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Impact of logging and plantation development on species diversity: a case study from Sumatra

Finn Danielsen
NORDECO (Nordic Agency for Development and Ecology)
Copenhagen

Morten Heegaard
Zoological Museum, University of Copenhagen

Abstract

This paper is based on a study in Sumatra of the responses of birds, primates, squirrels, tree-shrews, and bats to logging and replacement of tropical moist forest with plantations. The study investigated the composition and structure of the animal communities 7-10 years after logging, or after conversion to plantations of rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) and compared these with the composition and structure of the communities of an undisturbed primary forest.

The organization of the bird community was altered by logging, with abundant species occupying a higher proportion of the sample. Specialized insectivorous birds of the mature forest understory declined. In addition, logged forest held fewer bird species of importance to conservation. On the other hand, many insectivore-frugivore generalist bird species survived or increased, and even large frugivores such as hornbills (Bucerotidae) persisted in logged forest. Logging caused no change in the abundance of primate groups, squirrels and tree-shrews, but an increase in the proportion of dominant bat species and an overall decrease in bat species richness to 38-50%. Weighted by abundance, logging caused a 20-22% difference in bird species composition, a 28-32% difference in species composition of primate groups and a 54-65% difference in bat species composition.

Conversion of primary forest to rubber and oil palm plantations led to simple, species-poor and less diverse animal communities with fewer specialized species and fewer species of importance to conservation. In the plantations only 5-10% of the primary-forest bird species were recorded. Primates, squirrels and tree-shrews disappeared, except for one species of primate. Species richness of bats declined to 13-25%, and the community structure of bats changed. Weighted by abundance, conversion of forest to plantations caused a 61-81% difference in bird species composition, a 94-100% difference in species composition of primate groups and a 87% difference in bat species composition.

Overall, logged forest is very important to conservation of species diversity, but it *cannot* replace primary forest. Unfortunately, in many areas the authorities have been reluctant to create large protected areas of primary forest. Owing to the rapid pace of anthropogenic forest change, many countries are now running out of sites with primary forest. Plantations of rubber and oil palm are of little or no importance to biodiversity conservation. The massive replacement of Asia's natural forests with plantations of exotic trees will have serious impacts on the survival of many species of plants and animals.

Introduction

In large parts of South East Asia, primary forests are being modified by selective logging, or cleared and replaced with plantations of exotic trees such as rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*). There is little information available concerning the responses of tropical forest animals to these changes.

A number of studies have provided data on the impact of selective logging on primates of lowland rain forest (review by Johns and Skorupa 1987), but few studies have been published on the responses to logging of other species groups. The principal studies on the responses of birds are by Wong (1985; 1986) and Johns (1986b; 1988; 1989) for peninsular Malaysia, by Lambert (1992) for Sabah, by Holbech (1992) for Ghana, and by Thiollay (1992) for French Guiana. The responses of bats have been investigated by Pine and Wilson (see Johns 1992) in Panama, while the responses of termites and moths have been studied in Borneo by Collins (1980) and Henwood (Johns 1992), respectively.

We have not found any published studies on the impact on animals when lowland rain forest is converted to plantations of rubber or oil palm. However, the responses of mammals to plantations of *Albizia falcateria*, established for chip and pulp production in Sabah, have been studied by Duff *et al.* (1984) and Stuebing and Gasis (1989), while Mitra and Sheldon (1993) studied the responses of birds in the same area. Wilson and Johns (1982) examined a restricted set of mammal and bird species in a similar plantation in east Kalimantan. Ripley (*vide* Good *et al.* 1992) and Carlson (1986) carried out analogous studies of birds in plantations of sal (*Shorea robusta*) in India, and in plantations of conifer (*Pinus* sp.) in Kenya, respectively.

This paper is based on a study of the responses of birds, primates, squirrels, treeshrews, and bats to selective logging and the establishment of plantations of rubber and oil palm in Sumatra, Indonesia. Censuses from an area of unlogged forest were compared with censuses in other areas which in the past had been lightly logged, heavily logged, and converted to rubber and oil palm plantations. This paper describes the overall conclusions of the study, while a detailed analysis of the responses of the bird community to habitat changes will be provided elsewhere (Danielsen and Heegaard, in prep.).

Hevea brasiliensis (Euphorbiaceae) is native to the Amazon Basin (Raven *et al.* 1986). It has been introduced into large parts of tropical Asia. *Elaeis guineensis* (Palmae) is native to West Africa, but has been introduced into most tropical countries (Raven *et al.* 1986).

Study area

The study was conducted in the lowlands of eastern Sumatra in Seberida Subdistrict (0°35'S, 102°24'E, altitude < 180m), Riau Province, and the adjacent Bungotebo District, Jambi Province.

The natural vegetation is lowland evergreen dipterocarp rain forest (Whitmore and Samsoedin 1991). Primary forest had a three-layered forest crown canopy with an upper stratum above 30 m, a middle stratum from c. 20 to 30 m, and a lower stratum from c. 12 to 20 m (Mirmanto and Schumacher in prep.). On a 0.25 hectare plot 145 trees over 10 cm d.b.h. (57 species) were found, accounting for a basal area of 49 m^2 per hectare (Mirmanto and Schumacher in prep.); 8.3% of the trees had a diameter exceeding 60 cm. The most common species were *Aporusa stellifera*, *Baccaurea racemosa*, *Buchanania arborescens*, *Canarium littorale*, *Endiandra* sp., *Neoscortechinia kingii*, *Shorea acuminata*, *S. lepidota*, and *S. multiflora* (Mirmanto and Schumacher in prep.).

Narrow trail systems were established in five study areas with different land-use, each located in the middle of an extensive area characterized by the same land-use. The areas had a similar undulating topography, dissected by numerous small streams. The areas were 10-50 km apart. The logged forest study areas were structurally similar and were assumed to have had an original vegetation structure, habitat range, and animal community composition very similar to the undisturbed forest used for comparison. The plantation study areas were located in areas which were originally covered by rain forest. There was little or no hunting, except in the lightly logged study area where there was a hunting pressure on pheasants.

