Long-term impacts of logging on forest diversity in Madagascar

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Ecological perturbations can either be necessary for maintaining tropical forest diversity or responsible for its decline, depending on the scale, nature, and frequency of the disturbance. Anthropogenic disturbances such as logging and subsistence agriculture may promote the establishment of nonnative, invasive plant species, potentially affecting forest structure and diversity even long after the perturbation has ceased. We investigated the impacts of logging 50 and 150 years ago on tropical forest vegetation in Madagascar, a "hotspot" of biodiversity. Logging was the over-riding factor influencing establishment of nonnative plants. Sites once logged never recovered native species diversity because of the dominance and persistence of invasive species.

Temporal and spatial scales of disturbance affect forests differently. Disturbances over a range of scales are critical determinants of tropical forest composition, and the disturbance regime of tropical forests can be essential to maintaining native species diversity and community structure (1–4). Changes in disturbance type, frequency, scale, or intensity can also lead to the loss of species (5–10). The effect of selective logging on native tree diversity in tropical forests is a subject of speculation and of great current concern, but very limited data are available to assess its impact. Under some circumstances, logged tropical forests have been shown to contain as many tree species as unlogged forests (11, 12). Some disturbances may also facilitate colonization and establishment of invasive, nonnative plants when dominant native trees are removed (13, 14). The most critical questions about the establishment of invasive plants are not whether disturbance promotes establishment of nonnatives. Rather, it is essential to determine whether nonnative plant populations persist in tropical forests once established or are replaced by native species over time, and if persistent, whether the nonnative species have a negative impact on native tree diversity and forest community structure. Although the negative consequences of clear-cutting on the loss of biodiversity are well known, little is currently known about the long-term consequences for tropical forest diversity of selective logging and other more limited anthropogenic disturbances. The effects of colonization by nonnative species on native diversity under such conditions have rarely been considered, but may be important.

We investigated the effects of limited logging on the presence, persistence, and impact of invasive species on forest composition in Ranomafana National Park in southeastern Madagascar. The forests of Madagascar are considered a global "hotspot" of biodiversity, with among the world's highest levels of plant diversity and endemism. However, they are severely threatened by anthropogenic disturbances (15–19). We compared stands that were clear-cut and abandoned in about 1855, ≈150 years before the study, those selectively logged and abandoned in 1947, a stand that was never logged but was heavily damaged by a natural disturbance (a cyclone) 3 years before this study, and stands that were never logged and were relatively undisturbed.

Materials and Methods

Focal Species. There are a number of common invasive trees and large shrubs established in southeastern Madagascar. These include *Clidemia hirta* (Melastomacaceae), *Psidium cattleianum* Sabine (Myrtaceae), *Eucalyptus robusta* (Myrtaceae), *Lantana camara* (Verbenaceae), and *Syzygium jambos* (Myrtaceae). *P. cattleianum* is an understory tree that was introduced to Madagascar from South America in 1806 but has escaped from cultivation and spread throughout southeastern Madagascar (20). *P. cattleianum* was present in the forest ≈50 years before 1855, the estimated time of abandonment for the stands logged 150 years ago (ya). *E. robusta* is native to Australia, but its date of introduction to Madagascar is unknown. The tree is cultivated throughout Madagascar and is mostly used for firewood (20). The time and circumstance of the introduction of *S. jambos* are unknown, but it is distributed throughout Ranomafana, where it commonly grows along rivers and streams (20). *S. jambos* is native to the Malay archipelago. The remaining species, *C. hirta* and *L. camara*, are widely distributed throughout eastern Madagascar; however, unlike the previously mentioned species, they were not present in our plots.

