Interactions among Frugivores and Fleshy Fruit Trees in a Philippine Submontane Rainforest

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Abstract: *We assessed the potential effect of frugivore extinctions on forest regeneration in the North Negros Forest Reserve, a forest fragment that is one of the last remaining wet tropical rainforest ecosystems in the biogeographic region of the central Philippine Islands. We evaluated foraging observations of 19 species of birds, fruit bats, and other mammals in three successional habitats and identified tree species that are potentially at risk because their seeds are dispersed by frugivores that are seriously endangered. The relative abundance of zoochorous trees in this forest community was exceptionally high (80%), suggesting that the process of forest regeneration will change drastically if endangered frugivores are hunted to extinction. We grouped 45 tree species as early-, mid-, or late-successional species based on their population structure and we demonstrated that early-successional tree species were visited by a wide spectrum of frugivores, whereas mid- and late-successional species were visited mostly by hornbills (Bucerotidae) and fruit pigeons (Columbidae). Late-successional tree species were most specialized with respect to dispersers and could therefore be susceptible to extinction. We recommend tree species that could be useful for assisted natural regeneration projects in the reserve because they are visited by a variety of frugivores. Of those, we recommend early-successional trees for open-field plantations and mid-successional tree species for enrichment plantings.*

Interacción entre Especies de Frutívoros y Árboles de Frutas Carnosas en un Bosque Mesófito de Montaña Filipinas

Resumen: *Las interacciones entre animales frutívoros y árboles de frutas carnosas fueron estudiadas en un fragmento del bosque aún existente de las islas centrales de Filipinas. Parcelas de observación que cubrieron un área total de 8 has fueron trazadas en tres habitates sucesionales de la Reserva Forestal North Negros. Basadaos en observaciones de habitos forrajeros, identificamos especies arboreas que están enriesgo potencial debido a que sus semillos son dispersadas por frugívoros que están seriamente amenazados. La importancia de los árboles zoocoros en esta comunidad forestal fue excepcionalmente alta y se concluyó que el proceso de regeneración forestal será modificado severamente si las especies de animales frutívoros en peligro de extinctión son cazadas hasta extinguirse. Las especies forestales fueron agrupadas como tempranas, medias y tardias en la succesión, basados en la estructura de población de las tres parcelas. Se demostró que las especies arboreas de succesión temprana son dispersadas principalmente por pájaros pequeños y murciélagos frutívoros, las especies de succesión media dependen en gran medida de los buceros (Bucerotidae) y de las palomas frutívoras (Columbidae) para la dispersion de sus semillas. Varias especies arboreas de sucesión tardia fueron identificadas como suceptibles a extinguirse junto con los agentes de dispersión debido a su grado de especialización. Además, identificamos especies arboreas con potenciales de uso para proyectos con regeneración natural ayudada en la reserva, debido a que estas areas son visitadas por un gran numero de frugivóros. Especias arboreas de sucesión temprana fueron recomendadas para plantaciones a campo abierto y especias arboreas de sucesión media para diversificación de plantaciones.*

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Introduction

The central Philippine Islands, including Panay, Guimaras, Negros, Cebu, and Masbate, form a distinct faunistic region with a high proportion of endemic species (Dickinson et al. 1991; Bibby et al. 1992) They have also been identified as centers of plant biodiversity (Davis 1995) and fall into the World Conservation Union's category of the highest conservation priority (Dinerstein et al. 1995). The North Negros Forest Reserve, with an original area of 80,500 ha, contains the largest remaining fragment of wet evergreen rainforest in the central Philippine Islands. A recent survey revealed that only 9800 ha of old-growth forest remain in the little-protected reserve. At the same time it is one of the last refuges of many endemic animals, and captive breeding programs have been launched to save at least some of these species from extinction (W. Oliver 1993). Hunting pressure is an important problem for this relatively small forest fragment, and a number of endemic vertebrates are seriously threatened. Among them are the Visayan warty pig (*Sus cebifrons*), the Philippine spotted deer (*Cervus alfredi*), and several large birds, especially the Writhed-billed Hornbill (*Aceros waldeni*), the Visayan Tarictic Hornbill (*Penelopides panini*), and several species of fruit-pigeons (Columbidae).