The *primary forest* study area comprised 20-35 m tall forest with emergents reaching 50 m (Figure 1). It was within an area of approximately 160,000 hectares of primary forest. The *lightly logged forest* study area had been logged in 1980-81, with tractors being used to extract the timber, and the level of timber extraction was 4 trees per ha. Heights of canopy and emergents were the same as in the other forest study areas, but density of trees and basal area per hectare were slightly lower. The *heavily logged forest* study area had been logged in 1984,

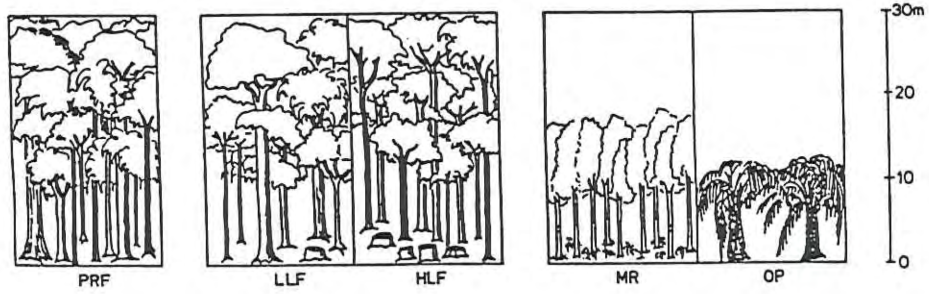

Figure 1. Schematic vegetation profile of the study areas in primary undisturbed forest (PRF), in lightly and heavily logged forest (LLF, HLF), and in modern rubber and oil palm plantations (MR, OP). The diagram shows the canopy height, the average density of the trees, and the number of trees logged per hectare. One tree in the diagram represents 100 ex. per hectare, while one stump represents 4 stumps per hectare.

again with tractors being used to extract the timber. The level of extraction was 15 trees per ha. It was a mosaic of several distinctly different types of vegetation. Approximately half of the study area had been severely damaged and contained very few large trees. Those trees that remained occured in very dense stands and were mostly less than 10 m tall. Such areas resembled gaps within the primary and lightly logged forest areas caused by treefalls. Vegetation was smothered with creepers and vines. Other areas had suffered little or no damage, and contained 20-30 m tall forest with emergents at 45 m. Where logging roads transversed the area the vegetation was distinct, the verges being dominated by trees of *Macarenga hosei*.

The *rubber plantation* study area consisted of mature rubber trees (*Hevea brasiliensis*) planted in 1982-83 in an area previously covered by rain forest. It was roughly 10,000 hectares, and surrounded by agricultural land, the nearest forested area lying 5 km away. The average height of the trees was 15.6 m (±1.2), with a density of 944 trees per hectare (±269). The undergrowth was being cut regularly. It was dominated by *Blechnum* sp. (Polypodiaceae) and *Pisum* sp. (Fabaceae), with patches of *Cyperus* sp. and *Imperata cylindrica*, and small bushes of *Melastoma affinis* (Melastomataceae).

The *oil palm* study area consisted of mature oil palms (*Elaeis guineensis*). The plantation was 10,000 ha and surrounded by rubber plantations, the nearest forest lying 6 km away. The average height of the palms was 11.1 m (±0.8), with a density of 162 trees per ha. The stems were densely covered by ferns and small plants. Within 1.5 m of the palms an area was kept free of vegetation. Otherwise, there were dead palm leaves and abundant ferns (*Blechnum* sp.) between the palms. More details are provided by Danielsen and Heegaard (in prep.).

Methods

All habitats were surveyed within a period of only two months (August and September 1991), using the same techniques in all habitats and all samples.

Birds, primates, and squirrels

A variable-distance line-transect method was used (Anderson *et al.* 1979). A line-transect survey route of 2,000 m was cut in a straight line in each habitat, regardless of logging roads, light gaps, etc. Easily recognizable markers were put up every 250 m, where detailed features of the habitat were recorded. The route was walked by one person with a speed of 250 m per 15 minutes. This speed allowed brief stopovers where vocalizing individual animals or primate groups were detected. Primates normally occur in groups; it is difficult to detect all group members, thus usually groups and not individual primates were detected. For each animal contact, we sought to record species name, number of individuals, perpendicular distance from the trail, height, and whether the animals were seen or heard. In order to minimize biases caused by differing detectability, all censuses were made during optimal conditions (between 6.00 h and 11.00 h, fine, dry weather). Though the survey was carried out during the dry season, the forest floor was humid and there were heavy showers every week. The route was surveyed four times per day. In each forest study area the route was surveyed for 40 hours (divided equally between the authors), while in each plantation area the route was only surveyed for 20 hours by MH.

The average number of animals (or primate groups) observed per transect day was compared between the study areas with one-way ANOVA, Tukey's Studentized Range test, and Studentized Maximum Modulus test after log(x+1) transformation (SAS 1990). Statistical significance was accepted at $P < 0.05$ for all tests.

Thirty-seven percent of birds, 7% of primate groups, and 73% of squirrels and tree-shrews detected were unidentified and only included in total community measures of abundance. Aerial insectivorous birds (*Eurostopodus temminckii*, *Collocalia* spp., *Hirundapus giganteus*, *Chaetura leucopygialis*, *Cypsiurus balasiensis*, *Hemiprocne longipennis*, *Hirundo rustica*) were excluded from analysis as they are almost impossible to detect in primary forest with more or less closed canopy. Few birds were recorded in mixed parties and most were territorial, probably because of breeding.

Species richness (number of species) *with a standardized effort* is probably a more meaningful value than various indices. However, to enable comparisons with other studies, bird diversity was assessed by Shannon's Index ($H' = -\sum p_i \ln p_i$). A proportional difference (PD) in species composition, weighted by abundance, was calculated by:

$$PD = \frac{100 * \sum |(xi - yi)|}{x + y}$$

where x and y are the total number of records and xi and yi the number of records of species i in each study area (Thiollay 1992); PD is zero when the communities are similar.