Land-Use History. The disturbance history for stands logged 50 and 150 years before the study and those never logged was established through interviews with local residents and Malagasy research assistants and corroborated by park officials and long-time local researchers. The selectively logged stands 1–3, identified as those logged 50 ya, were cut in 1947. Stands 4 and 5 were clear-cut in the early 1850s for subsistence agricultural purposes and later abandoned. Selective logging procedures were carried out with the use of nonmechanized methods, with ≈50–60% of mature stems removed (20). Stands 6–8 had never been logged, but stand 6 was heavily damaged by cyclone Geralda in 1994.

Field Survey. This study was undertaken in one of the largest areas of relatively intact protected forest in Madagascar, Ranomafana National Park, located between lat 21°02′ and 21°25′S and long 47°18′ and 47°37′E. The designated park consists of 43,500 ha of continuous moist humid forest (mid-altitude montane rainforest) with annual rainfall ranging from 1,700 to 4,300 mm. The high rainfall occurs from December to March, and September and October are consistently the driest months. Temperatures range from lows June–September (4–12°C) to highs December–February (36–40°C). The surveys for this study were conducted in Ranomafana National Park from May 1997 through July 1997.

Data from a total of 240 25-m² quadrats in eight stands were used in this study. In stands 1–3 and 5–8, one 900-m² plot was established in each site (Table 1). Each plot was subdivided into thirty 25-m² quadrats (for spacing purposes and to diminish disturbance of sampled plots, all thirty-six 25-m² quadrats were not surveyed). In stand 4, a 2,500-m² plot with fifty 25-m²

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Table 1. Characteristics of stands with different logging histories

Stands within logging classes	Elevation, m	Stems, N	Observed richness, S	Estimated richness, S_{max}	Fisher's α	Shannon index, H'	S_{250I}	Invasion, %
Logged 50 ya								
Stand 1	951	1,024	29	36	5.6	0.89	31	83
Stand 2	1,006	669	28	32	5.9	1.10	21	52
Stand 3	1,015	787	35	43	7.6	1.56	23	67
Logged 150 ya								
Stand 4	1,000	649	36	46	8.3	1.88	27	73
Stand 5	997	933	24	30	4.5	1.52	15	78
Unlogged								
Stand 6	1,024	173	32	42	11.6	3.04	34	0
Stand 7	1,050	255	44	60	15.4	3.06	43	0
Stand 8	1,100	247	45	63	16.2	3.11	45	0

Stand elevation, number of trees (N stems), number of species (S), Fisher's α, Shannon diversity (H'), estimated true species richness (S_{max}), standardized number of individuals (S_{250I}), and percent invasion (based on number of stems) are reported.

quadrats was established (to diminish disturbance to surrounding plots, the entire area was not used). We randomly chose 30 of the original 50 quadrats in stand 4 for use in all calculations. The following information was collected in each quadrat: the diameter at breast height (DBH) of all woody species with DBH >2.5 cm; the identity of all plant species except grasses; and the native or nonnative status of each plant species (20, 21). In cases where the plant has not been described yet, the local Malagasy name was used. Also reported (Table 1) are number, N, of stems with DBH >2.5 cm and percent invasion of nonnative trees, based on numerical abundance (stem counts).

Species Diversity. Four measures were used to characterize species diversity; each emphasizes a different aspect of diversity. These were as follows: species richness, S, the number of species per 900 m²; Fisher's α, $S = \alpha \ln(1 + N/\alpha)$, a formulation commonly used for highly diverse tropical forest data sets (22) (where S is the species richness, N is the number of individuals, ln means natural logarithm, and α is the sole parameter); Shannon's index, $H' = -\Sigma p_i \log_2 p_i$, which accords greater weight to contrasts in rare species; and S_{max} or estimated true species richness. We estimated S_{max} (asymptotic number of species) and B (species overlap) from the set of values for $S(n)$ generated from the species–area accumulation curves by fitting each curve to the two-parameter hyperbola,

