center of its torsional range, is optimally placed for the next gaze shift, which may go either CW or CCW [see K. Hepp, *Vision Res.* **35**, 3237 (1995) and D. Tweed, *ibid.* **37**, 1939 (1997)].

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Tree Species Diversity in Commercially Logged Bornean Rainforest

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The effects of commercial logging on tree diversity in tropical rainforest are largely unknown. In this study, selectively logged tropical rainforest in Indonesian Borneo is shown to contain high tree species richness, despite severe structural damage. Plots logged 8 years before sampling contained fewer species of trees greater than 20 centimeters in diameter than did similar-sized unlogged plots. However, in samples of the same numbers of trees (requiring a 50 percent larger area), logged forest contained as many tree species as unlogged forest. These findings warrant reassessment of the conservation potential of large tracts of commercially logged tropical rainforest.

Conservationists have despaired over destruction of tropical rainforest by logging, clearing, and burning. Most extant tropical rainforest has been logged or will be in the near future, with only relatively small fragments preserved (*1, 2*). Thus, commercially logged forest with low residual timber value is the only remaining option if large areas of tropical rainforest are to be conserved. The diversity of trees is fundamental to total rainforest biodiversity, because trees provide resources and habitat structure for almost all other rainforest species. In specially controlled, low-impact logging trials in Queensland, Australia, tree diversity was maintained (*3*). However, more typical of commercial, selective logging is the use of heavy machinery to remove marketable species; this kills additional trees, damages soils, alters habitat, and reduces timber growth potential (*4, 5*). Reductions in tree diversity might be anticipated, but the effects of commercial logging on tree species diversity over vast areas of rainforest in Southeast Asia, Latin America, and Africa remain largely unknown (*1, 6*).

Comparisons between logged and unlogged forest can be confounded by differences in soil, topography, and disturbance history that influence whether a site will be logged. We chose a site that allowed for controlled comparisons, including areas logged at different times in the past (1 year and 8 years before sampling) and which had already been surveyed for the gross, structural effects of logging (*4*). Loggers were unaware that the effects of logging would be assessed. At low elevations in West Kalimantan, Indonesia, local-scale topographic variation restricts mechanized logging; commercially valuable, well-drained lowland dipterocarp forest is frequently intermixed with patches of swamp forest impassable to heavy machinery. In the logging concession we studied, lowland dipterocarp forest (59% of area) and swamp forest (41%) form a complex spatial mosaic (*4*). Machine operators cannot reach all areas of lowland forest without long search paths and prohibitive costs. Patches (0.5 to 10 ha) that escape logging are determined by the placement of logging roads and the haphazard search patterns of operators, rather than by intrinsic differences among patches (*4*); thus, these patches provided convenient unbiased unlogged controls.

The unlogged lowland forest is species-rich, but the commercial species (mainly *Shorea laevis*, *S. hopeifolia*, and *Dryobalanops beccarii*, in the family Dipterocarpaceae) dominate, comprising 70% of total precut basal area (*7*). Logging removed 62% of dipterocarp basal area and 43% overall. One year after logging, 45% of lowland forest canopy was open or dominated by low pioneer vegetation (including roads and skid trails), 15% was unaffected, and 40% was disturbed in varying degrees (*4*).

Logging reduced both tree density and the number of tree species per 0.1-ha plot, for both large and small trees (unlogged versus 1-year sites; Table 1). For all trees >20 cm in diameter (*7*), density fell by 41% and the number of species per plot by 31%. The species-area curves 1 year after logging fell well below those for unlogged forest (Fig. 1, A and B). However, per plot richness alone is inadequate for assessing logging effects on tree diversity. In highly diverse communities, where rare species have few or single individuals in plot samples, the number of species per plot is sensitive to reductions in density by random deletions of individuals—"rarefaction" (*8*). If mortality due to logging were equivalent to rarefaction alone, the underlying species-individual relationship would be unchanged. Then it would only be necessary to sample proportionately larger areas in logged forest to obtain similar numbers of individuals, and thus similar species richness, to unlogged

Table 1. Numbers of species and abundances of trees, comparing plots logged 1 year and 8 years before sampling and plots unlogged at the time of sampling. Small trees are 20 to 30 cm in diameter (at 1.37 m high); large trees are >30 cm in diameter. U-1, 1-8, and U-8 are *P* values for Scheffe pairwise tests comparing unlogged versus 1-year logged forest, 1-year versus 8-year logged forest, and unlogged versus 8-year logged forest, respectively. Asterisks denote significance at $\alpha = 0.05$. See (*15*) for sampling details. ANOVA, analysis of variance.

