had coconut. Freshly fried coconut was used as bait because it yields high rodent captures in Eastern Arc forests (Stanley et al. 1998). A total of 1, 2, 2, and 3 transects bisected the 2, 9, 16, 31 ha fragments whereas 9 and 15 transects were distributed evenly in three widely separated sites in each of the larger and more extensive patches of 520 and 3500 ha forest, respectively. Traps were checked in the early morning or evening hours, and rodents were identified, marked and released.

Rodent censuses in 2001 were done using the lipid-rich seeds of the native *Allanblackia stuhlmannii* (Clusiaceae) tree and coconut. The sampling was done during the fruiting season of this tree species in January and February. Results revealed high abundance of the forest mouse *Praomys delectorum* in 2001 compared to 2002 and 2005, when trapping was done with *Leptonychia* fruits during July and August. Higher abundances of *Praomys delectorum* during the hot season from January to March than in other months of the year is similar to findings by Makundi et al. (2007) from the nearby West Usambara Mountains. Five other rodent species were infrequently captured: *Lophuromys flavopunctatus* (51 g) and *Hylomyscus arcimontensis* (24 g, *sensu* Carleton and Stanley 2005), and occasional captures of *Beamys hindoi* (61 g), *Graphiurus murinus* (22 g), and *Cricetomys gambianus* (>1 kg). Abundances of all rodents for the different sampling years are presented in Table A1.

The Tambourine *Turtur tympanistria* and Lemon *Aplopelia larvata* dove abundances were estimated through 136 point counts spread over four census periods between February 2000 and February 2001 (Table A2). The number of point counts was stratified by fragment size with 2, 2, 2, 4, 12 and 12 counts in the 2, 9, 16, 31, 520 and 3500 ha fragments, respectively. In the 520 and 3500 continuous forest patches, the 12 counts were divided as 4 counts in each of three widely distributed sites.

## Rodent and dove statistical analyses and results

We first tested if sites were independent in the two continuous forest tracts (520 and 3500s ha) with fragment size class as a fixed effect and year and site as random effects. The importance of the random effects was evaluated by simple inspection of the *t-value* of the coefficient estimates and respective standard errors (see also Moore and Swihart 2007). Given that all sites were independent of each other in the continuous forest tracts, we proceeded with further analyses without taking site into consideration.



TABLE A1. The  $t$  value, coefficient estimate, standard error (SE) and  $P$  value for random effects of census period and year in Proc Glimmix analyses of dove and rodent abundance.

Random effect	Coefficient estimate	SE	$t$ value	$P$
DOVES				
census period	0.3327	0.3328	0.9997	0.50
RODENTS				
year	0.9312	0.9608	0.9692	0.51

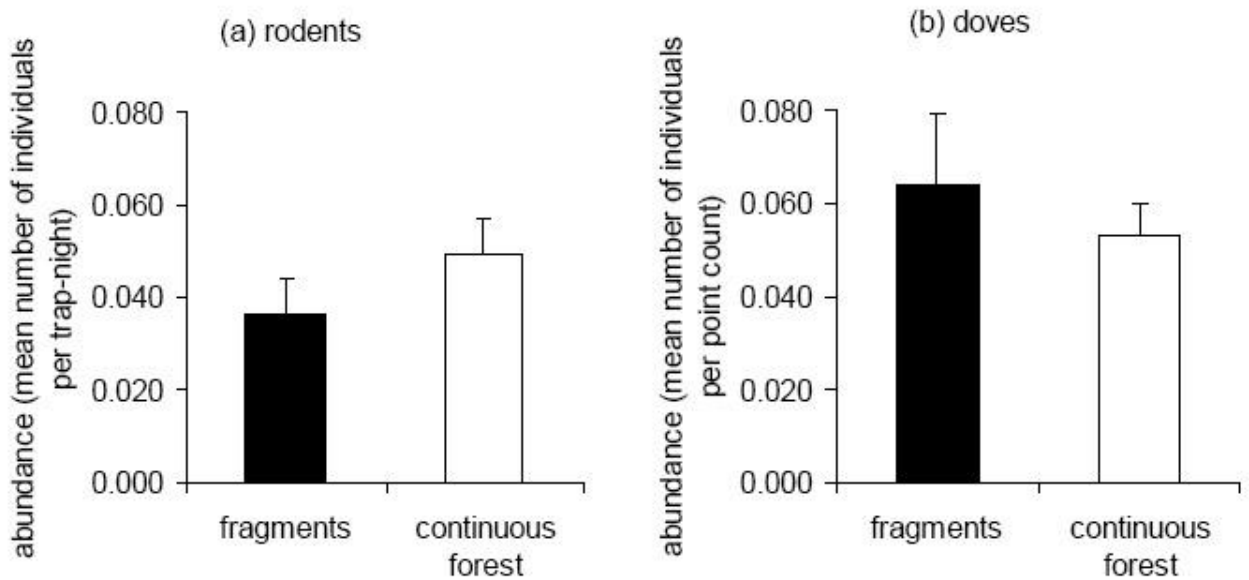


FIG. A3. Abundance of (a) rodents (individuals per trap night) and (b) doves (individuals per point count) in small isolated fragments and continuous forest in the East Usambara Mountains. Abundances of both rodents and doves did not significantly differ in fragments compared to continuous forest ( $P = 0.19$ , see *Results* section).

TABLE A2. Rodent abundance (mean number of individuals per trap-night  $\pm$  SE) over all three sampling years in East Usambara fragments and continuous forest.

