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Predicting which tropical tree species are vulnerable to forest disturbances

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Abstract

Tropical forest management often focuses on a few high-value timber species because they are thought to be the most vulnerable in logged forests. However, other tree species may be vulnerable to secondary effects of logging, like loss of vertebrate dispersers. We examined vulnerability of tree species to loss of vertebrate dispersers in Mabira, a heavily disturbed tropical rainforest in Uganda. Fruit characteristics and shade tolerance regimes of 269 tree species were compiled. Stem densities of tree species producing fruits of various sizes and having different shade tolerance regimes were computed for Mabira and compared with densities of conspecifics in Budongo, a less disturbed forest with similar floral composition. Seventy per cent of tree species in Mabira are animal-dispersed, of which 10% are large-fruited light demanders. These species are the most vulnerable because they rarely recruit beneath adult conspecifics and are exclusively dispersed by large vertebrates, also vulnerable in heavily disturbed forests. Comparison of densities between Mabira and Budongo showed that large-fruited light demanders had a lower density in Mabira. Other categories of tree species had similar densities in both forests. It is plausible that the low density of large-fruited light demanders is due to limited recruitment caused by dispersal limitations.

Key words: fruit/seed size, light demanders, logging, seed dispersal, shade tolerants

Résumé

La gestion des forêts tropicales se concentre souvent sur quelques espèces d'arbres de grande valeur parce qu'on pense que ce sont les plus vulnérables dans les forêts exploitées. Pourtant, d'autres espèces d'arbres peuvent s'avérer vulnérables aux effets secondaires des coupes forestières, comme la perte des vertébrés disperseurs. Nous avons examiné cette vulnérabilité à Mabira, une forêt pluviale tropicale très perturbée d'Ouganda. Nous avons compilé les caractéristiques des fruits et le régime de tolérance à l'ombre de 269 espèces d'arbres. La densité des jeunes plants d'espèces d'arbres produisant des fruits de différentes tailles et montrant un régime différent de tolérance à l'ombre a été enregistrée pour Mabira et comparée à celle des mêmes espèces à Budongo, une forêt moins perturbée où la composition florale est comparable. Soixante-dix pourcents des espèces d'arbres de Mabira sont dispersées par les animaux, dont 10% portent de gros fruits et exigent de la lumière. Ces espèces sont les plus vulnérables parce que les jeunes plants poussent rarement sous les adultes de même espèce et qu'ils sont exclusivement dispersés par de grands vertébrés, eux-mêmes vulnérables dans les forêts très dérangées. La comparaison des densités entre Mabira et Budongo a montré que les arbres à gros fruits et aimant la lumière étaient moins denses à Mabira. D'autres catégories d'arbres avaient des densités comparables dans les deux forêts. Il est possible que la faible densité d'arbres à gros fruits demandeurs de lumière soit due au recrutement limité causé par une dispersion réduite.

Introduction

The impacts of forest disturbances, especially logging, on tropical forest dynamics have been the focus of many ecological studies. Logging directly affects the forest ecosystem by removing mature individual timber trees that are often more fecund, causing incidental damage to seedlings and saplings during the logging operations and altering the physical structure of the forest, for example

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opening up the canopy (White, 1994; Pereira *et al.*, 2002). However, it is now recognized that the secondary effects of logging are equally or even more important especially for most mammal species. For instance, logging is accompanied by an increased incidence of hunting, fire and human occupation (Laurance *et al.*, 2006). It is, therefore, important for contemporary ecologists and forest managers to examine the chain of effects of logging disturbances to predict their impacts on forest dynamics as a prerequisite to developing comprehensive management strategies.

