REMOVING OTHER TREE SPECIES DOES NOT BENEFIT THE TIMBER SPECIES *CEPHALOSPHAERA USAMBARENSIS*

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ABSTRACT

The endemic canopy tree *Cephalosphaera usambarensis* is a valuable timber species in montane rainforest of Tanzania. Here we evaluate an experiment in which mature trees of species other than *C. usambarensis* were removed from an area in the East Usambara Mountains. We compared stage/size structure of the trees in this area to structure in three nearby control areas from which potential competitors had not been removed. The removal area contained a slightly higher density of large *C. usambarensis* trees than did control areas, but these trees had not grown bigger than those in control areas in the quarter century since removal. Furthermore, the removal area contained far fewer newly-dispersed seeds, seedlings, or small sapling trees. Thus there is no evidence that removal of potential interspecific competitors enhances the population density or biomass (tree size × density of individuals) of the *C. usambarensis* population. Instead, removing other trees not only sacrifices local forest biodiversity, but also may harm future timber yield of *C. usambarensis* by suppressing recruitment of new individuals into the population.

Key words: Biodiversity–Competition–Density–Experiment–Recruitment–Size Structure

INTRODUCTION

The Eastern Arc Mountains of eastern Tanzania and south-eastern Kenya rise from near sea level to elevations of several thousand meters. Before the Twentieth Century these mountains supported dense and species-rich rainforests between elevations of about 400m and 2000m a.s.l. (Lovett and Wasser 1993). In more recent times the forests have been selectively logged or clear-cut for agriculture and to harvest natural resources (Conte 2004), but the remaining forests still contribute importantly to the Eastern Afromontane biodiversity hotspot (Conservation International 2012; Myers *et al.*, 2000).

One example of a species that has been logged for timber is the endemic canopy tree *Cephalosphaera usambarensis*. Experimental plots were established approximately 25 years ago in the Amani Nature Reserve, Eastern Usambara Mountains, to evaluate a possible method for managing this valuable species (Raja, I., pers. communication.). In one area, large individuals of other canopy species were selectively removed, under the assumption that this could reduce interspecific competition and increase timber yield. Here we evaluate the effect of this treatment by comparing stage and size structure of the population in the area of removal to structure in areas from which potential competitor trees were not removed. This comparison suggests that removal may actually harm populations of the timber species, as well as harming forest biodiversity.

METHODS
Species description
The canopy tree *Cephalopshaera usambarensis* Warb. (nutmeg family, Myristicaceae; "*mtambaa*" or "*mtambala*" in the Kisambaa language) is endemic to Tanzania and restricted to montane rainforest of the Eastern Arc Mountains

(Schulman *et al.*, 1998; Lovett *et al.*, 2006). The species reaches highest densities in the East Usambaras between 800 and 1000m a.s.l. (AFIMPP 1988). Mature trees grow to 50m tall with a straight bole and a cylindrical crown. The species is dioecious; sexual maturity is reached at a size of approximately 20cm diameter at breast height (hereafter "dbh"). Females produce fruits after the "long rains" season from March to May. While still held on the tree, fruits split open to reveal a single large seed (dimensions circa 4cm × 6cm), which is partly covered with a thin yellow-to-orange-coloured aril. Fruit bats (family Pteropodidae) harvest the arils and may aid in dispersal of the seeds away from parent trees (Rajabu, I. Personal communication). Giant rats (*Cricetomys gambianus)* harvest seeds from the forest floor and, because they sometimes cache seeds before consuming them, may also serve as seed dispersers. Unharmed seeds germinate and establish as seedlings after the long rains. Seedlings grow rapidly: one planted at the Amani Nature Reserve reached a height of 43cm after six months and another reached a dbh of 28cm and height of 15m after 16 years.

Mature *C. usambarensis* trees are valuable for timber (AFIMPP 1988). They have been selectively logged in the East Usambara Mountains since at least the middle of the Twentieth Century (Conte 2004, p. 155). We studied *C. usambarensis* in the Amani Nature Reserve in the East Usambaras (5° 05' S, 38° 40' E), at elevations around 500m a.s.l., within "Block 2—Intact and Exploited Moist Forest" as mapped and described in AFIMPP (1988).