Bats

Systematic mist-netting was carried out with 15 to 20 nets (totalling 150-250 m), mainly set at 0.5-3 m height. Nets were tended continuously during the primary activity peak from early dusk (about 17.30 h) until about 21.00 h, and some were tended longer; nets were left open thereafter, and bats were removed at dawn. Voucher specimens were prepared in fluid, as skeletons, or as skins with partial skeletons, and have been deposited in the Zoological Museum, University of Copenhagen and the Museum of Zoology, Bogor.

Nomenclature follows Marle and Voous (1988) for birds and Corbet and Hill (1992) for other taxa.

Results

Line-transects

There was no significant difference between the number of species recorded by each observer during a day of transects ($t_{19}=0.98$, $p<0.10$, two-tailed test for matched pairs). Therefore, the two observers' data on species numbers were pooled.

Most animals were detected by voice (birds 77%, macaques 48%, langurs 66%, gibbons 96% and squirrels/tree-shrews 53%), making accurate estimation of their distance from the trail difficult. Experimental distance estimation showed a significant difference between perpendicular distances to vocalizing animals estimated by the two observers and actual distances ($t_{74}=12.48$, $p<0.001$ and $t_{74}=2.16$, $p<0.05$, two-tailed test for matched pairs). When the animal records were partitioned into species groups, however, there was no significant difference between the mean distance of observation data sets in each habitat, except for the squirrels and tree-shrews. Therefore, no correction factors have been applied to the transect data, and all inferences are from direct comparison, except for the squirrels and tree-shrews.

The number of individual birds recorded during a day of transects differed signifi-

Table 1. Results of line transects of birds. Sample size, composition, and structure of bird communities in undisturbed primary forest (PRF), in lightly and heavily logged forest (LLF, HLF), and in modern rubber and oil palm plantation study areas (MR, OP).

	PRF	LLF	HLF	MR	OP
No. of transect hours	40	40	40	20	20
Species recorded, total no.	67	59	79	27	17
Species recorded after 20 hours	53	46	65	27	17
Species pr. 4 transects (± s.d.)	34.0 ± 3.5	28.8 ± 4.4	43.6 ± 4.6	20.0 ± 3.0	15.5 ± 0.5
Diversity	3.12	3.19	3.75	1.59	2.17

cantly between the observers (t_{19}=4.70, p<0.01, two-tailed test for matched pairs), even when unidentified birds were excluded from the analysis (t_{19}=3.59, p<0.01). The number of primate groups and individual squirrels/tree-shrews recorded during a day of transects also differed significantly between the observers (t_{19}=2.85 for primates, t_{19}=3.11 for squirrels and tree-shrews, p<0.001). As the plantation study areas were surveyed by only one observer, only data from this observer were used when comparing abundance data between the primary forest and plantations.

Patterns of bird population changes

A total of 152 bird species were recorded along transects, but only 67 were recorded in pristine forest (Table 1). Some 61% and 72% of the primary forest species were found in the lightly logged forest and the heavily logged forest study areas, respectively. In the rubber and oil palm plantation study areas, 10% and 5% of the primary forest species were found (after equal effort, 20 hours of transect).

Diversity of birds did not differ among the three forest study areas but was significantly lower (Mann Whitney U tests, p<0.001) in the plantations (reduced to 51% in rubber and 70% in oil palm, Table 1).

The proportional difference (PD) in bird species composition, weighted by abundance, between the primary and other forests is not significant (lightly logged 20.4%, heavily logged 21.9%); but the difference between the primary forest and the plantations (rubber 81.0%, oil palm 61.3%) is highly significant (Wilcoxon matched pairs tests, p<0.005). The PD value for rubber is higher than that for oil palm plantation due to the lower overall frequency of birds in the latter habitat.

Trophic structures of bird communities

Bird species were sorted into 16 feeding guilds according to their principal food and ways of foraging (see Danielsen and Heegaard in prep.). Community structure with respect to feeding guilds was significantly different in all disturbed study areas compared to the primary forest (x^2_{5-12}= 618-49,000, p<0.001).

Two feeding guilds, the *sallying substrate-gleaning insectivores* and the *nectarivores/insectivores* decreased significantly in abundance to less than 50% from primary forest to both logged forest study areas (Table 2).

Table 2. Impact of logging and conversion to rubber and oil palm plantations on trophic structure of birds. Feeding guilds which were significantly (p<0.05) affected negatively and positively, or not affected. Guilds with less than 20 individuals were not tested. For species composition of feeding guilds, see Danielsen and Heegaard (in prep.).

Guild	Impact of logging				Impact of conversion to plantation			
	N[1]	neg.	pos.	n.a.	N[2]	neg.	pos.	n.a.
Diurnal predators	18				5			
Terrestrial insectivores	137			X	144		X[5]	
Arboreal foliage-gleaning insectivores	1021		X[3]		1772		X	
Bark-gleaning insectivores	242		X		44	X[5]		
Sallying substrate-gleaning insectivores	268	X			87	X		
Sallying insectivores	49			X	44			X
Arboreal foliage-gleaning insectivores/ frugivores	466		X[4]		82	X		
Arboreal frugivores/predators	365			X	91	X		
Arboreal frugivores	292	X[3]			548	X[6]	X[6]	
Terrestrial frugivores	5				358		X	
Nectarivores/insectivores	317	X			103	X		
Nectarivores/frugivores	13				2			
Nectarivores/insectivores/frugivores	160		X		33	X		
Terrestrial insectivores/frugivores	143	X[3]			48	X		
Terrestrial/arboreal omnivores	0				1266		X	
Miscellaneous insectivores/piscivores	5				36		X	

Notes:

1) Number of individuals recorded in primary forest, in lightly and heavily logged forest (40 h of line transects).
2) Number of individuals recorded in primary forest, in rubber and oil palm plantations (20 h of line transects).
3) Affected in lightly logged forest but not affected in heavily logged forest.
4) Not affected in lightly logged forest but affected in heavily logged forest.
5) Not affected in rubber plantation but affected in oil palm plantation.
6) Positively affected in rubber plantation, but negatively affected in oil palm plantation.