An important effect of logging is the loss of vertebrates caused by increased hunting due to improved access to forests (Laurance *et al.*, 2002). Vertebrates are crucial in the dynamics of tropical forests because they disperse the seeds of most tropical trees. In some forests, over 90% of tree species are dependent on vertebrates for their dispersal (Gautier-Hion *et al.*, 1985; Willson, Irvine & Walsh, 1989; Corlett, 1996; Silva & Tabarelli, 2000). Vertebrates disperse seeds of trees that provide them with a direct energetic reward such as the pulp of fleshy fruits or the aril of arillate seeds. However, other species that do not produce fleshy fruits also benefit from vertebrate dispersal through scatter hoarders. The scatter hoarders hide away excess seeds and forget about some, allowing survival and establishment of some individuals (Forget & Vander Wall, 2001). Consequently, the loss of vertebrates could affect tropical forest trees given that seed dispersal enhances their recruitment by facilitating escape of distance- and density-dependant mortality factors beneath adult conspecifics (Bell, Freckleton & Lewis, 2006; Hardesty, Hubbell & Bermingham, 2006). However, different tree species are unlikely to be equally vulnerable to the effects of loss of dispersers. Few studies have attempted to predict which tree species may be threatened by such forest disturbances, for example Hammond *et al.* (1996); Martini, Rosa & Uhl (1994); Pinard *et al.* (1999). In these studies, a number of ecological parameters including tree life history, geographical distribution and tree density were used to predict vulnerability. Given the large variation in forest composition and ecology found among tropical forests, the appropriate suite of characteristics useful for describing a tree species' vulnerability to disturbance will vary regionally. However, dispersal ability appears to be a universal factor. The major concern would then be how to measure dispersal ability for tree species in secondary forest landscapes. Perhaps of greater importance for tree population biology, are the limits that are set by fruit and seed allometry to the range of frugivores that are capable of dispersing their seeds. Only large-bodied vertebrates have the capacity to swallow or carry large seeds intact. As diversity of potential seed dispersers is negatively correlated with seed size, large-seeded tree species have a limited range of dispersers, mainly composed of large-bodied species. It is also well known that hunting and habitat degradation have a disproportionate effect on large vertebrates (Pimm, Jones & Diamond, 1988; Peres, 2001). This is because large vertebrates are more attractive to hunters and often have a lower reproductive rate (Bodmer, Eisenberg & Redford, 1997). Large vertebrates cannot adjust to persistent hunting pressures by becoming more behaviourally inconspicuous (Babweteera & Brown, 2009). Also, they require large contiguous habitats (Laidlaw, 2000), which means they are more vulnerable to fragmentation.

It seems therefore logical to hypothesize that the recruitment of large-seeded trees is likely to be more at risk in forest communities where large-bodied vertebrate seed dispersers have been decimated. This study examines the fruit characteristics of tree species in a heavily disturbed forest landscape with the aim of: (i) determining whether tropical trees form discrete fruit syndromes that can aid identification of vulnerable species and (ii) determining what proportion of tree species have a narrow range of seed dispersers and therefore are particularly vulnerable to the effects of their loss.

Materials and methods

Study area

The study took place in Mabira Forest and Budongo Forest Reserves in Uganda. Mabira is a moist semideciduous forest (32°52′–33°07′E and 0°24′–0°35′N), covering an area of 306 km^2, at an altitudinal range of 1070–1340 m above sea level. Due to its proximity to Kampala, the capital city in Uganda, Mabira, is one of the main sources of fuel wood and timber for the growing urban population. Moreover, the forest has been subjected to intense logging, hunting and conversion to agricultural land for several decades. For instance, over a period of 15 years (1973–1988), it is estimated that 29% of the forest cover was lost and the total forest edge-to-area ratio increased by 29%. The total area of heavily disturbed forest increased from 18% to 42% (Westman, Strong & Wilcox, 1989). This resulted in severe forest fragmentation with an estimated 50,000 people living in the associated enclaves. The vertebrate population in Mabira is not well studied although it is believed that most large vertebrates have been depleted (Howard, Davenport & Mathews, 1996). Early records suggested the existence of large-bodied animals such as chimpanzees, *Pan troglodytes*, black and white colobus monkeys, *Colobus guereza*, and buffaloes, *Syncerus caffer* (Kingdon, 1971), which are now extinct. Elephants, *Loxodonta africana*, were last recorded in the mid-1950s (Howard, 1991). Informal interviews with local people revealed that black mangabeys, *Lophocebus aterrimus*, and red tailed monkeys, *Cercopithecus ascanius*, are the only species of diurnal primates currently known to exist in the forest. However, their populations are thought to be diminishing.

Budongo is also a moist semideciduous forest to the north-west of Mabira (31°22′–31°46′E and 1°37′–2°03′N), covering an area of 853 km^2, at an average altitude of 1050 m above sea level. Budongo and Mabira had similar faunal and floral compositions less than a century ago (Hamilton, 1991; Howard, 1991). Although Budongo has been selectively logged for over 80 years, the forested area remains relatively intact (Plumptre *et al.*, 2007). The vertebrate community of the forest is well preserved, except for the elephants that are now extinct (Howard, 1991). Consequently, Budongo offers an effective control site to Mabira to determine whether the loss of dispersers affects the recruitment of certain categories of tree species.