Experimental removal of potential competitors
In the middle 1980s an experimental manipulation was applied to approximately 0.15ha of forest within Block 2, above the west bank of the Sigi River. The manipulation involved removing large trees of other species, trimming lower branches of mature *C. usambarensis* individuals, and slashing understorey vegetation other than *C. usambarensis*. In the approximately 25 years since removal no analysis of this experiment has been attempted, judging from our search of records at the Amani Nature Reserve and at the Tanzania Forestry Research Institute in Lushoto.

Census methods
In August 2012 we spent approximately 400 person-hours censusing a 30m × 20m plot (total area = 600 m^2) in the area of removal and an equal-sized plot in each of three nearby areas. One of these was a 'Slash-Control' plot that we demarcated about 85m downstream from the 'Removal' plot, in an area that was slashed at the same time as removal, but that had received no other treatment. We set out the final two plots ('Control 1' and 'Control 2'), about 295 and 340m downstream respectively from the other plots and on the opposite side of the Sigi River, in forest areas where no treatment was done.

Each plot was further divided into 6 parallel strips (hereafter "subplots") each of 5m × 20m. Within each subplot we counted all fresh seeds (i.e., those produced during the previous rainy season that had fallen to the ground; these are large enough to be quite visible with a systematic search), seedlings, saplings, and older individuals. We noted whether seeds were germinating, as indicated by an emerging radicle, and scored as seedlings those that had rooted and produced stems and first leaves. We measured dbh of all individuals above 6cm dbh, and scored individuals older than seedlings as saplings <1m high; saplings between 1m high and 6cm dbh; trees 6cm to 20cm dbh, and trees >20cm dbh.

These censuses yielded information on the present stage and size structure of populations. Population structure provides insights into past survival and growth of individual trees and into the recruitment of new individuals from seeds.

Data Analysis

We used chi-square tests to compare proportional representation of *C. usambarensis* individuals of various stage and size classes across different plots. Analysis of variance (ANOVA) based on the six subplots within each plot, followed by Tukey's HSD for *a posteriori* pairwise comparisons, allowed us to compare absolute numbers of individuals of different classes as well as overall densities of *C. usambarensis*. We used multivariate analysis of variance (MANOVA) to further explore which stage and size classes and which plots contributed the most to overall heterogeneity in population structure. We again used ANOVA to compare sizes of larger trees across plots, as well as proportions of seeds that were germinating. Finally, we explored the statistical associations among stage and size classes using pairwise correlation analyses. All analyses were done with JMP 5.0 software (SAS Institute, Cary, North Carolina, USA).

RESULTS

Population structure

The four study plots are similar in elevation, slope, and canopy cover (Table 1). However, their populations of *C. usambarensis* differed significantly in proportional representation of individuals of different stages and sizes (Fig. 1; $\chi^2 = 185.56$, df = 15, P < 0.001). Most of the overall heterogeneity was contributed by the 'Removal' plot (77.3% of total χ^2), which contained proportionally more trees in the two largest size classes (i.e., 6cm to 20cm dbh and >20cm dbh), proportionally fewer saplings in the smallest size class (i.e., <1m high), and absolutely no saplings of intermediate size (i.e., between 1m high and 6cm dbh). The second greatest contribution to overall hetereogeneity came from the 'Control 2' plot (11.2% of total χ^2), which contained proportionally fewer individuals within the three largest size classes and proportionally more saplings <1m high. Overall, most of the heterogeneity in structure came from different proportional representation of larger size classes (i.e., trees 6cm to 20cm dbh and >20cm dbh, $\chi^2 = 181.27$, df = 9, P < 0.001); seed and seedling classes contributed very little to overall heterogeneity.