<b>Fragment area (ha)</b>	<b>2001</b>	<b>2002</b>	<b>2005</b>
2	0.12	0.03	0
9	0.06 $\pm$ 0.03	0	0.02 $\pm$ 0.02
16	0.05 $\pm$ 0.02	0.05 $\pm$ 0.02	0.02 $\pm$ 0.02
31	0.07 $\pm$ 0.03	0.01 $\pm$ 0.01	0.04 $\pm$ 0.01
520	0.18 $\pm$ 0.02	0.02 $\pm$ 0.01	0.04 $\pm$ 0.01
3500	0.06 $\pm$ 0.01	0.02 $\pm$ 0.01	0.01 $\pm$ 0.00

TABLE A3. Dove abundance (mean number of individuals per point count  $\pm$  SE) over all four sampling periods in East Usambara fragments and continuous forest.

<b>Fragment area (ha)</b>	<b>Feb 2000</b>	<b>June 2000</b>	<b>Oct 2000</b>	<b>Feb 2001</b>
2	0.13	0.13 $\pm$ 0.13	0	0.19 $\pm$ 0.19
9	0.06 $\pm$ 0.06	0	0	0
16	0.06 $\pm$ 0.06	0	0.13 $\pm$ 0.13	0.06 $\pm$ 0.06
31	0.08 $\pm$ 0.06	0.02 $\pm$ 0.02	0.03 $\pm$ 0.03	0.14 $\pm$ 0.03
520	0.02 $\pm$ 0.02	0.02 $\pm$ 0.01	0.09 $\pm$ 0.02	0.09 $\pm$ 0.02
3500	0.07 $\pm$ 0.02	0.02 $\pm$ 0.01	0.08 $\pm$ 0.02	0.03 $\pm$ 0.01

Nonsignificant result of dry shoot and root biomass from the seedling transplant experiment

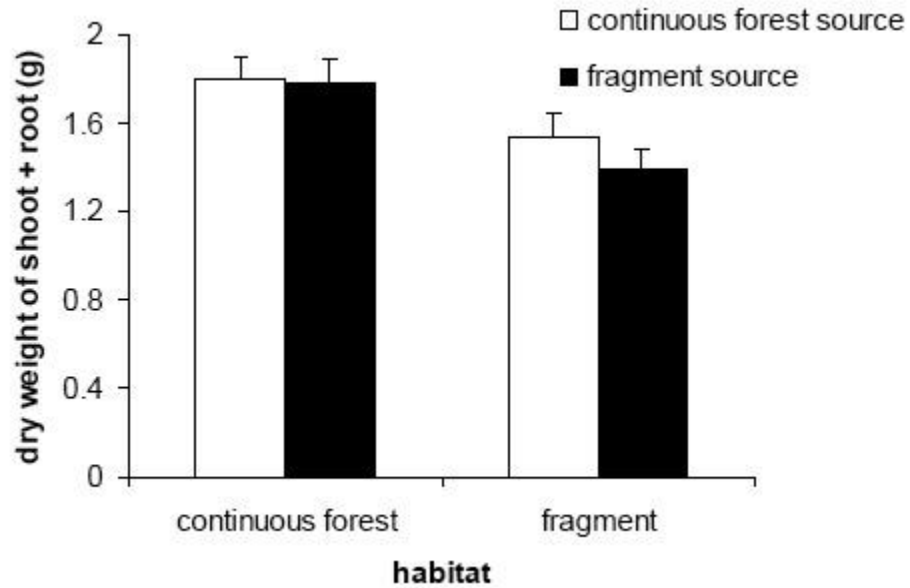


FIG. A4. Biomass (raw means  $\pm$  SE of dry mass) of *Leptonychia usambarensis* juveniles sourced from continuous forest and fragment trees reciprocally transplanted in continuous forest and fragment habitats. There was no significant effect of habitat ( $P = 0.61$ ) or seed source ( $P = 0.14$ ) on juvenile growth. See text for details.

Nonsignificant result of seedling to juvenile survival from the seedling transplant experiment

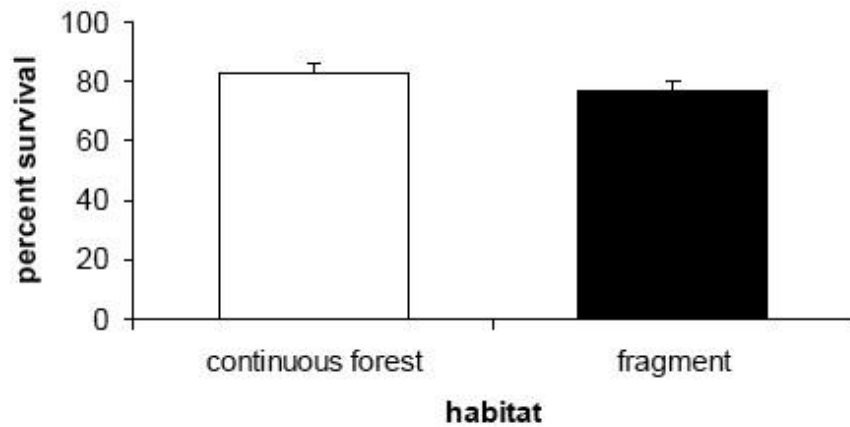


FIG. A5. Percent survival (raw means  $\pm$  SE) of *Leptonychia usambarensis* juveniles 16 months after establishing the experiment in the field. Seeds were sourced from continuous forest and fragment trees and seedlings were reciprocally transplanted in continuous forest and fragment habitats. There was no significant effect of habitat on survival ( $P = 0.38$ ). See text for details.

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