Tree fruit characteristics and ecological guild

Fruit characteristics of 269 tree species (representing over 95% of total number of tree species found in Mabira) were compiled from measurements taken during the study (83%) and from published literature (17%) (Eggeling, 1940; Taylor, 1960; Dale & Greenway, 1961; Palgrave, 1983; Souane, 1985). Considering fruit characteristics measured during the study, a minimum of 30 fruits from at least five randomly selected trees were measured. However, the characteristics of most species were derived from published literature. The following fruit characteristics were assessed as follows: (i) fruit types: categorized as berries, drupes, capsules, follicles, pods, nuts or samaras; (ii) ripe fruit colour; (iii) number of seeds per fruit: coded as: '1' = 1 seed; '2' = 2–3 seeds; '3' = 4–10 seeds; and '4' = >10 seeds; (iv) fleshy pulp: fruits were categorized to indicate whether they were fleshy or nonfleshy. The former are supposed to be dispersed by animals. Among the nonfleshy fruits, a distinction was made between those with arillate seeds and others. The nonfleshy arillate species were considered to be animal-dispersed as well; and (v) fruit size: corresponding to the maximum length or diameter, whichever was bigger. Although seed size was another important trait to measure, it was not considered in this study because most literature quoted only the fruit size. Nonetheless, fruit and seed size showed a strong positive correlation for species where both measurements were available (Spearman's correlation, $r = 0.52, P < 0.05$, N = 42). The fruit sizes are presented in a score system (Table 1) that represents the different seed dispersing vertebrate guilds.

In addition to the fruit traits, trees were classified into three ecological guilds namely pioneer, nonpioneer light demander and shade tolerant depending on their light requirements. This classification was aimed at determining tree species' tolerance to shade and hence their potential to recruit beneath adult conspecifics. The pioneers include species that establish within the first or second year of a gap being formed. They may germinate but rarely survive for long under a closed canopy. Pioneers require dispersal to maximize the probability that seeds reach open habitats. Nonpioneer light demanders include trees that often become dominants in the forest canopy. They require gaps for release although they are capable of growing under a closed canopy. They are probably less prone to dispersal limitations than the pioneers. Shade-tolerant species form the subdominant trees in the middle canopy but may eventually become dominants especially in old mature forest. This group also includes understorey species that establish under a closed canopy and rarely grow beyond

Table 1 Scores used for classifying fruit size

Score	Definition	Notes
1	<10 mm	Dispersed by most frugivores including small birds
2	10–30 mm	Rarely dispersed by small birds but dispersed by larger birds (including hornbills and turacos) and most primates and ungulates
3	31–50 mm	Occasionally dispersed by small primates and predominantly dispersed by large primates such as chimpanzees
4	>50 mm	Occasionally dispersed by large primates and predominantly by large ungulates such as elephants

10 m in height. Many shade-tolerant species are capable of establishing beneath adult conspecifics and thus may be least affected by lack of dispersal. The classification of trees into ecological guilds is based on literature (Eggeling, 1940; Synnott, 1985). (A complete list of the tree species and their respective characteristics is presented in the Table S2.).

Stem abundance

To test whether trees with different fruit sizes and shade tolerance are differentially affected by forest disturbances, we conducted an inventory for 45 tree species that occur in Mabira and Budongo Forest Reserves (a list of the 45 tree species is presented in the Table S2). The inventory was conducted in 2012/2013 during which seventy 4-hectare plots were established in each forest site. In each plot, trees of the selected study species that were above 10 cm dbh were enumerated. Of the 45 study tree species, thirteen were light demanders producing large fruits (>30 mm diameter), twelve were shade tolerants with large fruits, ten were light demanders with small fruits (<10 mm diameter), and ten were shade tolerants with small fruits.