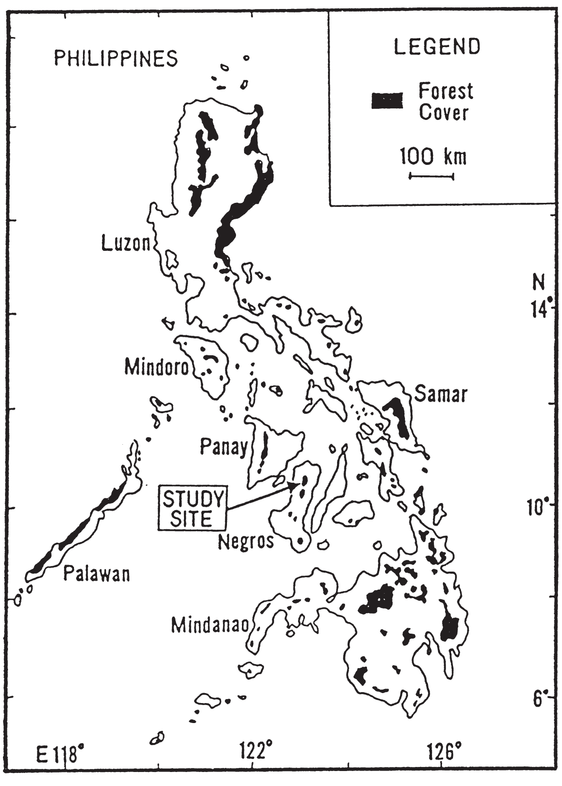

Figure 1. Location of the study site in the North Negros Forest Reserve, Province of Negros Occidental, Philippines.

Numerous studies have investigated ecological and evolutionary aspects of the linkage between fruit consumption by vertebrate frugivores and seed dispersal of tropical forest trees (e.g., Estrada & Fleming 1986; Howe 1986; Fleming & Estrada 1993). Moreover, case studies suggest that regeneration of a tree species will suffer if its dispersal capability is lost (e.g., Becker & Wong 1985; Martinez-Ramos & Alvarez-Bullya 1986; Gibson & Wheelwright 1995). The importance of this interdependence is well recognized with respect to conservation programs and has recently been reviewed for the Southeast Asian region by Payne (1995). We studied the community-wide visitation of forage trees by frugivores and assessed the impact of extinctions among frugivores on the process of forest regeneration. By grouping trees into early-, mid-, and late-successional species, we investigated which stages of forest regeneration are most likely to be affected. Further, we screened this forest community for tree species that are potentially at risk because their seeds are dispersed by endangered frugivores. Our data are also valuable for assisted natural regeneration projects, in which forage trees are planted to attract dispersers into areas to be regenerated (Green 1993, 1995). We identified fruit trees that are potentially useful for assisted natural regeneration because they are visited by a large number of frugivore species.

Methods

Study Site

The study was conducted within an upland tropical rain forest near Patag, Silay City district, on the island of Negros, lat 10°41′N, long 123°11′E (Fig. 1). The study plots lie on the northwest slope of Mt. Mandalagan within several hundred meters of each other at an average elevation of 1000 m. Weather records from this mountain range are available for only 1 year with a total rainfall of 4650 mm and an average temperature of 25.4° C. There was a short dry season during April. Three forest stands of different successional stages were chosen in which to set up observation plots, including a 1.7-ha area cleared for pasture and abandoned in approximately 1975, a 1.9-ha area destroyed by bombing during World War II, and a 4.4-ha area of old-growth forest. They are hereafter referred to as early-, mid-, and late-successional plots (plots E, M, and L, respectively). All trees on these plots with $\leq$10 cm diameter at breast height (dbh) were measured, permanently tagged, and identified (Hamann et al. 1999).

