NOTE BRÈVE

IMPACTS ON TREE DIVERSITY IN A MALAGASY LOWLAND RAINFOREST OF SOIL TYPE, A DEVASTATING CYCLONE AND AN INVADING PIONEER

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RÉSUMÉ. — *Impacts du type de sol, d'un cyclone dévastateur et d'une plante pionnière envahissante sur la diversité des ligneux d'une forêt pluvieuse malgache de basse altitude.* — Deux relevés de toutes les plantes ligneuses (diamètre ≥ 5 cm) ont été effectués en octobre 2005 dans la Réserve Spéciale de Manombo (forêt de basse altitude, au sud-est de Madagascar), l'un sur une parcelle (50 × 50 m) sur sable blanc, l'autre sur une parcelle (50 × 48 m) sur sol ferralitique d'origine volcanique (basaltique). La forêt sur sol sableux est utilisée par les villageois tandis que la parcelle sur sol basaltique, qui a subi peu d'action anthropique (sauf la disparition des lémuriens), fut dévastée par un cyclone en janvier 1997 et se trouve envahie par l'espèce pionnière introduite *Cecropia peltata*. On compte 37 espèces pour les 453 tiges de la parcelle sur sol sableux et *ca* 145 espèces pour les 777 tiges de la parcelle sur sol basaltique. La composition floristique diffère bien davantage entre ces deux parcelles qu'entre les relevés effectués sur des parcelles de 50 x 50 m dans les Réserves Spéciales d'Analamazaotra (à 1 000 m d'altitude) et d'Ambohitantely (à 1 500 m d'altitude) éloignées l'une de l'autre de 200 km. La diversité des espèces ligneuses de la parcelle de Manombo sur sol basaltique non seulement n'a pas été diminuée par le passage du cyclone mais, qui plus est, les espèces d'origine de cette forêt sont en train de surcimer et vont probablement remplacer l'espèce envahissante *Cecropia peltata*.

At Manombo Réserve Spéciale (23° S, 47° E), lowland rainforest occurs both on ferralitic soil of volcanic (basaltic) origin, and, just a few kilometers eastward, on white sand. Much of the forest on basaltic soil was devastated by cyclone Gretelle on 24 January 1997. In some parts of this forest the cyclone snapped or knocked over most trees over 10 m tall. Introduced *Cecropia peltata* recruited copiously in devastated areas, and seemed poised to take over the forest. In October 2005, we censused stems ≥ 5 cm dbh on two plots of approximately 0.25 ha apiece, one in devastated forest on basaltic soil, one in less damaged, intensely managed forest on white sand, to assess diversity and species composition on the two soil types. This paper centers on three questions: (1) How does soil quality affect diversity and species composition? (2) Did cyclone Gretelle diminish tree diversity in devastated areas of the reserve? (3) Is *Cecropia peltata* simply an early successional species, which more shade-tolerant native species will replace?

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Rev. Écol. (Terre Vie), vol. 62, 2007.

MATERIAL AND METHODS

STUDY AREA

The plot on volcanic soil was on Parcelle I of the Manombo Réserve Spéciale, < 2 km west of Route Nationale 12. We reached it by driving through the village of Manombo, 37 km S of Farafangana, bearing right just north of a nearby schoolhouse, following the jeep track through the gateway into the reserve, and driving about 500 m through forest to a tongue of savanna with an abundance of the invasive exotic *Psidium cattleianum*, where we parked. A path descended to a stream < 100 m away, and up a gentle, forested slope. A few hundred meters beyond the stream, we established our plot a few meters to the right of the trail.

The soil here, "sol ferralitique rouge," was shallow. It formed from basalt derived from Cretaceous lava flow. Despite the cyclone damage, the forest here was cool, shady and pleasant. There was little sign of cutting or other human disturbance near our plot, although at the top of our hill, several hundred meters further on, an agricultural field, now abandoned, had been cleared from the forest. We never saw a lemur, however, the whole time we worked in and near these plots. The neotropical invader *Cecropia peltata* was present but rare in this forest before 1995 (CSIR ORIMPAKA, 1995). Cyclone Gretelle allowed this species to spread and multiply. *Psidium cattleianum,* however, was absent from the forest.