Data analysis

To determine whether there are discrete fruit syndromes among trees, a nonmetric multidimensional scaling (MDS) ordination was performed using the fruit characteristics compiled [CAP v3.0 (Seaby & Henderson, 2004)] for the 269 tree species. Chi-square tests were performed to determine relationships between seed dispersal mode and fruit size category for the 269 tree species. To determine the proportion of trees most vulnerable to forest disturbances, a cross-tabulation of fruit size and ecological guild was performed. Given that large-fruited trees unable to recruit beneath adult conspecifics are the most vulnerable to the effects of loss of dispersers, the cross-tabulation was aimed at identifying the proportion of large-fruited light-demanding species. To compare stem densities, *t*-tests were performed on $\log_{10}(1 + X)$-transformed abundances of large-fruited light demanders and large-fruited shade tolerants, and small-fruited light demanders and small-fruited shade tolerants between Mabira and Budongo. The *t*-tests were performed in consideration of the 45 selected tree species in Budongo and Mabira.

Results

Fruit types

Tree species did not form any discernible discrete fruit syndromes with an MDS ordination using all five fruit characteristics. However, most trees produce berries, drupes or capsules. Sixty per cent of tree species produce fleshy fruits, although an additional 10% that produce nonfleshy fruits with arillate seeds implies that the proportion of animal-dispersed trees is 70% (Fig. 1).

Zoochorous (animal-dispersed) trees produce smaller fruits than anemochorous or autochorous (wind or ballistic dispersed) trees ($X^2 = 61.6$, df = 3, $P < 0.001$). Eighty-three per cent of zoochorous trees produce fruits whose diameter is inferior to 30 mm. The majority of anemochorous or autochorous species produce large fruits (Fig. 2). Over 75% of animal-dispersed species produce fruits with fewer than three seeds, with the majority producing one-seeded fruits. The animal-dispersed trees that produce more than ten seeds per fruit are mainly *Ficus* species (Moraceae). In contrast, 60% of trees dependant on wind or ballistic dispersal produced more than four seeds per fruit.

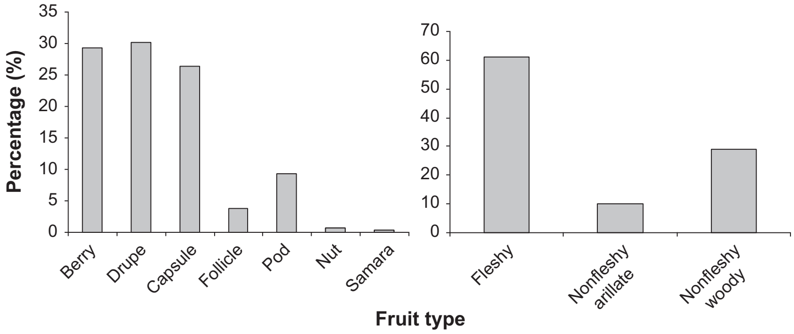


Fig 1 Proportion of the different type of fruit produced by trees species in Mabira Forest Reserve (Uganda; N = 269)

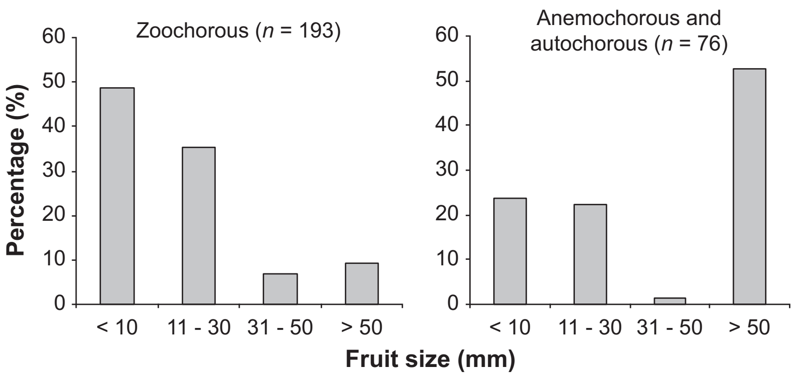


Fig 2 Proportion of the different fruit size produced by tree species in Mabira Forest Reserve (Uganda). Tree species are presented as dispersed by animals (left) and other modes (right)

Proportion of vulnerable animal-dispersed tree species

The results of a cross-tabulation between ecological guild and fruit size of trees revealed that 10% of animal-dispersed trees in Mabira are light demanders that produce large fruits (>30 mm in diameter; Fig. 3 and Table S1). The animal-dispersed large-fruited light demanders constitute 7% of the total number of tree species in Mabira Forest Reserve. A further consideration of trees producing fruits >10 mm in diameter (those rarely dispersed by small birds but can be dispersed by primates and ungulates) showed that the number of tree species vulnerable to the effects of disperser limitation increased to 31% of animal-dispersed trees. In the context of all tree species, the vulnerable trees represented 23% of the total number of tree species in Mabira.