The three plots were visited monthly from August 1995 to June 1996. Bird species foraging in fruiting trees were recorded during 5 days of each month, and between 10 and 30 fruits per tree species were collected and preserved in 70% alcohol. In addition, we caught birds and fruit bats with mist nets for species identification. Mist nets were set up over 24-hour periods in the vicinity of the plots near fruiting trees at heights ranging from ground level to 20 m. Foraging activities of fruit bats and other mammals could not be observed directly because these animals are mostly nocturnal. Therefore only pellets of fruit pulp, animal traces under fruiting trees, and feces allowed the identification of frugivores that utilized fruit tree species.

Grouping of Tree Species and Frugivores

We grouped tree species as early-, mid-, and late-successional based on frequency diagrams using 5-cm size-class intervals constructed for each plot. The theoretical diameter distribution of a balanced, uneven-aged population of trees represents a composite of the component age-class distributions, in which each age class occupies a more or less equivalent amount of space. Such a balanced distribution is shaped like a reversed *J*. If a species does not regenerate and recruit into larger size classes, this distribution will gradually become symmetrical due to lack of individuals in small size classes, and eventually the species will phase out in the stand (C. D. Oliver 1990). We defined late-successional tree species as those that had a balanced (reversed-*J*-shaped) distribution on all plots. Small individuals of mid-successional species were absent on plot L, and small individuals of early-successional species were absent from plots M and L, or from all plots.

Further, we grouped trees by dispersal syndrome according to Van der Pijl (1982). A fruit was considered bird-dispersed if it was fleshy, red or black in color, and of small to medium size or if it was dry but with fleshy seed appendages (arils). Odorous fruits of dull color, borne on large branches or stems, and of medium size were considered fruit bat–dispersed. Large, juicy fruits with few well-protected seeds were classified as fruits dispersed by mammals. Dehiscent, winged fruits were classified as wind-dispersed, and all fruits that did not fall into any of these categories were classified as presumably dispersed by gravity.

We arbitrarily grouped frugivores into the categories of hornbills, fruit pigeons, other birds, fruit bats, and other mammals in order to make more general statements regarding interactions among frugivores and fruit trees.

Data Analysis

Because it is difficult to directly measure fruit quantity produced at the community level, we used relative abundance of forage trees as an approximation for fruit production, where relative abundance of a tree species is its proportion of the total basal area plus its proportion of the total number of individuals divided by two. We used analysis of variance to compare plots E, M, and L with respect to relative abundance of forage trees and dispersal syndromes. The analysis was based on 10 subplots of 0.1 ha randomly located on a coordinate system for each of the three successional stands. These pseudoreplications were evaluated by the general linear model procedure and the Student-Newman-Keuls test of the SAS-software package (SAS Institute 1995).

For statistical analysis we arranged foraging observations as a matrix of binomial data (foraging observed or not observed) for each combination of frugivore and tree species. A table of proportions was then derived for all group combinations, in which the number of observed utilizations (successes) was divided by the total number of possible combinations of frugivores and tree species within each group (sample size). Subsequently we could use z or chi-square tests for proportions to compare the utilization percentage of, say, early-successional tree species by hornbills with corresponding percentages of mid- and late-successional trees. The hypothesis that all proportions were the same was tested with the chi-square test for proportions according to Rosner (1982):

$$\chi^2 = \sum((x_i - X(n_i - x_i)N^{-1})(X(n_i - x_i)N^{-1})^{-1})^2,$$

where n_i is the sample size of each proportion; N is the total sample size; x_i is the number of successes of each proportion; and X is the total number of successes. If the null hypothesis was rejected, we used the z test for proportions for pair-wise comparisons according to Rosner (1982):

$$z = |p_1 - p_2|(p(1-p)(n_1^{-1} + n_2^{-1}))^{-1/2},$$

where p_1, p_2 are the proportions under investigation; p is the pooled proportion $(x_1 + x_2)(n_1 + n_2)^{-1}$; n_1, n_2 are the sample sizes of each proportion; and x_1, x_2 are the number of successes in each proportion. The test statistics were calculated with the frequency procedure of the SAS software package (SAS Institute 1995). To adjust for the inflation of the experiment-wise Type I error due to multiple comparisons, we used a critical z value calculated analogous to Bonferroni's compensation for multiple-range tests: $z_{crit} = z_{\alpha/2m}$, where m is the number of possible comparisons and $\alpha = 0.05$.