The plot on white sand was in Parcelle II of this same reserve, east of Route Nationale 12, near the sea. To reach it, we started from an ANGAP campsite on the east side of the highway, 4 km N of Manombo village. We followed a track southeastward for 10 minutes through rolling country, grassland with scattered spiny *Strychnos madagascariensis*, past a draw filled with *Ravenala madagascariensis*. Near the sea we reached flat country. A few minutes short of the sea, we turned right and drove, seemingly cross-country, for four minutes to the edge of a forest. Here, a clear jeep track of white sand led us to the gate to Parcelle II. The nearly straight track led through the forest, which extended hardly more than 100 m to either side. The forest was intensely but carefully managed, with many cut stumps, often with one or more tree-sized resprouts from the same rootstock. The villagers clearly realized that on such poor soil, regeneration is primarily by resprouting (Riswan & Kartinawata, 1991). Unfortunately, subsistence farmers are encroaching on the forest from the two sides, leaving only a relatively narrow strip along the track. Although the white-sand plot had more than twice as many trees ≥ 30 cm dbh as its basaltic counterpart, the white-sand forest cast far less shade, thanks to the steep inclination of the leaves and the narrow, non-overlapping tree crowns.

Judging by climate data from Farafangana, 37 km north of Manombo, this forest's climate is everwet, with the driest month averaging over 100 mm of rainfall (Tab. 1). Manombo's climate is probably slightly drier than Farafangana's, but the difference probably matters little to the forest. October 2005, when we censused our plots, was quite dry. There were only three days with rain between October 4 and October 25, and the total rainfall during this period was probably less than 25 mm. In mid-October, fires burned much of the savanna east of the reserve's Parcelle I, including our parking place, but these fires hardly entered the forest. Fires also burned much of the grassland east of Route Nationale 12, but did not approach the forest of Parcelle II.

TABLE I

Monthly averages of the daily maximum temperature T_{max}, the daily minimum temperature T_{min}, and rainfall, P (mm) T/A denotes the total or average for the year

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	T/A
Tmax	29.0	29.4	28.7	27.6	26.0	24.6	23.8	23.9	24.8	25.8	27.0	28.3	26.6
Tmin	23.1	22.8	22.2	20.7	18.2	16.1	15.8	16.2	17.3	19.3	20.9	22.2	19.6
P	300	317	338	290	204	183	206	147	109	139	175	310	2717

METHODS

In Parcelle I, the plot was laid as 12 contiguous rows of ten 5 × 4 m quadrats apiece, each row extending nearly perpendicularly from the trail, but starting a few meters from it, so the plot was not visible from the trail. The plot was accordingly a 50 × 48 m rectangle (about 0.24 ha in total) of 120 5 × 4 m quadrats. In Parcelle II, the plot was laid out as ten contiguous rows of ten 5 × 5 m quadrats apiece, each row extending seaward, perpendicular to the trail. This plot, which was visible from the trail, was therefore a 50 × 50 m square (about 0.25 ha in total) of 100 5 × 5 m quadrats. All plots were laid out by tape-measure and demarcated by string: their areas were only approximately as described.

In every quadrat, each stem ≥ 5 cm in diameter at breast height (dbh, taken 1.3 m above the ground) was identified by Benja Rakotonirina, and given a temporary label with a number ranking it in order of encounter on the plot (number 1 being the first of the plot's trees to be sampled). Each censused tree had its dbh measured, its height and degree of crown exposure estimated, and its architectural model (Hallé & Oldeman, 1970, as modified by Leigh, 1999) identified where possible. Neither trees nor quadrat boundaries were permanently marked.