Absolute numbers of individuals of different stage/size classes and total density also varied among plots (Fig. 2; $F_{3,23} = 61.63$, P < 0.0001; ANOVA using ln-transformed values to achieve normality and homoscedasticity of model residuals). The 'Control 2' plot contained many more seeds, seedlings, and saplings than any other plot, and thus supported a significantly higher density of *C. usambarensis*. Conversely the 'Removal' plot contained few or no individuals in these smaller stage/size classes, and thus supported a significantly lower overall density. 'Control 1' and 'Slash-Control' plots were intermediate and statistically indistinguishable (pairwise comparisons, not shown). One consequence is that the four plots differed greatly in their ratios of potential new *C. usambarensis* recruits—seeds plus seedlings—relative to sexually mature trees >20cm dbh (Ratios of 16.8, 34.6, 10.0, and 1.4 respectively for 'Control 1', 'Control 2', 'Slash-Control'', and 'Removal' plots).
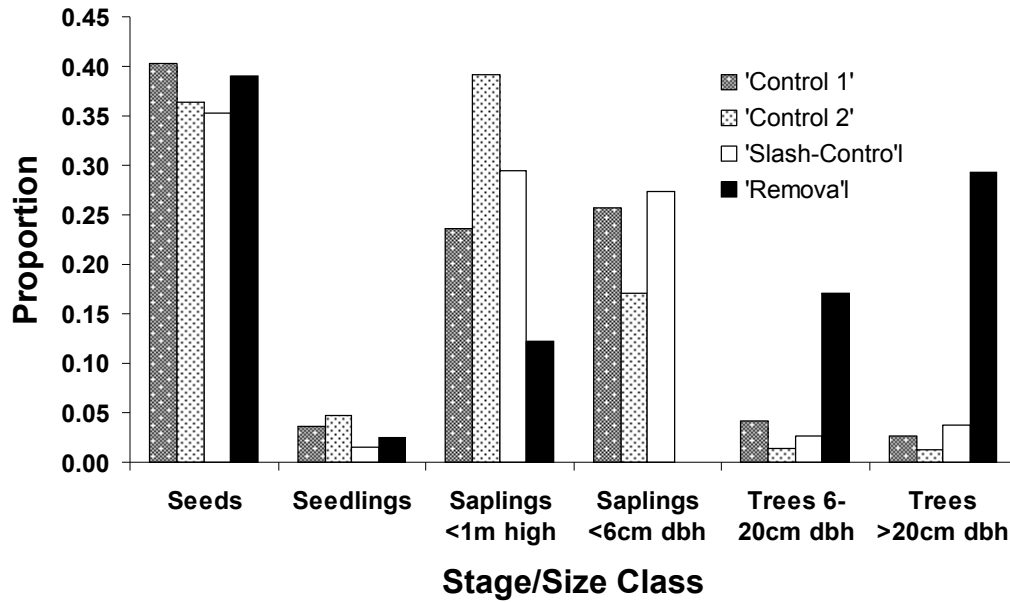
Figure 1: Proportional structure of *C. usambarensis* populations in the four study plots. Histograms are proportions of the populations in each of six stage/size classes.
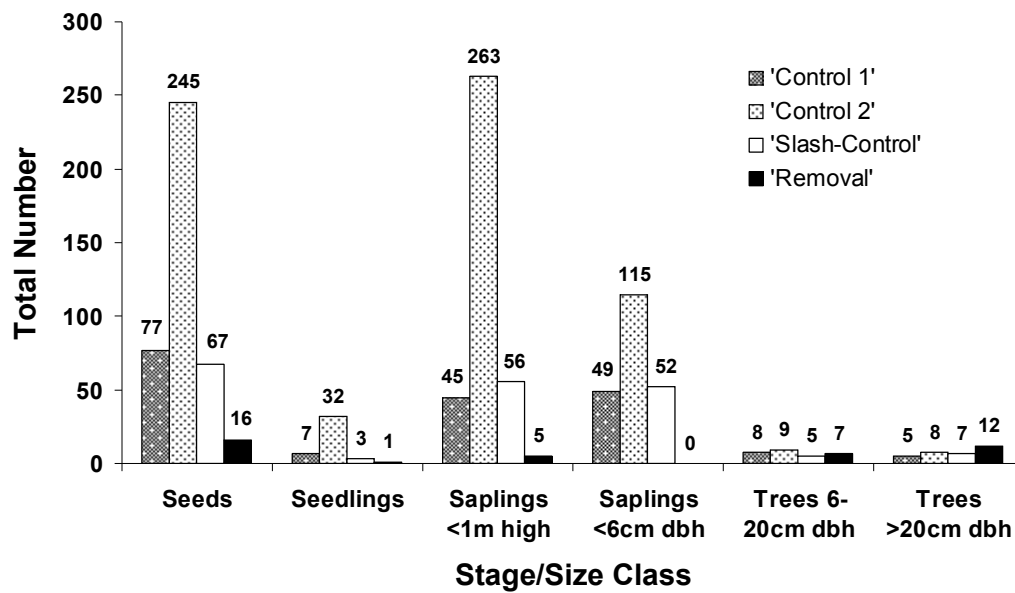