$$S(n) = \frac{S_{max} * n}{B + n},$$

where $S(n)$ is the number of tree species in each 25-m² quadrat generated from the accumulation curves, n is the number of quadrats, and S_{max} and B are fitted constants (23). The species accumulation curves were constructed by using ESTIMATES (statistical estimation of species richness and shared species from samples, Version 5; http://viceroy.eeb.uconn.edu/EstimateS). Data are means for plots for stands logged 50 ya ($n = 3$), stands logged 150 ya ($n = 2$), and unlogged stands ($n = 3$). The species accumulation curves are means from 100 randomization of the order of addition of sample plots within each logging class (24). The species individual curves were obtained by converting the cumulative area to cumulative numbers of stems. S_{250I}, the estimated species richness for 250 stems, was calculated by interpolation from the species-individual curves; 250 was the number of individuals in the site with the smallest total number of individuals.

Statistical Analyses. The effects of logging on number of stems (N), species richness (S), Fisher's α, Shannon index (H'), S_{max}, S_{250I}, and percent invasion were tested by using separate single-classification ANOVAs. *A priori* post-ANOVA comparisons between the three logging classes was conducted by using orthogonal contrasts to test the effects of logging (logged vs. unlogged stands) and time since logging (stands logged 50 ya vs. stands logged 150 ya). The sequential Bonferroni procedure was used to correct the significance levels in the ANOVAs (25), because six tests (for the six outcome variables) were run on the data.

We used partial Mantel tests (26) to evaluate the correlations between percent invasion, logging history (categorical), and diversity (S_{max}), while holding elevation constant statistically. The Mantel test is a nonparametric randomization procedure based on distance matrices, in which the statistical significance of the correlation between two distance (or difference) matrices is tested by creating a distribution by re-randomizing one of the matrices many times. Partial correlations can be constructed to evaluate the correlation between two distance matrices (e.g., percent invasion and diversity) while holding the values in a third matrix (e.g., elevation) constant statistically and can be tested in a similar manner. The distance matrix for invasion was based on the differences between the relative abundances (proportion of stems) of nonnative plants in each plot, compared to every other plot. Mantel tests were carried out by using PASSAGE (Pattern Analysis, Spatial Statistics, and Geographic Exegesis, Version 1.1.1.3; http://lsweb.la.asu.edu/rosenberg/Passage); each partial correlation was tested by using 999 permutations of the data.

We tested the effects of logging on species composition in stands with different logging histories by using Multiple Response Permutation Procedures (MRPP), a multivariate, nonparametric method for testing differences among predefined groups (27, 28). MRPP offer a way to test for differences among predetermined groups (e.g., logging categories) when the outcome is multivariate (here, species abundances) and where the data may not conform to parametric assumptions, such as normality and homogeneity of variances (27). The MRPP statistic is based on the average within-group distances and is tested against a distribution determined by randomly reassigning the data into the groups many times. Logging history (none, 50 ya, and 150 ya) was used as the grouping variable, and where *P. cattleianum* abundances may have biased our results, they were omitted from the analyses. The MRPP test was carried out by using PC-ORD (MjM Software, Glenden Beach, OR).

Results and Discussion

Regardless of how long ago trees were clear-cut or selectively removed, logging decreased species diversity, as indicated by
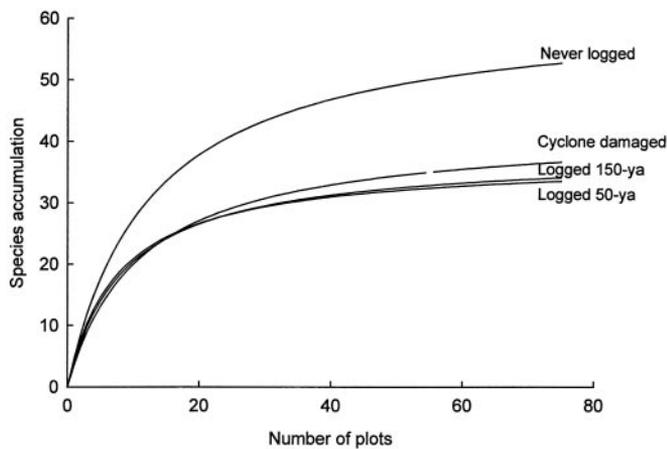
Fig. 1. Species accumulation curves for stands that were never logged, a cyclone-damaged site, 50-year-old logged stands, and 150-year-old logged stands. The graph shows estimated true species richness (S_{max}) for each stand type. Data are means for one 900-m^2 plot in montane rainforests in Ranomafama National Park.