With the conversion of forest to rubber or oil palm plantations, eight feeding guilds decreased significantly in abundance (Table 2). Six guilds disappeared entirely or decreased to less than 10-50%, including the *sallying substrate-gleaning insectivores*, the *arboreal foliage-gleaning insectivores/frugivores*, the *arboreal frugivores/predators*, the *nectarivores/insectivores*, the *nectarivores/insectivores/frugivores* and the *terrestrial insectivores/frugivores*.

There were also major differences between the forest and plantation study areas in the numerical dominance of guilds. While the forest study areas comprised an avian fauna of 15 feeding guilds with little dominance by any of them, four mainly terrestrial guilds strongly dominated in the plantations. In addition, there were many species per feeding guild in forest, while in plantations most guilds comprised only 1-3 species.

Conservation importance of bird species affected by logging and forest conversion

Eleven bird species currently listed as globally threatened or near-threatened (Collar and Andrew 1988), but no restricted-range species (global range < 50,000 km² *sensu* BirdLife 1992), occur in the area. None of these species were recorded in the rubber or oil palm plantations.

To assess in more detail how logging and forest conversion affect bird species of differing importance to conservation of biodiversity, we grouped species according to their global range, habitat range, and population density.

The first group comprised species of most importance to conservation, defined here as species endemic to the Greater Sundas, and peninsular Malaysia, known to breed in only one habitat (King *et al.* 1975, Lekagul and Round 1991), and to occur in low population densities where they occur (pers. obs.). A total of 17 species of importance to conservation were recorded in the study areas. In plantations we recorded one species (6%). We recorded 5 (29%) and 6 (35%) species in heavily logged forest and lightly logged forest, respectively, while in primary forest we recorded 10 (59%) of these species.

The second group comprised species of least importance to conservation. This group comprised species that were not confined to the Greater Sundas and peninsular Malaysia, which were known to breed in more than one habitat, and to occur in high population densities. A total of 77 species were placed in this category. They comprised 25% of the species in the transect in primary forest, 25% in lightly logged forest, 23% in heavily logged forest, and 72% of those in plantations of rubber and oil palm combined.

Bird species of most importance to conservation were more abundant in primary forest than in logged forests and plantations. However, the difference was only significant between primary forest and plantations ($F_{5,18}=5.55$). Similarly, species of least importance to conservation were 3-9 times as abundant in plantations as in any other forest type ($F_{5,18}=84.11$).

Primates

A total of 199 primate groups were recorded (Table 3). Six species were identified. There was no significant difference in abundance of primate groups between the primary and logged forest study areas. In the plantation study areas there were significantly fewer groups of macaques (*Macaca* spp.) and gibbons (*Hylobates* spp.). Colobines (Colobinae) were absent from the oil palm plantation study area, but occurred in the rubber plantation with the same group abundance as in the primary forest study area.

Table 3. Number of primate groups, tree-shrews and squirrels recorded in the study areas in primary undisturbed forest (PRF), in lightly and heavily logged forest (LLF, HLF), and in modern rubber and oil palm plantations (MR, OP). "+" indicates the species was recorded at the study site but not on transect counts. No entry denotes that the species was not recorded. Forest study areas were surveyed for 40 h each, and plantation study areas for 20 h each.

	PRF	LLF	HLF	MR	OP	Total
Macaca nemestrina	+		+			
Macaca fascicularis		+				
Macaca sp.			1			1
Presbytis melalophos	6	1		1		8
Semnopithecus cristata		3			3	
Unidentified Colobinae	4	21	11	3		39
Hylobates agilis	+	7	8			15
Hylobates syndactylus	45	39	32			116
Hylobates sp.	1	2	1			4
Unidentified Primate	5	5	3			13
Primates, total	61	78	56	4		199
Tree-shrews and squirrels	73	45	38	1		157

Weighted by abundance, the proportional difference (PD) in species composition of primate groups between the primary and other forests is not significant (lightly logged forest 27.7%, heavily logged 31.6%); but the difference between the primary forest and the plantations (rubber 93.9%, oil palm 100%) is significant (Wilcoxon matched pairs signed-ranks tests, $p<0.05$).

Squirrels and tree-shrews

A total of 157 squirrels and tree-shrews were recorded (Table 3). Twenty-seven percent were identified to species; they included the common tree-shrew (*Tupaia glis*), lesser tree-shrew (*T. minor*), large tree-shrew (*T. tana*), giant squirrel (*Ratufa affinis*), Prevost's squirrel (*Callosciurus prevostii*), plaintain squirrel (*C. notatus*), Low's squirrel (*Sundasciurus lowii*), slender squirrel (*S. tenuis*), horse-tailed squirrel (*S. hippurus*), three-striped squirrel (*Lariscus insignis*) and black-eared pigmy squirrel (*Nannosciurus melanotis*).

Mean estimated perpendicular distance to squirrels and tree-shrews was 20.6 m in the primary forest study area, but 10.7 m and 14.4 m in the lightly and heavily logged forest study areas, respectively. When corrections were made for this (by multiplying the number of individuals with quotient between the mean distance in the primary forest and the logged forest study area), there was no significant difference between abundance of squirrels/tree-shrews in the primary and logged forest study areas. Squirrels and tree-shrews were extremely rare in the rubber and oil palm plantation study areas.

Bats

Our sampling effort (3,170 net-meter nights) resulted in the capture of 204 bats of eleven species, including 191 fruit bats (Pteropodidae) of five species, seven horseshoe bats (Rhinolophidae), four leaf-nosed bats (Hipposideridae), one slit-faced bat (Nycteridae) and one vespertilionid bat (Vespertilionidae) (Table 4). Mist-net sample size for most species was small, making comparisons of species captured in each study area questionable. Nevertheless, a few clear differences in species richness and community structure are apparent.