ANALYSES

To assess cyclone damage in our Manombo plots, we compared the distribution of diameters of stems ≥ 5 cm dbh on our plots with the distribution on a 50 × 50 m subplot of a montane forest plot (1000 m) censused at the Indri Reserve of Analamazaotra (18° 28′ S, 48° 28′ E) by Abraham *et al.* (1996). We compared the diversity and taxonomic composition of our plots with those of the aforementioned 50 × 50 m plot at Analamazaotra, and a 50 × 50 m subplot of a plot censused by Abraham *et al.* (1996) in plateau forest at 1 550 m at Ambohitantely Réserve Spéciale (18° 10′ S, 47° 17′ E). To assess how the cyclone affected tree diversity on basaltic soil at Manombo, we compared the diversity of trees ≥ 10 cm dbh on our basaltic soil plot in 2005 with the diversity of trees ≥ 10 cm dbh on a 1-ha plot censused in the same reserve before the cyclone (Rabevohitra *et al.*, 1996). To compare diversity, we used Fisher's α, a quantity which is relatively independent of sample size (Abraham *et al.*, 1996). It is calculated from the number N of trees on a plot and the number S of species among them by the formula $S = \alpha \ln(1 + N/\alpha)$ (Fisher *et al.*, 1943).

RESULTS AND DISCUSSION

Of the 777 stems ≥ 5 cm dbh sampled on our basaltic-soil plot, there were only 126 stems ≥ 10 cm dbh, 20 stems ≥ 20 cm dbh, and 10 stems ≥ 30 cm dbh. Trees ≥ 10 cm dbh were far scarcer than on the 50 × 50 m subplot at Analamazaotra, and trees ≥ 30 cm dbh were far scarcer than on the 50 × 50 m Manombo plot on white sand (Tab. II). The lower number of trees reflects destruction by the cyclone. Although six of the plot's trees ≥ 30 cm dbh were ≥ 20 m tall, two of which were 25 m tall, this plot had only 22 trees > 10 m tall. Of the remaining stems ≥ 10 cm dbh, ≤ 10 m tall, 34 had diameters that were ≥ 2% of their height, a contrast with the 1% usual for stems ≤ 10 m tall in lowland forest (Oldeman, 1974: 46-50). Of our 120 quadrats, 84 had at least one tree ≤ 6 m tall whose crown was nearly fully exposed to the sun.

TABLE II

Number of trees exceeding selected diameters, number of species among them, and Fisher's α in selected 50 × 50 m plots (Manombo I, on basaltic soil, is 50 × 48 m, or 0.24 ha; Manombo II is on white sand)

	≥ 5 cm dbh	≥ 10 cm dbh	≥ 20 cm dbh	≥ 30 cm dbh
Analamazaotra, 0.25 ha				
Number of trees	682	251	57	26
Number of species	147	96	40	21
Fisher's α	57.6	56.8	59.6	50.9
Manombo I, 0.24 ha				
Number of trees	777	126	20	10
Number of species	145	55	15	8
Fisher's α	52.5	37.2	27.3	18.5
Manombo 11, 0.25 ha				
Number of trees	453	136	33	21
Number of species	37	20	8	7
Fisher's α	9.5	6.5	3.4	3.7
Ambohitantely, 0.25 ha				
Number of trees	1 038	--	--	--
Number of species	84	--	--	--
Fisher's α	21.6	--	--	--

Although the plot on white sand showed fewer obvious signs of cyclone damage, only ten of its 453 stems ≥ 5 cm dbh were over 10 m tall. The tallest tree was only 18 m tall. Why might this be? The plot had 21 trees ≥ 30 cm dbh, a number nearly normal for its size. Trees on poor soils devote more of their resources to competing below-ground for nutrients rather than above-ground for light (Keyes & Grier, 1981; Leigh, 1999), and indeed, this forest cast little shade. As in the most nutrient-starved mangroves (Ball *et al.*, 1988), most plants here hold their stiff leaves, which are costly to replace, nearly upright, which avoids damage from overheating

(Medina *et al.*, 1978; Ball *et al.*, 1988) and excessive transpiration (Givnish, 1984). Leaves are not arranged to shade neighbours, so great height has few advantages to weigh against the greater likelihood that taller trees have of succumbing to cyclones.