Results

Plot Characteristics

The relative abundance of zoochorous trees was substantial in all three successional stands (Fig. 2). Trees with wind or bird dispersal syndromes were equally abundant on all plots and not significantly different at $p < 0.05$. Trees with a fruit bat dispersal syndrome were significantly less abundant on plot M than on plots E and L. For trees with a mammal dispersal syndrome, plot mean E was significantly lower than plot mean L.

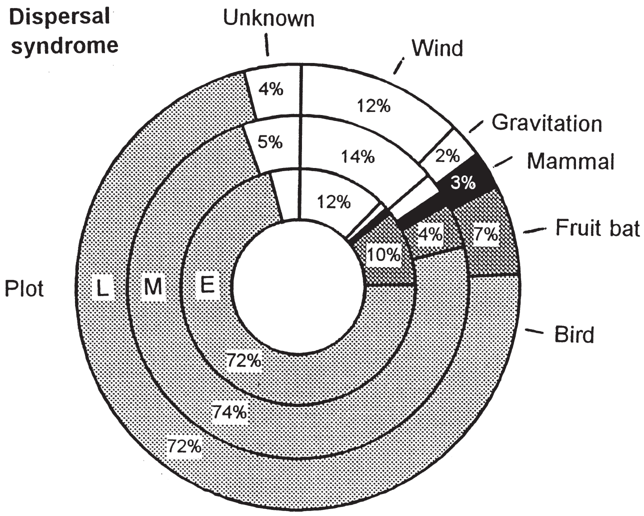

Figure 2. Relative abundance of trees with certain dispersal syndromes on the early- (E), mid- (M), and late-successional (L) plots.

Based on data on visitation of trees by frugivores instead of on dispersal syndromes, plots differed in abundance of forage trees for each group of frugivores (Fig. 3). The greatest abundance of trees visited by hornbills and fruit pigeons, for example, was on the mid successional plot, whereas the early-successional plot showed the greatest abundance of trees visited by small birds and fruit bats. (The relative abundance of forage trees added over groups of frugivores exceeds 1 because most tree species were visited by more than one group.)

Analysis of the Utilization Matrix

Evaluation of interactions among frugivores and fruit trees was limited to the 19 most common or readily observable frugivores and the 45 most abundant tree species for which observations were considered fairly comprehensive. The average number of foraging bird species declined from early- to late-successional tree species, whereas the average size of seeds and fruits increased (Table 1). Most frugivores we investigated utilized 10–15 tree species, and there were no obvious differences among frugivore groups with respect to the number of forage trees (Table 2).

Foraging observations were summarized by groups of frugivores and tree species as proportions (Table 3), where the proportions represent observations of foraging divided by all possible combinations of trees and frugivores (e.g., 15 early-successional species $\times$ 7 fruit pigeons = 105 possible combinations; in 33 of these cases [31%] visitation was observed). Subsequently we compared these proportions (Table 3) according to the following example for the row "total frugivores." After rejection of the hypothesis of all proportions being equal