Logging caused an overall decrease in species richness to 38-50%, while conversion of primary forest to plantations of rubber and oil palm caused a decrease in species richness to 13-25%. Seventy-three per cent of the species detected occurred in the primary forest study area, 27-36% in the logged forest and 18% in the plantation study areas combined.

The lesser dog-faced fruit bat (*Cynopterus brachyotis*) was the most abundant species in all study areas and accounted for 89% of all records, while other species only accounted for 1-3% each. The proportion of lesser dog-faced fruit bats increased with logging and with conversion to plantations. This species comprised 42% of the records in the primary forest study area, 50% and 77% of the records in the lightly and heavily logged forest, and 99% of the records in the plantation study areas combined.

Weighted by abundance, the proportional difference (PD) in bat species composition between the primary and logged forest study areas was approximately 60% (lightly logged 65%, heavily logged 54%), while the difference between the primary forest and the plantation study areas combined was 87%.

Based on their principal feeding guild, we grouped species into frugivores/nectarivores and insectivores (Table 4). Community structure with respect to feeding guilds was significantly different at the combined plantation study areas, compared to the primary forest ($x^2_3= 69.4$, $p<0.001$). Insectivorous bats appeared to be more susceptible to logging and conversion to plantations than frugivores/nectarivores.

Discussion

Study area assumptions

We assumed that the logged forest study areas had an original vegetation structure, habitat range and animal community composition very similar to the undisturbed forest used for comparison. In tropical forest, however, there can often be wide variation in species abundance and species distribution over even quite small distances (Whitmore 1984). The primary forest in this part of Sumatra differs considerably from place to place in stature, notably in the abundance of giant emergent trees and canopy height (Whitmore and Samsoedin 1991). To minimize bias from this we made censuses in two logged areas, and based our conclusions on results from both areas. More objective information could be gained, however, by continuing studies in a single forest area throughout a logging and management cycle (Johns 1992).

Table 4. Sample size and species composition of bats mist-netted in the study areas in primary undisturbed forest (PRF), in lightly and heavily logged forest (LLF, HLF), and in modern rubber and oil palm plantations (MR, OP). The first five species are principally frugivorous/nectarivorous, the remaining are insectivorous (based on Payne *et al.* 1985).

	PRF	LLF	HLF	MR	OP	Total
No. of net-meter nights (x 100)	8.9	8.2	8.1	5.2	1.3	31.7
No. of individuals caught	26	8	9	161		204
No. of species caught	8	4	3	2		11
Cynopterus brachyotis	11	4	7	6	154	182
Cynopterus horsfieldii	1			1		2
Megaerops ecaudatus		1				1
Megaerops wetmorei			1			1
Balionycteris maculata	4		1			5
Nycteris javanica		1				1
Rhinolophus trifoliatus	4	2				6
Rhinolophus lepidus	1					1
Hipposideros cervinus	3					3
Hipposideros diadema	1					1
Murina cyclotis	1					1
Frugivores/nectarivores	16	5	9	161		191
Insectivores	10	3	0	0		13

Biases caused by variable detectability

One potential bias of the line-transect census method is habitat variations causing differences in detectability. The more open canopy in the logged forest than in the primary forest study areas resulted in more sightings of birds in flight (Danielsen and Heegaard in prep.), and perhaps more chance of seeing animal species in the canopy. On the other hand, the denser understory would be expected to make it more difficult to see understory and terrestrial species. Although one might therefore expect a difference in the mean estimated distance to animals recorded in habitats with different land-use, except for squirrels and tree-shrews no such difference was found, perhaps because most were detected by their vocalizations. A change in vertical or horizontal foraging space could also change the detectability. In New Guinea and Australia, species of fantail (Rhipiduridae) shifted their foraging height, often feeding lower in logged than in undisturbed forest (Driscoll and Kikkawa 1989). However, except in two bird species, no change in foraging height of birds could be attributed to logging or forest conversion (Danielsen and Heegaard, in prep.). Capture rates of birds mist-netted in the study areas were higher in heavily logged than in primary and lightly logged forest (Danielsen and Heegaard in prep.). Increased capture rates of birds in logged forest were also found by Lambert (1992) in Sabah. He suggested this indicated either an increase in bird population density or a change in activity or ranging behaviour, as suggested by Wong's (1985) study in peninsular Malaysia. A change in ranging behaviour may change the detectability of animals in heavily logged forest and cause a wrong estimation of the impact of logging. Further research is needed to quantify this potential bias.

Responses of birds to logging

This study supports the conclusions of other studies that most forest birds may utilize selectively logged forest (McClure and Othman 1965; Johns 1989; Holbech 1992; Lambert 1992). We found a number of species in logged forest which other studies failed to find in this habitat. Thus, results from one area cannot necessarily be used to predict the species-specific effects of logging on the avifauna of another, even when original species composition is almost the same (Lambert 1992). On the other hand, we found more species with small global range, narrow habitat requirements and low population densities in primary forest than in logged forest. This finding has important implications for biodiversity conservation (see below).

The line-transect censuses of the present study were carried out within a brief period of time, yet the total effort was equal to most corresponding studies. Even after 40 h of survey, however, the line-transect censuses in the forest study areas continued to reveal bird species which had not been recorded previously in the area. It is possible that more effort in the forest study areas would give different results. More likely, however, increased effort would result in recording more species of importance to conservation in the primary forest study area, which would strengthen the results already found. Many bird species of importance to conservation are so rare that much effort is needed before they will be detected.