Figure 2: Absolute numbers of *C. usambarensis* individuals in the four study plots. Histograms and the numbers above them are the numbers of individuals of six different stage/size classes.

Table 1: Properties of the four study plots*

Plot	UTM	Elevation	Aspect	Slope	Cover
'Control 1'	0461153, 9436152	470m	340°	24.5°	82%
'Control 2'	0460777, 9435806	502m	340°	23.5°	84%
'Slash-Control'	0460819, 9436100	480m	60°	20.5°	83%
'Removal'	0460822, 9436014	477m	80°	20.5°	79%

*UTM coordinates (easting, southing), compass aspect, and elevations a.s.l. were taken with a Garmin Model GPSmap 76CSx handheld GPS device, using map datum WGS84. Forest canopy cover was measured with a Lemmon Model C spherical densitometer, and slope was measured with a Suunto PM-5/360 PC clinometer.

Differences among plots in numbers of individuals were confirmed by MANOVA based on numbers of individuals within the six subplots of each plot (Wilks' lambda = 0.053, $F_{18,42.9}$ = 4.34, P < 0.0001). The first eigenvector explained 92.8% of variance across plots; it contrasted numbers of mature trees >20cm dbh (negative coefficient) with all other stage/size classes (positive coefficients). 'Removal' subplots (low canonical scores) and 'Control 2' subplots (high canonical scores) differed significantly from each other and from 'Slash-Control' and 'Control 1' subplots (intermediate canonical scores); these latter two plots did not differ.

The four study plots were similar in some other regards, however.   For example, mean sizes of all individuals above 6cm dbh did not differ significantly across plots (Means of 23.0, 23.1, 21.4, and 23.7cm dbh respectively for 'Control 1', 'Control 2', 'Slash-Control', and 'Removal' plots; $F_{3,60}$ = 0.06, P = 0.98, ANOVA), nor did the proportions of seeds that were germinating at the time of censuses (Means of 0.39, 0.30, 0.27, and 0.50 respectively for 'Control 1', 'Control 2', 'Slash-Control', and 'Removal' plots; $F_{3,23}$ = 1.21, P = 0.33, ANOVA using square-root transformed values to achieve normality and homoscedasticity of model residuals).

Associations among stage/size classes
The abundances of seeds, seedlings, saplings <1m high, and saplings between 1m high and 6cm dbh were positively correlated with one another based on counts within the six subplots of each study plot (Table 2). Thus the strikingly low ratio of seeds plus seedlings relative to large trees in the 'Removal' plot corresponds as well to low ratios of saplings to large trees.   In contrast, there was no detectable association between numbers in the smaller stage/size classes and numbers of trees 6cm to 20cm dbh or >20cm dbh. Numbers in smaller classes appeared to be weakly negatively correlated with numbers in larger size classes (P ≈ 7%), but sample sizes were small.

DISCUSSION
The East Usambara Mountains are renowned for their montane rainforest with its relatively large extent and species diversity compared to nearby areas (Huang *et al.* 2003).   Selective removal of tree species from a site, as was done in the 'Removal' treatment about a quarter century ago, reduces this diversity locally. Is such a biodiversity sacrifice balanced by a perceptible gain in timber productivity of *C. usambarensis*?   Our comparisons of population structure provide no evidence for increased productivity.   If removing potential competitors does increase the rate of growth of *C. usambarensis* trees and their survival, there should have been more mature trees in the 'Removal' plot as a result of growth of small trees at the time of removal as well as survival of existing mature trees.   Furthermore, those trees

should have been bigger than trees in the 'Control' or 'Slash-Control' plots. Neither effect was evident. Similarly, if selective removal did help seed production or seedling recruitment, then the 'Removal' plot should have contained many small individuals and a high ratio of seeds to mature trees. Neither was the case; instead,

the 'Removal' plot was strikingly impoverished in saplings <1m high, completely lacked those between 1m high and 6cm dbh, and had a low ratio of seeds and seedlings relative to large trees when compared to 'Control' and 'Slash-Control' plots.