	ANOVA		Plot means			Scheffe pairwise tests		
	F	*P* value	Unlogged	1 yr	8 yr	U-1	1-8	U-8
			Trees per plot					
All trees	11.43	0.0002*	23.8	14.1	15.8	0.0004*	0.77	0.0007*
Large trees	7.51	0.002*	12.5	7.2	7.8	0.005*	0.93	0.02*
Small trees	4.41	0.02*	11.3	6.9	8.0	0.03*	0.80	0.15
			Species per plot					
All trees	5.04	0.013*	18	12.4	13.7	0.02*	0.81	0.11
Large trees	4.29	0.023*	9.7	6.6	6.6	0.05*	0.99	0.07
Small trees	6.12	0.006*	10	5.7	7.8	0.006*	0.30	0.27
			Species per individual					
All trees	4.6	0.02*	0.75	0.85	0.89	0.14	0.59	0.02*
Large trees	2.9	0.07	0.80	0.92	0.89	0.09	0.90	0.26
Small trees	3.9	0.03*	0.90	0.83	0.98	0.34	0.03*	0.37

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forest. Alternatively, if physical disturbances and ecological changes associated with logging influenced some species negatively (or positively), thus changing their relative abundances, a change in species-individual relationships and species per unit area would be expected.

Although only trees >50 cm in diameter were harvested, the immediate effect of logging (unlogged versus 1-year sites) was to reduce the number of species per plot most (by 43%) for small trees (20 to 30 cm in diameter; Table 1, see also Fig. 1B). Species-individual curves (*3, 9*) were similar for unlogged and 1-year logged forest (Fig. 1D), suggesting that the death of small trees, due to incidental damage, was random with respect to species (rarefaction). In contrast, logging targeted the most common species of larger trees. Compared to 1-year logged plots, 8-year logged plots had similar species-individual ratios for large trees, but significantly higher ratios for small trees (Table 1). Thus, growth of trees into the 20- to 30-cm diameter class apparently increased diversity in 8-year compared to 1-year logged sites. Consequently, even on a per unit area basis, species richness of small trees in 8-year logged sites approached that of unlogged forest (Fig. 1B). The reason for the high richness of trees recruiting to the 20- to 30-cm diameter class is unclear, but may be associated with increased habitat heterogeneity after logging, due to patchy canopy disturbance (*4*).

After 8 years, tree densities remained lower in logged than in unlogged forest (Table 1); this was taken into account by comparing tree diversity in terms of species-individual ratios. By this measure, tree species richness (for all trees >20 cm in diameter) was significantly higher in 8-year logged forest than in unlogged forest (Table 1). The steep species-individual curves for logged forest, especially for small trees (Fig. 1D), reflected the high species-individual ratios in logged forest (Table 1). Thus, while the number of species per plot remained depressed in 8-year compared to unlogged forest (Fig. 1A), that reduction was less than would be expected by rarefaction alone.

The species accumulation curves in Fig. 1 are far from asymptotic, and our purpose was not to estimate the total number of tree species in the community. However, an index designed for that purpose provides one means of comparing the entire samples of logged and unlogged forest. The nonparametric Chao 2 index (*10*), recommended (*11*) for small samples, yielded similar estimates of 329 species for unlogged forest and 340 for 8-year logged forest. Another aspect of diversity, the overall evenness of species' abundances [Pielou's J; (*12, 13*)] increased from 0.77 in unlogged forest to 0.89 in 8-year logged sites for trees >20 cm in diameter. All these measures are consistent with the conclusion that, 8 years after logging, the impoverishment of tree species >20 cm in diameter was, if anything, less than expected due to reduction in density alone. The reduction in dominance of commercial species by selective logging, together with the increase in species-individual ratios for small trees, combined to mitigate the effects of reduced densities on species area relations.

Nor did logging cause major changes in the family-level taxonomic composition of trees >20 cm in diameter. Dipterocarpaceae dominated not only unlogged forest (15 species and 31% of trees) but also 8-year logged forest (16 species and 35% of trees). Although logging removed many large dipterocarps, logged species were well represented in the smaller trees. The largest family-level change was in the Burseraceae, with 6 species (7% of stems) in unlogged compared to 12 species (14% of stems) in 8-year logged forest. In general, the species present in logged forest were also characteristic of unlogged forest; there were only two stems of pioneer species (*Macaranga* spp.) in our 8-year logged forest samples. These patterns might differ in forests (such as in the neotropics) with high species richness of pioneer trees that respond positively to logging.