Fisher's α and the Shannon index, and greatly increased percentage invasion (Table 1). The unlogged stand damaged by a cyclone had diversity values comparable to those of the unlogged sites and like these sites was uninvaded. There were no consistent statistical or biologically meaningful differences between forests that were selectively logged 50 ya and those clear-cut 150 ya. Logging history significantly altered species composition; native species' presence and abundance was different in logged and unlogged stands (MRPP, $P = 0.017$). Although lower-elevation sites were more likely to be logged than those at higher altitudes, the association between logging, invasion, and native diversity are not simply an artifact of covariation with elevation. Logging and plant invasion were strongly positively correlated when altitude was statistically held constant ($r_{mantel} = 0.575$, $P = 0.036$), whereas estimated true richness (S_{max}) and logging were negatively correlated when altitude was held constant ($r_{mantel} = -0.288$, $P = 0.048$). Logging itself, rather than altitude or time since disturbance, appears to be the overriding force driving plant invasions in this system, and plant invasion is a major predictor of reduced native species diversity.

The establishment of *P. cattleianum* is particularly strongly facilitated by logging. Once established, it can form monospecific stands that exclude establishment of other plant species, as it has

in Hawaii and elsewhere (29). Both in stands that were clear-cut 150 ya and those selectively logged 50 ya, *P. cattleianum* has become the dominant tree species, whereas it is absent from the stands that were never cut. The other nonnative, invasive plants present in these sites were not as pervasive or abundant as *P. cattleianum* (i.e., *E. robusta* and *S. jambos*).

These data suggest that the establishment of invasive species in forests logged in the past prevents recolonization by native species, even after 150 years. Species accumulation curves graphically suggest that logging, even 150 ya, leaves a characteristic signature on the plant community (Fig. 1). The cyclone-damaged, unlogged site had a species–area curve and asymptote similar to that of the logged sites (Fig. 1). However, differences in the estimated true species richness on an area basis (S_{max}) did not differ significantly among sites with different logging histories (Table 2).

Comparison of species–individual and species–area curves in highly diverse tropical forests is important for fully understanding ecological responses of these communities to disturbance (12, 24). Rare species represented by few individuals are likely to become lost from individual plot samples by chance, and species–area curves for disturbed and undisturbed plots will differ because of these random losses. If species losses in disturbed sites are due to such chance ''rarefaction'' effects alone, individuals belonging to rare species are more likely to be encountered when comparing the same numbers of individuals (stems) among sites than when comparing equal areas, and the species–individual curves will be similar for disturbed and undisturbed sites. If, however, rare species are disproportionately lost because of logging and associated changes such as invasion, species–individual curves as well as species–area curves will reveal those losses.

There were strong contrasts between the species–individual accumulation curves of logged and unlogged stands (Fig. 2). The differences in estimated richness for 250 stems (S_{250I}) between logged and unlogged stands based on species–individual curves were statistically marginally significant (Table 2). The stand that experienced the cyclone blow-down in 1994 had a species–individual curve more similar to those of the unlogged stands than those of the logged stands. The logged stands were characterized by large numbers of smaller, understory invasive plants. Unlogged stands were, in contrast, characterized by fewer, larger-diameter native trees (Table 2 and Fig. 3). The cyclone-affected stand (stand 6) resembled the logged stands in the number of stems, total DBH, and distribution of tree sizes (Table 2 and Fig. 3); individuals were lost across size classes, but no saplings or nonnative species have become established there