Stem densities of selected tree species

Analysis of the relative abundances of trees (stems/ha) showed no significant differences between Budongo and Mabira ($t = 0.7$, df = 222, $P > 0.05$). A Pearson correlation showed that species that were the most abundant in Mabira were similarly the most abundant in Budongo ($r = 0.9$, $P < 0.001$). Analysis by tree species' categories showed that both in Mabira and Budongo, small-fruited trees are more abundant than the large-fruited, and shade tolerants are more abundant than light demanders (Fig. 4).

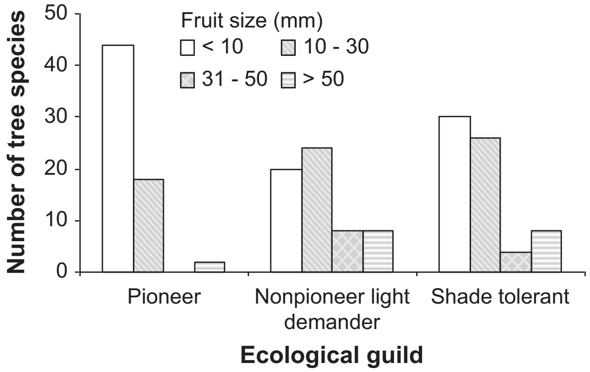


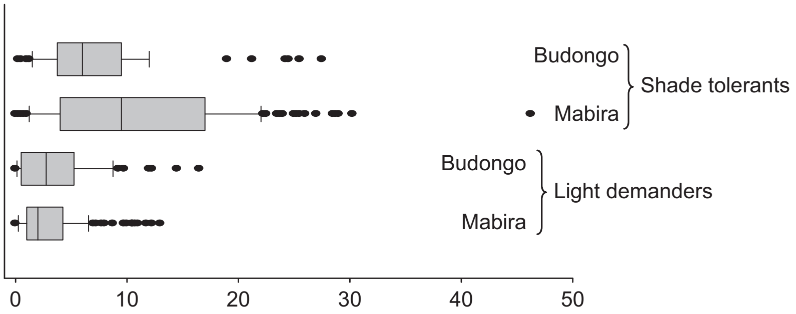
Fig 3 Proportion of the different fruit sizes produced by tree species for the different ecological guilds in Mabira Forest Reserve (Uganda; N = 269)

A comparison of abundances between Mabira and Budongo showed that light-demanding large-fruited trees (>30 mm fruit diameter) occur at lower densities in Mabira compared to Budongo ($t = 4.8$, df = 222, $P < 0.001$), whereas the abundances of large-fruited shade tolerants did not differ between the forests ($P > 0.05$). The abundances of small-fruited light demanders ($t = 0.656$, df = 16, $P > 0.05$) and small-fruited shade tolerants ($t = 1.49$, df = 16, $P > 0.05$) were not significantly different between the two forests, although small-fruited shade tolerants were more abundant in Mabira.

Discussion

Trees did not form any discernible discrete fruit syndromes. Although some studies (Gautier-Hion *et al.*, 1985; Dew & Wright, 1998) argue for the existence of fruit syndromes characteristic of particular vertebrates, this study showed that fruit traits vary and were not clearly correlated. This possibly augments the evidence for a lack of coevolution between fruit characteristics and the dispersers of their seeds provided by recent studies, for example Chapman & Chapman (2002). Consequently, the use of fruit morphological characteristics, probably with the exception of fruit size, seems to be of little use in categorizing tree species' vulnerability to forest disturbances.