Table 2: Pairwise correlations between the numbers of individuals of *C. usambarensis* in different stage/size classes found within 5m × 20m subplots of the four study plots

Variable	by Variable	Correlation	P
Seedlings	**Seeds**	**0.71**	**0.0001**
Saplings <1m high	**Seeds**	**0.75**	**<0.0001**
Saplings <1m high	**Seedlings**	**0.43**	**0.035**
Saplings <6cm dbh	**Seeds**	**0.85**	**<0.0001**
Saplings <6cm dbh	**Seedlings**	**0.52**	**0.0091**
Saplings <6cm dbh	**Saplings <1m high**	**0.82**	**<0.0001**
Trees 6cm-20cm dbh	Seeds	0.01	0.950
Trees 6cm-20cm dbh	Seedlings	−0.10	0.654
Trees 6cm-20cm dbh	Saplings <1m high	0.27	0.203
Trees 6cm-20cm dbh	Saplings <6cm dbh	0.11	0.610
Trees >20cm dbh	Seeds	−0.10	0.652
Trees >20cm dbh	Seedlings	0.02	0.914
Trees >20cm dbh	Saplings <1m high	−0.06	0.763
Trees >20cm dbh	Saplings <6cm dbh	−0.24	0.264
Trees >20cm dbh	**Trees 6cm-20cm dbh**	**−0.38**	**0.069**

*Boldface indicates significant correlations ($P < 0.05$). Abundances of the smaller stages and sizes are positively and significantly correlated within the 24 subplots, but are not correlated with abundances of larger trees. Abundances of smaller and larger individuals appear to be negatively correlated.

Why did removal of potential competitors fail to substantially enhance the density of larger *C. usambarensis* trees or their size after a quarter of a century? Although we cannot provide a precise mechanism for this lack of effect, a general finding for tropical trees is that interspecific competition has weak effects on recruitment and growth, whereas intraspecific density-dependence (intraspecific competition) is much stronger (e.g., Wright 2002; Piotto *et al*. 2003).

Why did removal of other tree species appear to suppress recruitment of new *C. usambarensis* individuals? Here we can think of several possibilities. First,

although the 'Removal' plot did not differ conspicuously from the other plots in elevation or slope, removal itself does change at least one physical aspect of a site, the penetration of sunlight below the canopy, and the 'Removal' plot did have slightly lower canopy cover than other plots even a quarter century after the experimental manipulation. While light often limits the growth of tropical trees, canopy species usually are shade tolerant and may be outcompeted by shade-intolerant species at high light levels (e.g., Wright 2002). Mugasha (1978) reported that logging of 7 to 17 *C. usambarensis* stems per ha impaired recruitment of new individuals, which is consistent with a

negative effect of light on seedling germination and growth, although it also might have been caused by a lower production of *C. usambarensis* seeds in logged areas. Second, low recruitment could also result from responses of seed consumers or dispersers to the removal treatment. Fruit bats, which disperse *C. usambarensis* seeds, may not roost as frequently in thinned forests, and this may result in lower seed deposition there. Consistent with this possibility, Velho *et al.* (2012) found fewer large-bodied frugivores birds, and lower recruitment of large-seeded, bird-dispersed tree species, in tropical forests of north-eastern India that had been thinned by logging.

We cannot at present evaluate these possible mechanisms for the observed differences in *C. usambarensis* population structure. However, our results suggest that reducing the density of potential competitor species does harm recruitment by some mechanism(s), and does not lead to short-term enhancement of density or size of trees. Thus removal does not appear to work as a management practice that improves yield. Furthermore, removal of other species reduces biodiversity of the forest, which is likely to impair valuable "ecosystem services" in the form of watershed protection and nutrient retention that enhance the health of populations of all canopy tree species (Naeem *et al.* 2012). This possibility is worth investigating, as it has important implications more generally for the effective management of tropical forest resources.

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