Five major studies have investigated birds in selectively logged tropical lowland rain forest. Two studies, however, used methods which are likely to be seriously biased towards species which frequent the highly disturbed vegetation in logging tracks and gaps. This vegetation is very different from the vegetation generally prevalent in logged areas. Johns (1986b; 1988; 1989) counted birds mainly along old logging roads to document changes in bird populations in selectively logged forest at various stages of regeneration in peninsular Malaysia (Lambert 1992). Thiollay (1992) used a point-count method of 0.25 hectare sample plots, centered on tracks or gaps, to investigate changes in bird populations in French Guiana. Untouched forest patches in the logged forest were not sampled. A third study, by Holbech (1992), used a strip-census line-transect method to document changes in the bird populations of logged forests in Ghana.

The remaining two studies were carried out in Malaysia. Wong (1985; 1986) conducted a ringing programme in peninsular Malaysia, comparing the understory bird community of 600 hectares of virgin forest with an adjacent logged area. Lambert (1992) used mist-netting and variable-distance line-transect methods with survey routes located independent of logging roads in Sabah. Comparisons are constrained by the use of different survey methods and by difference in time elapsed since logging. In the study by Wong (1985; 1986), 23-25 years had passed since logging, while in the study of Lambert (1992), only 8-9 years had passed. The three Indo-Malayan studies are compared below (from Danielsen and Heegaard, in prep.).

Wong (1985; 1986) found no significant difference in the relative importance of feeding guilds, either in terms of species richness or in abundance of individual species. This contrasts strongly with the results obtained by us and by Lambert (1992). The differences may be explained, however, by the longer regeneration time in the forest studied by Wong (1985; 1986).

The most noticeable change in avifauna found by Lambert (1992) was an increase in both specialized and generalized nectarivore species with logging. In contrast, Wong (1985; 1986) found that sunbirds and spiderhunters (Nectariniidae) decreased in abundance with logging, which is supported by the present study (the *nectarivores/insectivores* guild). The divergent results suggest that other factors than logging *per se*, such as the occurrence of flowers, may be key determinants of the abundance of these species. Flowers are highly patchily distributed in time and space, and the high abundance of the guild in unlogged forest coincided with a high frequency of plants with flowers visited by birds (Wong 1985; 1986). Often, however, flowering herbs and shrubs abound along edges and in light gaps.

The data of Lambert (1992) agreed with our findings that the abundance of the *sallying substrate-gleaning insectivores* guild, comprised of trogons (Trogonidae), broadbills (Eurylaimidae) and drongos (Dicruridae) declined with logging. In the present study the most numerous taxa in this guild were black-and-yellow broadbill (*Eurylaimus ochromalus*) and greater racquet-tailed drongo (*Dicrurus paradiseus*), while in the study of Lambert (1992), trogons and white-throated jungle flycatcher (*Rhinomyias umbratilis*) were also numerous. No such decline was found by Wong (1985; 1986), perhaps because she only recorded a few broadbills and drongos. However, she did find that logging was associated with a significant decrease in abundance in her flycatching insectivore guild, which mainly comprised flycatchers (Muscicapidae). In our and Lambert's (1992) studies, the number of flycatchers was too small to justify any conclusions.

Our results support the findings of Lambert (1992) that the abundance of the *arboreal foliage-gleaning insectivores/frugivores* guild, comprised of bulbuls (Pycnonotidae), leafbirds (*Chloropsis* spp.), flowerpeckers (Dicaeidae) and some sunbirds increased with logging. Most of these taxa are not understory birds and were recorded in relatively low numbers in the study of Wong (1985; 1986).

We found that woodpeckers (Picidae), the *bark-gleaning insectivores* guild, increased significantly in abundance with logging, while data of Lambert (1992) indicate a decrease. This may be attributed to a difference in the species composition or density of large trees or dead trees still standing in the study areas. In our study area there seems to be a lower density of timber-sized trees than in most of Borneo, while the density of tree trunks was comparatively high (Mirmanto and Schumacher in prep.).

To summarize, all three studies in Indo-Malaya consistently showed that logging deleteriously affects *sallying insectivores*, whether substrate-gleaning or not, such as trogons, broadbills, drongos and flycatchers, while bulbuls, leafbirds, flowerpeckers and some sunbirds generally benefit from logging. It is not understood what happens to woodpeckers.

Whatever the methodological shortcomings, all major studies on birds in selectively logged tropical rain forest reached overall conclusions similar to some of those of this study (Wong 1985; 1986; Johns 1986b; 1988; 1989; Holbech 1992; Lambert 1992; Thiollay 1992): organization of the bird community was altered by logging with abundant species occupying a higher proportion of the sample; and specialized insectivores of the mature forest understory declining. On the other hand, many insectivore-frugivore generalists, notably from gaps, survived or increased, and even large frugivores such as hornbills (Bucerotidae) persisted in logged forests.

The species richness and the species diversity of birds, however, did not decrease with logging. Indeed, only the studies of Johns (1986b; 1988; 1989) and Thiollay (1992), using potentially biased methods, found significant decreases in species diversity with logging. In the present study, as in all major studies except those two, the number of species colonizing the logged forest or increasing after logging largely compensated for the loss or decrease of primary forest species. In contrast to the conclusions of Thiollay (1992), the gaps, disturbance and habitat heterogeneity created by heavy selective logging seem to increase species richness and diversity and compensate for the decline of primary forest species, as sometimes seen in managed temperate forests. As discussed by Connell (1978), disturbed habitats may show a higher species diversity than undisturbed. But this does not mean that, in addition to new species, logged forest will continue to support all species of undisturbed forest (Johns 1992).

Responses of birds to complete conversion of the forest habitat

Overall, the small number of bird species colonizing the rubber and oil palm plantations or increasing after the complete conversion of the forest habitat far from compensated for the loss or decline of forest species. The conversion of primary forest to plantations led to a simple, species-poor and less diverse bird community. The plantations held fewer specialized species, fewer arboreal species, and fewer species with small global range, narrow habitat requirements, and low population density. On the other hand, widespread, generalist, and common species were much more abundant in plantations.