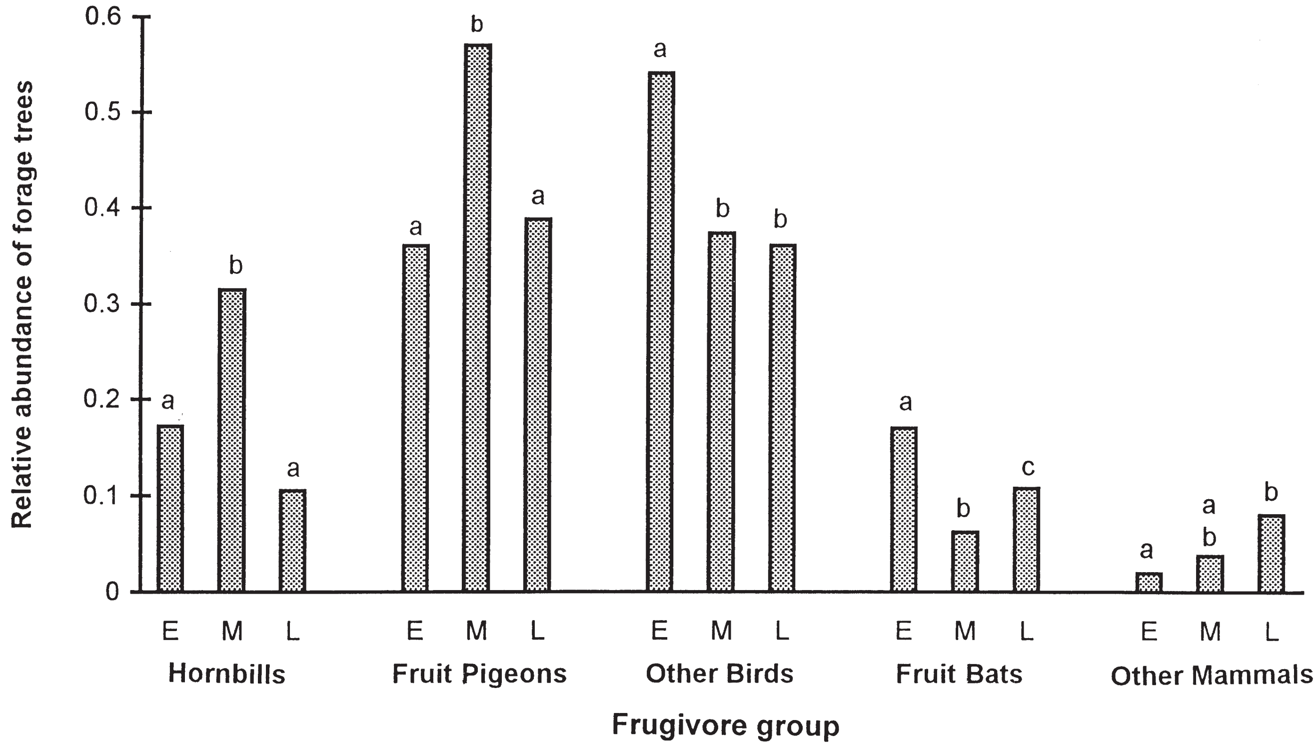

Figure 3. Relative abundance of forage trees for frugivores on early- (E), mid- (M), and late-successional (L) plots. Plot means with the same letter (a, b, c) are not significantly different at $p < 0.05$.

Table 1. Early-, mid-, and late-successional tree species with their average fruit size, seed size, and number of bird species observed foraging on their fruits.