(a) Small-fruited tree species



(b) Large-fruited tree species

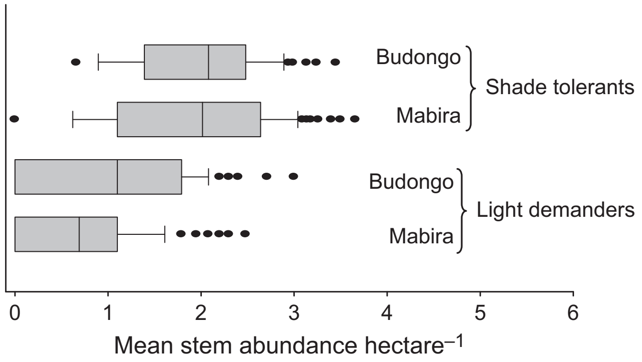


Fig 4 Box plots showing abundances of tree species producing (a) small fruits and (b) large fruits with different ecological requirements in Budongo and Mabira Forest Reserves. The boxes enclose the middle half of the data between the 25th and 75th quartiles. Vertical lines represent the median; horizontal lines show the range of the data value. Outliers are shown as (●). Note the different scales used for stem abundance in a and b

Fifty per cent of animal-dispersed trees produce small fruits (<10 mm diameter) that are probably dispersed by many avian species. Many of the small bird species capable of consuming these small fruits are ubiquitous and rarely affected by forest disturbances (Dranzoa, 1998). Consequently, 50% of animal-dispersed trees in Mabira Forest are probably not severely affected by anthropogenic disturbances. Fewer trees produce fruits that are bigger and are dispersed by a smaller subset of specialist large frugivores vulnerable to anthropogenic disturbances. For instance, 17% of animal-dispersed tree species produce large fruits (>30 mm diameter) that are dispersed by the large and more vulnerable frugivores. This result is similar to Peres & van Roosmalen (2002) finding. They estimated that large-seeded trees constitute nearly one-fifth of the woody flora in a Brazilian Amazon forest. Similarly, Kitamura *et al.* (2005) estimated that close to one-third of plant species in a Thailand national park were dispersed by large frugivores only. However, these estimates of vulnerable trees include shade-tolerant species that might be capable of recruiting beneath adult conspecifics and are therefore little affected by loss of dispersers. A consideration of ecological guilds among the large-fruited trees in Mabira revealed that nearly 10% of animal-dispersed trees are light demanders and are therefore the most vulnerable to loss of vertebrate seed dispersers.

A comparison of species' abundance of different tree categories in Mabira and Budongo showed that the large-fruited light-demanding tree species are less abundant in the former, which is heavily disturbed, whereas other categories showed no differences in relative abundance. Light-demanding trees are adapted to regenerate in the canopy gaps formed by natural and anthropogenic disturbances. Consequently, secondary forests such as Mabira are ideal for the recruitment of such species. However, the low abundance of large-fruited species in Mabira compared to the less disturbed Budongo (Fig. 4) could indicate a lack of dispersal of large fruits due to loss of large frugivores in Mabira Forest. A similar observation was made by Chapman & Onderdonk (1998) who showed that reduced numbers of large-bodied primates were correlated with lower seedling densities of large-seeded forest trees in tropical forests. The highest risk of tree species loss could be considered for at least 10% of the tree species in Mabira Forest. This represents a significant proportion of trees and would lead to compositional and structural changes to the forest landscape. First, this group of tree species (i.e. large-seeded light demanders) constitutes the upper canopy layer that supports a rich array of invertebrates (Basset, 2001). Secondly, limited recruitment of light-demanding species could lead to dominance in the forest landscapes of shade-tolerant species that are capable of recruiting successfully beneath adult conspecifics (Terborgh *et al.*, 2002). Most tree species that are favoured by the tropical timber industry are light-demanding trees (Kityo & Plumptre, 1997). This is because shade-tolerant species are slow-growing, have low timber quality and rarely attain large stem diameters for timber production. Consequently, an increase in basal area of nonmerchantable shade-tolerant trees would imply a reduction in the value of such forests as timber reserves.

In conclusion, knowledge of the ecological requirements of individual species and their interaction with vertebrate seed dispersers may help to identify the tree species that are most vulnerable to anthropogenic disturbances and thus provides a meaningful parameter for predicting tree regeneration following anthropogenic disturbances. It could also help to set priorities in tree species involved in artificial regeneration and enrichment practices. Contemporary forest managers need to monitor population dynamics of the large-fruited light-demanding tree species to set management parameters such as minimal harvesting diameter and extraction rates. In addition, harvesting regimes should be planned to maximize regeneration potential. Similarly, enrichment planting of the vulnerable species could be carried out where economical.

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Supporting information

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

Table S1 A list of large-fruited light demanding tree species in Mabira Forest.

Table S2 Fruit characteristics and ecological guild of tree species in Mabira Forest Reserve.