Table 2. Results from a single-classification ANOVA (df = 2, 5), followed by orthogonal contrasts based on decomposition of the two degrees of freedom among the three treatments

	ANOVA		Contrast 1		Contrast 2		Sites		
							Logged	Logged	
Variable	F	P	F	P	F	P	50 ya	150 ya	Unlogged
N stems	22.899	0.0030	45.646	**0.0005**	0.067	0.8044	A	A	B
S	2.259	0.2000	4.600	0.0757	0.014	0.9097	A	A	A
Fisher's α	13.9414	0.009	28.0678	**0.0018**	0.00032	0.9863	A	A	B
H'	46.418	0.0006	82.851	**0.0001**	5.520	0.0571	A	A	B
S_{max}	3.248	0.1248	6.456	0.0404	0.014	0.9097	A	A	A
S_{250I}	7.350	0.0325	14.989	**0.0083**	0.508	0.5028	A	A	B
Invasion, %	79.272	0.0002	161.679	**0.00002**	0.728	0.4263	A	A	B

The first contrast tested logged versus unlogged stands (Contrast 1; df = 1, 6), and the second tested logging 50 ya vs. 150 ya (Contrast 2; df = 1, 6). Logging classes with the same letters are not significantly different. The variable N stems was square root-transformed, and the invasion percentage was arcsine transformed. The probability values featured above are test-wise error rates. The results were interpreted in terms of experiment-wise error rates based on the sequential Bonferroni procedure. The experiment-wise error rates of 5%, 1%, and 0.1% correspond to test-wise error rates of 0.01000, 0.00167, and 0.00014, respectively. Test-wise P significant at experiment-wise error rates of 0.05 are presented in bold.
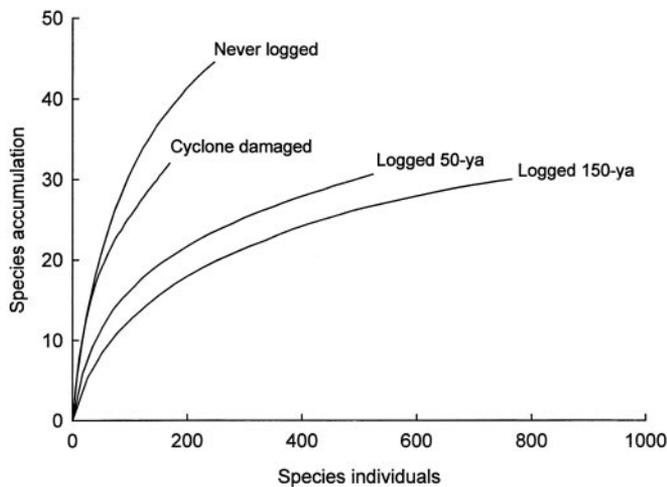
Fig. 2. Species–individual relationships for the same forest stands shown in Fig. 1.

periods of a half-century to a century or more. The recently naturally disturbed site had characteristics intermediate between those of the logged and unlogged stands and may undergo succession to eventually recover diversity and resemble the forest composition and structure of undisturbed stands. If it becomes invaded, however, it may never fully recover its original diversity.

Our results confirm that invasive plants are not transient members of postlogging tropical forests in Madagascar but maintain long-term viable populations after their initial colonization and can dramatically alter the trajectory of forest succession. *P. cattlieanum* does not invade closed, unlogged mature forests. It is unknown whether it will eventually colonize forests subject to natural disturbances; that may depend on their proximity to sources of propagules and other factors. The recent increases in abundance and availability of propagules of invasive plant species in logged sites in tropical forests worldwide may therefore require rethinking the affects of anthropogenic disturbances, with potentially profound implications for the viability of tropical forest diversity after even selective logging.

in the 3 years since the cyclone. Anthropogenic land use history has been shown to have long-persistent effects (40–60 years) in other tropical forests as well (30).