The pronounced decline in bird species richness corresponds with studies of plantations of *Pinus caribaea* and *Albizia falcateria* in Kalimantan (hornbills and pheasants, Wilson and Johns 1982) and plantations of sal in India (Ripley *vide* Good *et al.* 1992) and conifer in Kenya (Carlson 1986).

In contrast, about 60% of primary forest bird species used young plantations of the exotic *A. falcateria* in Sabah (Mitra and Sheldon 1993). The *Albizia*, however, provided space and light for the development of a substantial secondary forest replete with animal and plant food (Mitra and Sheldon 1993). The *Albizia* groves were 1-2 km from primary forest and near to areas of active logging; they thus had a ready source of avian forest species, and there was still microhabitat structure (e.g., stumps and logs) left from clearing primary forest (Mitra and Sheldon 1993). In addition, the *Albizia* trees were infested with caterpillars, which attracted birds. In comparison, the rubber and oil palm plantations in the present study had an undergrowth of mainly ferns (*Blechnum* sp.), which were cut regularly, allowing no second growth forest to develop. Our study areas were 5-6 km from the nearest forest, and there were no stumps or logs left from clearing primary forest. Furthermore, our study areas were visited almost daily by labourers, while the *Albizia* groves were not yet cropped (Mitra and Sheldon 1993) and perhaps only rarely visited by humans. The response of birds to plantations depend on many factors, including plantation species and age, proximity to forest, microhabitat structure, and level of human disturbance.

Responses of primates and squirrels to logging and forest conversion

Our findings on the responses of primates to logging correspond with previous studies, which found that frugivorous/folivorous primates such as colobines and gibbons are able to survive well under conditions of logging (Johns and Skorupa 1987), because they are able to change their diet and feeding behaviour to a considerable extent (Johns 1986a). Macaques which are largely frugivorous but opportunistic (Johns and Skorupa 1987), have even been reported to be more common in disturbed than in primary forests (Marsh and Wilson 1981). The critical period for many primates, when the fewest fruits will be available, is the period directly following logging (Marsh and Wilson 1981) and not 7-10 years after logging as in the present study. On the other hand, stresses exerted at the period directly following logging may affect parameters such as birth rates rather than population densities (directly) and thus may show up in population samples only after many years (Marsh and Wilson 1981; Johns and Skorupa 1985).

Few data are available on the responses of primates to plantations.In the literature there do not seem to be any published records of macaques or gibbons occurring in rubber or oil palm plantations, but the colobine *S. cristata* is known to occur in rubber plantations (MacKinnon 1986). We found no difference in the number of colobine groups in primary forest and in plantations of rubber.

We do not know, however, if the actual number of primate individuals had changed because of changes in group size. In very disturbed areas, primate groups may fragment and split into several smaller groups or lone animals (MacKinnon 1986). For instance, groups of *P. melalophos* have been found to be larger in primary forest than in logged forest (MacKinnon 1986).

There was no change in the total abundance of squirrels and tree-shrews with logging, but there might have been a change in species composition. In a study by Johns in peninsular Malaysia (*vide* Duff *et al.* 1984) giant squirrels were found to be more abundant in primary forest than in logged forest. In our study there were unfortunately too few squirrels and tree-shrews identified to species level to make comparisons of species composition. In a brief study in East Kalimantan, Wilson and Wilson (1975) also found that squirrels survived in logged forest but with a lower abundance than in primary forest. They used a strip-census method, but they did not, however, make any corrections for potential changes in detectability with logging.

It is remarkable that we had only one observation of a squirrel or tree-shrew in the rubber plantation and none in the oil palm plantation study area. Common tree-shrews have been observed eating unripe fruits of oil palm in Sabah (Davies and Payne 1982). Our findings contrast with studies in mixed plantations of mainly *Eucalyptus* and *Albizia* in Sabah, where tree-shrews were found to occur (Duff *et al.* 1984).

Responses of bats to logging and forest conversion

Except in the plantations, only a small proportion of the bat species present in each area was captured. Mist-netting was carried out for a short period in each study area and only in the lower strata of the vegetation. Flying insects (Sutton and Hudson 1980; Sutton 1983), and flowers and fruits of many plants are concentrated within or above the upper forest canopy, and a number of species would only occasionally be captured in the lower vegetation strata. In addition, it is not known if bats are better at detecting and avoiding mist-nets in some habitats than in others.

Megaerops wetmorei is in the Philippines probably limited to primary forest (Heaney *et al.* 1989), while in the present study we found it in disturbed habitats such as heavily logged forest. This indicates that results from one area cannot necessarily be used to predict the species-specific effects of disturbance on the bat fauna of another, even when original species composition is the same.

Decline in species richness and increase in proportion of dominant species with disturbance of forest were also found in Panama, where two species of one genus made up three-quarters of a total netted sample of frugivore bats (Johns 1992).

Replacement of forest with rubber and oil palm plantations led to a very simple, species-poor and less diverse bat community. All bats disappeared except the dog-faced fruit bats (*Cynopterus* spp.). Lesser dog-faced fruit bat and Horsfield's fruit bat (*C. horsfieldii*) are also known in Malaysia to be more common in disturbed habitats such as rubber estates than in forests (Mickleburgh *et al.* 1992).

Management implications

This study was concerned with logging operations that are typical for production forests of tropical Asia. The number of trees logged per hectare in the heavily logged forest study area equals what is extracted in an average Malayan dipterocarp forest (Whitmore 1984). However, logging here was carried out by conventional tractors while in some forests logging is carried out by cable systems, which causes less soil compaction but more disturbance to the vegetation. Moreover, in contrast to what is frequently seen elsewhere, there were no human settlements in the forest. Hunting pressure was significant only in the lightly logged forest area.

Little is known about the extent to which responses of one species group to habitat changes such as logging reflect the response of other species groups (Johns 1992). The difference in species composition, weighted by abundance, was larger for bats (54-65%) than for birds (20-22%) or primates (28-32%). In contrast with the assumption of Johns (1992) that the greater the species richness of a species group, the more sensitive it is likely to be to habitat changes, this difference in species composition indicates that bats may be more sensitive to habitat changes than birds (or primates). Sample size for bats was small, however, and only birds showed a significant change in community structure with respect to feeding guilds.