Code and species	*Family*	*Fruit size (mm)*	*Seed size (mm)*	*No. of bird spp.*
Early-successional species				
1 *Alphitonia excelsa* (Fenzl) Reiss.	Rhamnaceae	14	2	
2 *Bischhofia javanica* Bl.	Euphorbiaceae	11	4	17
3 *Ficus congesta* Roxb.	Moraceae	35	1	
4 *Ficus heteropleura* Bl.	Moraceae	10	1	16
5 *Ficus septica* Burm. f.	Moraceae	23	1	
6 *Ficus variegata* Bl.	Moraceae	28	1	
7 *Ficus* sp. 01	Moraceae	30	1	
8 *Grewia multiflora* Juss.	Tiliaceae	17	4	7
9 *Guioa pleuropteris* (Bl.) Radlk.	Sapindaceae	15	3	9
10 *Homalanthus alpinus* Elm.	Euphorbiaceae	10	5	8
11 *Leucosyke capitellana* (Poir.) Wedd.	Urticaceae	16	1	
12 *Macaranga bicolor* Muell.-Arg.	Euphorbiaceae	17	8	10
13 *Mallotus molissima* (Geisel) A. Shaw	Euphorbiaceae	10	3	8
14 *Strebus glaber* (Merr.) Corner	Moraceae			12
15 Tiliaceae sp. 01	Tilaceae	10	3	
	Average	17.6	2.7	10.9
Mid-successional species				
16 *Astronia cumingiana* Vid.	Melastomaceae			
17 *Ficus heteropoda* Miq.	Moraceae	35	1	
18 *Homalanthus rotundifolius* Merr.	Euphorbiaceae	10	5	8
19 *Lithocarpus* spec.	Fagaceae	21	21	
20 *Litsea quercoides* Elm.	Lauraceae	19	12	4
21 *Macaranga tanarius* (L.) M.A.	Euphorbiaceae	10	3	10
22 *Microcus stylocarpa* (Warb.) Burret	Tiliaceae	25	10	6
23 *Platea excelsa* (Heine) Sleum.	Icainaceae	29	21	5
24 *Prunus fragrans* (Elm.) Kalkm.	Rosaceae	22	12	3
25 *Syzygium garciae* (Merr.) Merr. & Perr.	Myrtaceae			
26 *Syzygium gracile* (Korth.) Amsh.	Myrtaceae	25	15	8
27 *Syzygium* sp. 01	Myrtaceae	19	10	
28 *Syzygium* sp. 02	Myrtaceae	22	11	9
29 *Syzygium* sp. 03	Myrtaceae	23	10	9
30 *Ternstroemia megacarpa* Merr.	Theaceae	51	20	3
31 unidentified sp. 01		20	14	4
	Average	23.6	11.8	6.3
Late-successional species				
32 *Aglaia sp.* 01	Meliaceae	45	25	2
33 *Canarium asperum* Benth.	Burseraceae	12	8	4
34 *Dillenia reifferscheidia* Elm.	Dilleniaceae	60	4	
35 *Elaeocarpus cumingii* Turcz.	Elaeocarpaceae	23	12	4
36 *Garcinia busungaensis* Merr.	Guttiferae	25	13	
37 *Laportaea luzoniensis* (Wedd.) Warb.	Urticaceae			
38 *Litsea luzonica* F.-Vill.	Lauraceae	18	9	7
39 *Memexylon lanceolatum* Blco.	Melastomaceae	11	8	3
40 *Myristica ceylanica* A. DC.	Myristicaceae	45	17	2
41 *Palaquium* sp. 01	Sapotaceae			4
42 *Palaquium* sp. 02	Sapotaceae			
43 *Pometia pinnata* J. R. & G. Forst	Sapindaceae	40	25	2
44 Sapotaceae sp. 01	Sapotaceae			
45 unidentified sp. 02		20	15	4
	Average	29.9	13.6	3.6

(the test statistic of $\chi^2 = 31.0$ was larger than the critical value of $\chi^2 = 6.0$ for df = 2 and $\alpha = 0.05$), pairwise comparisons showed that early-successional trees were visited by significantly more frugivores than mid- and late-successional species (test statistics $z_{\text{early-mid}} = 3.3$, $z_{\text{early-late}} = 5.4$ were all larger than the critical z value of 2.6 for $m = 3$ and $\alpha = 0.05$, whereas $z_{\text{mid-late}} = 2.4$ was slightly lower). This trend was due mainly to the groups "fruit bats" and "other birds" visiting early-successional trees more often than mid- and late-successional species, as the analysis of the other rows suggests (Table 3). Correspondingly, mid- and late-successional trees were vis-

Table 2. Important frugivore species encountered in the North Negros Forest Reserve and fruit trees they have been observed using.