The persistent diversity of trees >20 cm diameter, which will provide most of the reproductive inputs to the community in the near future, points to high conservation value of logged forest. To include equivalent numbers of tree species and species abundances, a conservation area in the logged forest (8-year) should be larger by some factor than for unlogged forest, because of reduced tree densities. To estimate this factor, we assumed (conservatively) that species-individual ratios were similar for logged (8-year) and unlogged forest. A crude estimate is the ratio of densities in unlogged to 8-year logged forest—that is, 23.8/15.8 (Table 1) or a multiplication factor of approximately 1.5.

This study does not include the effects of logging on landscape-scale fragmentation or changes in land use. On the time scale of decades and longer, the ecological potential for the maintenance of tree species diversity in commercially logged forest will depend on the species-specific dynamics of tree regeneration, which may be influenced by altered animal communities (*1, 14*), and remain largely unquantified. Generalization of our findings to logged tropical rainforest in Southeast Asia or elsewhere will depend on larger samples across a variety of sites.

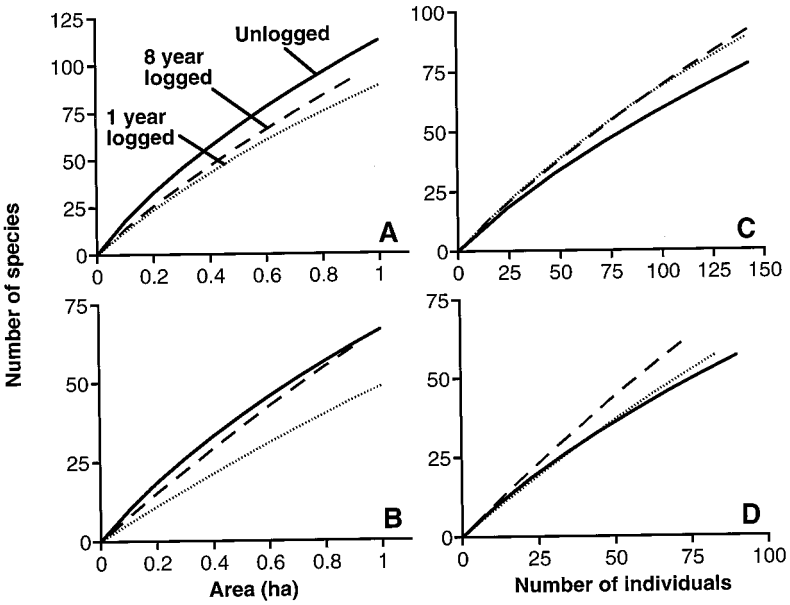

Fig. 1. Cumulative species-area relationships for (**A**) all trees >20 cm in diameter and (**B**) small trees 20 to 30 cm in diameter. Cumulative species-individual relationships for (**C**) all trees >20 cm in diameter and (**D**) small trees 20 to 30 cm in diameter. See (*16*) for details.

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15. Data are means for 20 m by 50 m (0.1 ha) plots in lowland dipterocarp rainforest in West Kalimantan, Indonesia (1°10′S, 110°20′E). In unlogged forest, n = 12 plots; in forest logged 1 and 8 years before sampling, n = 12 and 9 plots, respectively. Logged plots were on randomly oriented 1.5-km transects, of total length 15 km in the 8-year site, sampling from an area of ~15 km^2, and 7.5 km in the 1-year site, sampling from an area of ~6 km^2. Plots were located randomly on transects, within sampling strata defined by disturbance level, to ensure that samples reflected the degree and variability of disturbance characteristic of logged forest. See (*4*) for details of logging disturbance. Unlogged plots were randomly placed within primary forest remnants in both logged sites. One plot in 1-year logged forest, containing only trees >30 cm diameter, was excluded from the species-per-individual analyses for small trees in Table 1.
16. Data for cumulative numbers of species in Fig. 1, A and B are means from 1000 replications of the order of addition of plot samples within each of unlogged, 1-year, and 8-year samples. The abscissa in Fig. 1, C and D, was obtained by converting the abscissa of Fig. 1, A and B (cumulative area), to cumulative numbers of trees, using known densities of trees per plot in 1-year, 8-year, and unlogged forest, so that species richness could be compared between logged and unlogged forest with samples of the same numbers of trees.

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