Bats play an important role as pollinators and seed dispersers. They are responsible for the propagation of many plants useful to man, including timber trees and fruit trees (Mickleburgh *et al.* 1992). Twelve of the major timber species in Malaysia depend on bats for dispersal. If species richness of bats is changed by logging it would be very valuable to know the impact on pollination and seed dispersal.

Specialized insectivorous birds of the mature forest understory declined in abundance with logging, and insectivorous bats declined in species number, perhaps because the associated disturbances changed the species composition and abundance of insects in the forest understory. Short-term moth-trapping programmes demonstrated a considerable difference in species composition between unlogged and logged forest (Johns 1992), and termite studies have indicated dominance by a few species in logged forest (Collins 1980). More studies are needed to investigate the impact of logging on understory insects. Indeed, current views on the impact of logging on species diversity are biased by the responses to larger animals, which are only a part of the total biological diversity of the forests (Johns 1992), while the numerically most important group, the invertebrates, have hardly been studied.

Our study suggests that selective logging may not be as detrimental to birds as previously thought, as long as large unlogged patches are maintained. The patch size and dispersion necessary to support viable populations of birds on the patches, however, remain to be determined (Lambert 1992). The species richness and the species diversity of birds did not decrease with logging, but logged forest held fewer species of importance to conservation. Whether all bird species present in logged forest are able to breed there is also uncertain (Lambert 1992). Wong (1985) reported lowered reproductive success in selectively logged forest in peninsular Malaysia. Certain species such as great argus (*Argusianus argus*) (Johns 1986b) and Storm's stork (*Ciconia stormi*) (Danielsen *et al.* 1995) may survive the short-term effects of logging, but be unable to breed. Juveniles of many bird species were netted in the logged forest study areas (Danielsen and Heegaard 1994) but it is not certain that they had fledged locally.

The responses of one species group to clearing of forest and replacement with rubber and oil palm plantations reflected well the response of other species groups, probably because of the magnitude of the habitat disturbance. The species richness of all species groups declined substantially. The difference in species composition, weighted by abundance, was relatively similar (birds 61-81%, primates 94-100%, bats 87% in rubber and oil palm plantations, combined). Not surprisingly, botanists who studied the same areas found a number of threatened species of plants in primary and logged forests, but none in plantations of rubber and oil palm (Schumacher 1994).

Plantations of rubber and oil palm are of little or no importance to conservation of species diversity. At present, major plantation programmes are being established in South East Asia at a rate unparalleled at any time or place in world history. More than 10 million ha of industrial plantations are planned to be established in the region by early next century (Turvey 1994). In Indonesia, most plantations are being developed within natural production forests. This massive conversion of natural forests to plantations will have a serious impact on the survival of many species of plants and animals.

For conservation of the biodiversity of tropical forests, logged forest cannot replace primary forest. In many areas the authorities have, however, been reluctant to create large protected areas of primary forest (e.g., Aiken 1994). Owing to the rapid pace of anthropogenic forest change, many countries are now running out of sites with primary forest. Conservation of biological diversity must come to rely more and more heavily on the wise management of logged forests. Since logged forests cover much larger areas than primary forests, it is the logged forest areas, not the protected areas of primary forest, that harbour most of the region's species diversity. If the logged forests are managed so as to support the long-term production of diverse natural timbers, they should, however, also support the long-term conservation of at least some of the animal and plant species of undisturbed forest (Johns 1992). For various reasons, such as their role in the pollination and seed dispersal of many forest trees (e.g., Stiles 1985), wildlife will, in any case, be an integral part of a successful forest management operation (Johns 1992). Still, however, logged forest should be maintained only in addition to, and not in place of, protected areas of primary forest.

To develop biodiversity monitoring methods and define quantifiable achievement indicators for conservation projects it is often suggested that single "indicator" species be identified whose presence, absence, or abundance may be used in a rapid assessment of the status of a forest. However, since results from one area cannot necessarily be used to predict the species-specific effects of habitat changes such as logging on the fauna of another, even when original species composition is almost the same, it may be impossible to identify appropriate species.

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Does "deforestation" always result in serious soil erosion?

Lawrence S. Hamilton[1]
Islands and Highlands Environmental Consultancy

Abstract

Serious soil erosion is usually one of the impacts of deforestation, but not always. It is important to note the range of diverse activities commonly included under the umbrella of "deforestation", and examine their specific impacts before making policy or management decisions. This paper makes a plea for more precision in defining the rain forest impactor in question. Only then can on-target recommendations be made for minimizing soil losses following rain forest disturbance, whether modest or drastic.

There is a continual struggle, both by nature and humans, to counteract the effect of gravity and reduce the rate at which the earth's productivity moves downhill. A review of the three principal erosion types in the wet tropics (and their importance) is followed by a brief discussion of the processes of erosion control operating in forests, and how these are disrupted by disturbance.

With this background, the paper points out that in some cases erosion consequences are over-rated, while in others, the seriousness of the consequences is ignored and yet they can be the most damaging of any impact. A set of general statements of causes and effects are presented as policy and management guidelines.

Introduction

Humans and nature must struggle continually, to counteract the effect of gravity and reduce the rate at which the earth's productivity moves downhill. Productivity is lost onsite due to erosion, leaching, and the transport of nutrient-bearing products off-site (usually downhill). Plants and animals in the undisturbed forest "grab" molecules of productivity from the soil and the atmosphere and incorporate them in their tissue, thus retarding the movement of nutrients to the sea from the uplands. Nutrient cycling in relatively closed systems keeps undisturbed tropical rain forests in productive condition, yielding an exuberant diversity of species of flora and fauna, and frequently also stands of high biomass. Much of the nutrient capi-

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