Frugivore species	*Tree codes*
Hornbills (Bucerotidae)	
Writhed-billed Hornbill (*Aceros waldeni*)	4, 23, 30, 40, 43
Visayan Tariktic Hornbill (*Penelopides panini*)	2, 4, 9, 20, 21, 22, 23, 26, 28, 29, 30, 32, 33, 43, 45
Fruit pigeons (Columbidae)	
Common Emerald Dove (*Chalcophaps indica*)	8, 9, 10, 12, 13, 14, 18, 21, 26, 29, 28, 39
Pied Imperial Pigeon (*Ducula bicolor*)	2, 4, 14, 22, 20, 23, 24, 26, 29, 28, 31, 33, 34, 35, 41, 45
Pink-bellied Imperial Pigeon (*Ducula poliocephala*)	2, 4, 20, 22, 23, 24, 28, 29, 31, 33, 34, 35, 38, 41, 45
Reddish Cuckoo Dove (*Macropygia phasianella*)	2, 8, 9, 10, 12, 14, 21, 31, 39
White-eared Browne Dove (*Phapitreron leucotis*)	2, 4, 8, 9, 12, 13, 14, 21, 24, 26, 29, 28, 30, 39
Yellow-breasted Fruit Dove (*Ptilinopus occipitalis*)	2, 4, 20, 22, 23, 24, 26, 28, 29, 31, 33, 34, 35, 38, 41, 45
Spotted Dove (*Streptopelia chinensis*)	2, 8, 9, 12, 13, 14, 26, 38
Rhabdornis (Rhabdornitidae)	
Stripe-headed Creeper (*Rhabdornis mysticalis*)	2, 4, 8, 10, 12, 14, 18, 21
Barbets (Capitoniadae)	
Coppersmith Barbet (*Megalaima haemacephala*)	2, 4, 26
Orioles (Oriolidae)	
Black-naped Oriole (*Oriolus chinensis*)	2, 4, 9, 12, 13, 14, 21
Bulbuls (Pygnonotidae)	
Yellow-vented Bulbul (*Pycnonotus goiavier*)	2, 4, 8, 9, 10, 12, 13, 14, 18, 21
Philippine Bulbul (*Hypsipetes philippinus*)	2, 4, 8, 9, 10, 12, 13, 14, 21, 29, 28
Starlings (Sturnidae)	
Coleto (*Sarcops calvus*)	2, 4, 8, 9, 10, 12, 13, 14, 18, 21, 22, 24, 28, 29, 35, 38, 41
White Eyes (Zosteropidae)	
Yellow White-Eye (*Zosterops nigrorum*)	2, 4, 8, 10, 12, 13, 14, 18, 21
Fruit bats (Macrochiroptera)	
Cynopterus brachyotis	2, 3, 4, 5, 6, 7, 17, 22, 34
Ptenochirus jagori	2, 3, 4, 5, 6, 7, 17, 22, 34, 36
Other mammals	
Visayan Warty Pig (*Sus cebifrons*)	19, 23, 34

ited by large avian frugivores more frequently than all other groups, whereas the trend was the opposite for early-successional species. It should be noted that the power of detecting differences in comparison with "other mammals" was low because of the small sample size for this class.

Discussion

The overall frequency of zoochory was exceptionally high in all successional stages of this submontane rainforest. In contrast, lowland forests in Southeast Asia are dominated by wind-dispersed dipterocarps (Whitmore 1990). Montane forests generally have a larger proportion of wind-dispersed species such as conifers, Casuarinaceae, and Aceraceae (Merlin & Juvik 1994). For the maintenance of these forest communities and regeneration of adjacent areas, it seems crucial not only to prevent further cutting of trees but also to preserve the remaining frugivore populations.

Difficult logistics and steep terrain prevented us from establishing permanent inventory plots at several places in the reserve. Lacking true replications of successional plots for statistical evaluation, we interpreted the size structure of tree populations to determine the species

Table 3. Utilization matrix by groups of frugivores and fruit tree species in which observed cases of utilization, total number of possible observations, and this ratio (%) are given.*

	Tree species			
Frugivores	*Early-successional*	*Mid-successional*	*Late-successional*	*Total trees*
Hornbills	4/30 (0.13) A a	8/32 (0.25) A ab	9/28 (0.32) A a	21/90 (0.23) ab
Fruit pigeons	33/105 (0.31) A ab	37/112 (0.33) A a	21/98 (0.21) A a	91/315 (0.29) a
Other birds	45/105 (0.43) A b	17/112 (0.15) B b	3/98 (0.03) C b	65/315 (0.20) ab
Fruit bats	14/30 (0.47) A b	2/32 (0.06) B b	3/28 (0.11) B ab	19/90 (0.21) ab
Other mammals	0/15 (0.00) A a	2/16 (0.13) A ab	1/14 (0.07) A ab	3/45 (0.07) b
Total frugivores	96/285 (0.34) A	66/304 (0.22) B	37/266 (0.14) B	199/855 (0.23)