Of the 777 stems ≥ 5 cm dbh censused on our volcanic-soil plot, 402, representing 55 species, were fully identified, 338 were identified to genus and sorted into 78 more species, 17 were identified to family and sorted into five species, 14 other recognizable unknowns were sorted into 7 species, and six unknowns were not classified. There were roughly 145 species, representing at least 46 families, among these 777 stems. As in the plots reported by Abraham *et al.* (1996), no one species dominated (Tab. III). Eighteen species were represented among the 22 trees > 10 m tall.

Table III

Numbers of trees (≥ 5 cm dbh), and names, of the ten commonest species on selected 50 × 50 m plots. Manombo I is a 50 × 48 m plot on basaltic soil, Manombo II is a nearby 50 × 50 m plot on white sand

Analamazaotra	Manombo I	Manombo II	Ambohitantely
69 *Blotia madagascariensis* (Euphorbiaceae)	56 *Dypsis fibrosa* (Palmae)	167 *Intsia bijuga* (Leguminosae)	83 *Podocarpus madagascariensis* (Podocarpaceae)
42 *Suregada laurina* (Euphorbiaceae)	49 *Mascarenhasia* sp. (Apocynaceae)	39 *Pandanus* sp. (Pandanaceae)	83 *Uapaca densifolia* (Euphorbiaceae)
27 *Erythroxylum corymbosum* (Erythroxylaceae)	41 *Macaranga obovata* (Euphorbiaceae)	25 *Ixora* sp. (Rubiaceae)	57 *Rhus tarentana* (Anacardiaceae)
22 *Blotia oblongifolia* (Euphorbiaceae)	40 *Cecropia peltata* (Cecropiaceae)	22 *Dicoryphe stipulacea* (Hamamelidaceae)	49 *Vaccinium* sp. (Ericaceae)
19 *Lautembergia multispicata* (Euphorbiaceae)	37 *Anthostema madagascariensis* (Euphorbiaceae)	21 *Dracaena madagascariensis* (Dracaenaceae)	48 *Micronychia tsiramiramy* (Anacardiaceae)
18 *Ocotea cymosa* (Lauraceae)	20 *Blotia hildebrandtii* (Euphorbiaceae)	18 *Rhus* sp. (Anacardiaceae)	39 *Weinmannia rutenbergii* (Cunoniaceae)
18 *Gaertnera* sp. (Rubiaceae)	20 *Uapaca densifolia* (Euphorbiaceae)	14 *Diospyros* sp. 2 (Ebenaceae)	35 *Symphonia clusioides* (Guttiferae)
17 *Cryptocarya thouvenotii* (Lauraceae)	20 *Dracaena* sp. (Dracaenaceae)	13 *Diospyros* sp. 1 (Ebenaceae)	35 *Calophyllum milvum* (Guttiferae)
16 *Polyalthia emarginata* (Annonaceae)	19 *Grewia rotunda* (Tiliaceae)	13 *Vernonia* sp. (Compositae)	31 *Evodia fatraina* (Rutaceae)
14 *Noronhia* sp. (Oleaceae)	18 *Diospyros* sp. (Ebenaceae)	12 *Rhodolaena* sp. (Sarcolaenaceae)	31 *Protorhus microphylla* (Anacardiaceae)

Of the 453 stems ≥ 5 cm dbh on our white sand plot, 249, representing 11 species, were fully identified, 197 were identified to genus and sorted into 23 species, one was identified to family, and 6 unknowns were classified into two additional species. In total, there were 37 species, representing at least 23 families, on this plot. This forest was dominated by *Intsia bijuga*: 167 of the plot's 453 stems ≥ 5 cm dbh, 91 of its 136 stems ≥ 10 cm dbh, 20 of its 33 stems ≥ 20 cm dbh, and 14 of its 21 stems ≥ 30 cm dbh, belonged to this species. Yet only four of the ten trees > 10 m tall belonged to this species. Three other species had trees taller than 13 m, the height of the tallest *Intsia* on the plot.