Taken together, these results suggest that both natural and anthropogenic disturbances reduce observed species richness and diversity. In the presence of invasive plants, logged stands did not recover species diversity even after 150 years, with characteristics of recent disturbance seemingly fixed even after

Fig. 3. Size distribution for representative stands from each logging classification. (*A*) A site (stand 2) logged 50 ya. (*B*) A site (stand 4) logged 150 ya. (*C*) A site (stand 6) never logged but cyclone-damaged. (*D*) A site (stand B) never logged. The size classes are based on DBH measurements up to 60 cm.

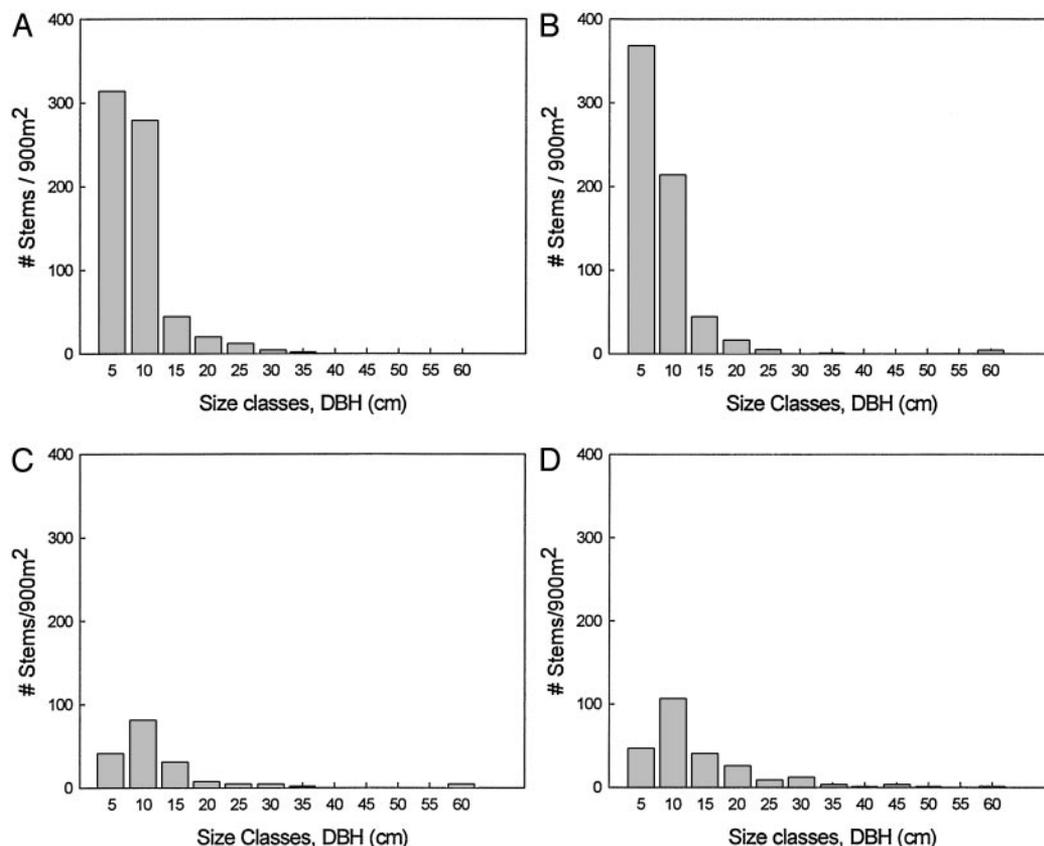1. Hartshorn, G. S. (1978) in *Tropical Trees as Living Systems*, eds. Tomlinson, P. B. & Zimmermann, M. H. (Cambridge Univ. Press, Cambridge, U.K.), pp. 617–638.
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