**Ratios with the same capital letter in rows and the same small letter in columns are not significantly different at* $p < 0.05$.

competitiveness at different stages of stand development. Because the size structure reflects the relative performance of different age classes at the same site, it eliminates site factors that could be confounded with successional stage of the plots (C. D. Oliver 1990). When comparing the relative abundance of forage trees by means of pseudo-replications, we could not eliminate confounding of successional stages with other factors specific to the plots. We believe, however, that the plots chosen for our study differ little in anything but successional stage, and the following statements are likely to apply to comparable forest stands in the reserve. Nevertheless, the following hypotheses of preferred forage areas for certain frugivores should be tested by studying the occurrence of frugivores in additional areas of different successional stages.

The high abundance of forage trees available to hornbills and fruit pigeons in the mid-successional plot suggests that these older, regenerating stands are visited regularly by large avian frugivores, many of which are endangered because of hunting pressure. In the North Negros Forest Reserve, regenerating forest stands occur mostly on the periphery of the old-growth forests. They are easily accessible and common hunting grounds. In delineation of wildlife protection zones, mid-successional stands therefore should be given high priority rather than being classified as multiple-use buffer zones. The mid-successional plot, however, appeared to be of minor importance for fruit bats. The lack of fruit bat–dispersed species in this area is an interesting phenomenon. Fruit bat–dispersed trees were either early-successional species or small trees that occurred in the understory layer of the old-growth plot. For mammals such as the Visayan warty pig or the long tailed macaque (*Macaca fascicularis*), the old-growth forests appeared to be the prime forage area. Long-tailed macaques were also observed on several species of large strangler figs, which are not listed in Table 1 because of their low relative abundance.

Our study further suggests that a number of tree species are potentially at risk because they are visited by only a small number of frugivores. If we assume that the animals are neither fruit thieves nor seed predators, late-successional tree species appear to be most specialized with respect to their dispersal agents. Also, dispersers of late-successional trees are mostly endangered species, namely hornbills and three species of fruit pigeons (*Ducula bicolor*, *Ducula poliocephala*, and *Ptilinopus occipitalis*). In fact, 60% of all late-successional species would lose all dispersal agents observed if large avian frugivores were hunted to extinction. *Myristica ceylanica*, *Pometia pinnata*, and *Aglaia* sp. appear to depend solely on the two species of hornbills for seed dispersal, and these are considered critically endangered (Collar et al. 1994). *Lithocarpus* sp. and *Dillenia reifferscheidia* appear to depend entirely on the Visayan warty pig for seed dispersal. Our data suggest that the early phases of forest regeneration will remain unaffected by continued hunting pressure on large avian frugivores. Nevertheless, the subsequent process of succession and the composition of the mature forest will change drastically if large avian frugivores and mammals are lost.

Government agencies and nongovernmental organizations currently reforest degraded areas in the reserve to create buffer zones and to restore watershed properties. Previously, these agencies planted exotic species exclusively. Now they also plant indigenous fruit trees for assisted natural regeneration projects. The rationale is that fruit trees included in plantations or planted into slowly regenerating areas serve not only as a future seed source but also as centers for the reestablishment of other species by attracting seed-dispersing animals to the vicinity. Among the tree species we investigated, there are several candidates for potential use in such a program because they are visited by a wide spectrum of frugivores. For open-field plantations we recommend early-successional trees such as *Bischofia javanica, Ficus heteropleura*, *Strebus glaber*, and *Macaranga bicolor.* For enrichment plantings in existing plantations or in slowly regenerating areas we recommend more shade-tolerant species such as *Macaranga tanarius, Homalanthus rotundifolius, Microcus stylocarpa*, and *Syzygium* spp.

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