The cyclone did not significantly reduce the diversity of trees ≥ 10 cm dbh on Manombo I (the volcanic-soil plot). Manombo I had 55 species among 126 trees ≥ 10 cm dbh, giving a Fisher's α of 37.2; the pre-cyclone census of a 1-ha plot at Manombo found 119 trees among 787 trees ≥ 10 cm dbh, giving a Fisher's α of 39.0. This result is not surprising. In other hurricane-prone forests, devastating hurricanes do not reduce tree diversity: indeed, they sometimes increase it (Vandermeer *et al.*, 2000; Tanner & Bellingham, 2006).

Moreover, the cyclone is not allowing *Cecropia peltata* to take over the forest. There was only one *Cecropia*, 15 m tall, among the 22 trees on the basalt-soil plot that were over 10 m tall. Although there were a few *Cecropia* with much-branched, well-shaped crowns, most supported a few leaves atop an unbranched pole. *Magnistipula tamenaka* (Chrysobalanaceae) is a native species, some members of which have grown rapidly after the cyclone. One tree of this species in the plot is 17 m tall, another is 15 m tall. It appears that the Manombo forest will also master its pioneering invader.

Rubiaceae and Lauraceae were among the most speciose families on all four plots (Tab. IV). Nonetheless, the two Manombo plots differed remarkably in species composition. Of the 19 most common species on the Manombo volcanic soil plot, three, the 13th, 18th and 19th most common, also occurred on the Manombo white sand plot. Three other basaltic plot species, representing two additional genera, had congeners on the white sand plot. This difference was much greater than that between the 50 x 50 m plots at 1000 m in Analamazaotra and at 1550 m in Ambohitantely, 200 km away and 500 m higher. To be sure, only three of the 19 most common species on the Analamazaotra plot, the 9th most common, and two tied for the 11th most common, occurred on the Ambohitantely quadrat. Eleven other species on the Analamazaotra quadrat, however, representing eight additional genera, had congeners on the Ambohitantely plot. The soil differences between the two Ambohitantely plots had a most remarkable effect on their tree floras.

TABLE IV

Number of species in each of the most common families on selected 50 × 50 m plots. Manombo I is a 50 × 48 m plot on basaltic soil. Where there are two numbers separated by a slash, the first number includes lianas ≥ 5 cm dbh

Manombo 11	Manombo 1	Analamazaotra	Ambohitantely
6 Salicaceae	13 Rubiaceae	15/13 Rubiaceae	8 Rubiaceae
3 Rubiaceae	13 Salicaceae	14 Lauraceae	6 Lauraceae
2 Dracaenaceae	12 Lauraceae	11 Euphorbiaceae	5 Anacardiaceae
2 Sarcolaenaceae	12 Euphorbiaceae	11 Guttiferae	5 Guttiferae
2 Ericaceae	5 Leguminosae	7 Myrtaceae	4 Euphorbiaceae
2 Ebenaceae	5/4 Moraceae	6 Anacardiaceae	4 Myrtaceae
2 Lauraceae			
18 (in ≥ 16 other families)	86 (in ≥ 40 other families)	83/78 (in 41/39 other families)	52 (in 34 other families)

Soil differences can radically alter species composition at even smaller scales. On a 52-ha plot at Lambir Hills National Park, Sarawak, the 21 species with the most trees ≥ 20 cm dbh in a 4-ha subplot on fertile udult soil include only two of the 21 most common tree species ≥ 20 cm dbh in a 4-ha subplot on infertile humult soil (Lee *et al.*, 2002: 390-395). In Allpahuayo-Mishana National Reserve, near Iquitos, Peru, there are analogous differences between tree species composition on clay soil and that on interfingering white sand. Experiments at this reserve show that these differences in species composition are driven by the trade-off between fast growth on clay soil and survival on white sand (Fine *et al.*, 2004, 2006).

In short, tree diversity was far lower, and species composition very different, on a white sand plot at Manombo compared to a plot on basaltic soil a few km further west. Although a cyclone had severely damaged the forest on volcanic soil in January 1997, it did not reduce the forest's diversity, nor did it allow the invasive neotropical pioneer *Cecropia peltata* to take over this forest.

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