



Species Diversity, Susceptibility to Disturbance and Tree Population Dynamics in Tropical Rain Forest

Author(s): David F. R. P. Burslem and Timothy C. Whitmore

Source: *Journal of Vegetation Science*, Vol. 10, No. 6 (Dec., 1999), pp. 767-776

Published by: Opulus Press

Stable URL: <http://www.jstor.org/stable/3237301>

Accessed: 26/08/2008 05:31

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=opulus>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

# Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest

Burslem, David F.R.P.<sup>1\*</sup> & Whitmore, Timothy C.<sup>2</sup>

<sup>1</sup>Department of Plant and Soil Science, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, UK;

<sup>2</sup>Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK

\*Author for correspondence; Fax +441224272703; E-mail d.burslem@abdn.ac.uk

**Abstract.** In 1964 a census of all trees > 9.7 cm diameter at breast height (DBH) was conducted on 22 plots totalling 13.2 ha in lowland tropical evergreen rain forest on Kolombangara, Solomon Islands. Over the following 30 yr (1964-1994), populations of all individuals > 4.85 cm DBH of the 12 most common tree species and amounts of disturbance have been monitored on a declining number of these plots (in 1994, nine plots totalling 5.4 ha were still being recorded). Between November 1967 and April 1970, Kolombangara was struck by four cyclones, although only two of these caused substantial amounts of damage to the canopy structure. Multivariate analysis has identified six forest types on Kolombangara (Greig-Smith et al. 1967). The species richness and diversity of trees in the 1964 census, turnover rates of the populations monitored over 1964-1975, and the amount of disturbance sustained during a cyclone in 1970, were all positively correlated across five of the forest types. The sixth forest type was a consistent outlier in these analyses and is believed to have been seriously disturbed by humans about a century ago. The floristics, turnover and disturbance data support Connell's intermediate disturbance hypothesis. The most species-rich forest types contained a higher proportion of fast-growing individuals and species that are early-successional and which have low density timber. Properties of these species rendered them more susceptible to damage when struck by the 1970 cyclone. They showed higher turnover rates because disturbance-dependent species are also characterised by higher mortality and recruitment rates. Thus, periodic cyclones appear to favour the maintenance of differences in species diversity and composition between forest types.

**Keywords:** Anthropogenic impact; Cyclone; Forest dynamics; Intermediate disturbance hypothesis; Large-scale disturbance; Solomon Islands.

**Nomenclature:** Stevens (1980) for *Calophyllum*; Prance (1987) for *Parinari*; M.J.E. Coode (pers. comm.) for *Elaeocarpus* and Whitmore (1966) for all other genera.

## Introduction

The interpretation of relationships between turnover rates and tree diversity in tropical rain forests has been

the subject of a recent lively debate (Phillips et al. 1994, 1997; Sheil 1996, 1997, 1999a). The controversy was triggered by a pan-tropical comparison of forest dynamics and tree species richness from permanent plot data (Phillips et al. 1994), which found a higher turnover (the mean of mortality and recruitment rates) associated with greater richness (measured as species per 500 stems). Phillips et al. (1994) concluded that the different turnover rates (thus 'small-scale disturbance') determined differences in community species richness, and that species richness may be at an equilibrium in the forests they studied (Phillips et al. 1997).

We have recently reviewed studies of tropical forest composition and dynamics (Whitmore & Burslem 1998) and questioned whether the composition of any tropical forests studied has not been influenced more by large-scale than small-scale disturbance events. In addition, Sheil (1996, 1997) has recently pointed out that cause and effect are difficult to disentangle using permanent plot studies, and has invoked Connell's (1978) intermediate disturbance hypothesis as one explanation of the positive relationship between turnover rates and species richness observed by Phillips et al. (1994). Connell's hypothesis proposes that diversity will be maximal in communities or stands at the mid-point of succession, or where disturbance occurs at intermediate frequencies or intensities. According to Connell, early-successional communities, or early-successional patches within communities, are dominated by a species-poor assemblage of light-demanding pioneers, which are progressively superseded by shade-tolerant species; diversity eventually declines as these totally replace the pioneers. Thus species richness is not at equilibrium at the spatial scale corresponding to the scale of the typical disturbance regime. In tropical rain forests, it is well known that species differ in the extent of canopy disturbance in which they successfully regenerate (Whitmore 1974, 1984; Denslow 1987; Swaine & Whitmore 1988) and it is likely that all local tropical forest species pools include some species requiring strong disturbance.

Species that depend on strong disturbance have higher turnover (recruitment and mortality) than others (e.g. Manokaran & Kochummen 1987; Swaine et al. 1987; Swaine & Whitmore 1988; Sheil 1996). Forests with sufficient disturbance for these species to co-exist with others are therefore bound to have a higher turnover and to be more species-rich than forests with lesser disturbance in which they cannot exist. One reason for the high mortality of species requiring strong disturbance is their weaker timber or low density (Swaine & Whitmore 1988; Burslem & Whitmore 1996a). This makes them particularly prone to mortality in the face of disturbance.

To our knowledge, the intermediate disturbance hypothesis has not been addressed explicitly in tropical rain forests, except for the Ugandan forests studied by Egging (1947) which provided one of the case studies on which it was based (Connell 1978). The Ugandan Budongo forest contains a series of vegetation types which Egging (1947) interpreted as a successional sequence reflecting time since first colonisation of grassland. Multivariate analysis of the original data supports this hypothesis, but changes in tree species composition since the 1930s, when measurements began, mostly do not (Sheil 1999b). The end-point of the Budongo succession proposed by Egging (1947) is a species-poor monodominant forest containing a very high abundance of *Cynometra alexandri*. So-called 'monodominant' forests have now been described from all the tropical regions (Connell & Lowman 1989; Hart et al. 1989). In most cases, the tree species diversity of these forests is markedly lower than nearby 'mixed' forests, which led Connell (1978) to propose that they are examples of late-successional communities in which species diversity has declined as a result of competitive exclusion. According to this model, adjacent species-rich communities represent an earlier stage in succession and are not, therefore, at equilibrium.

Thus, there are two alternative views on the factors that determine species richness in relation to disturbance. High richness is correlated with high turnover, but this either depends on local factors intrinsic to each forest type and is in equilibrium (Philips et al. 1994, 1997) or, alternatively, is a consequence of an external stochastic disturbance in the not too distant past from which the forest is recovering and is not in equilibrium (Connell 1978).

The two views can best be tested by local comparisons, i.e. where there are unlikely to be inter-site differences in the pool of available species. According to the non-equilibrium model, the more species-rich forests ('stands' or 'communities') will have experienced a more recent or greater intensity or frequency of large-scale disturbance, and differences in species composition

should reflect these varying histories (assuming that the disturbance event was not so recent that the sample is dominated by pioneers).

We are able to test some of these predictions using data from a study of the dynamics and response to disturbance for tree populations on replicated permanent sample plots in tropical rain forest in the Solomon Islands (Whitmore 1974, 1989; Burslem & Whitmore 1996b; Burslem et al. 1998). In this study, all trees greater than one foot girth (9.7 cm DBH) were censused in 1964. These data were used to identify forest types defined by floristic criteria and to characterise the tree species richness and diversity of those forest types (Greig Smith et al. 1967). The populations of the 12 most abundant tree species on the plots have been re-censused periodically, along with semi-quantitative scoring of disturbance. These data were used to determine turnover rates of the monitored populations and the rates of disturbance to the forest types. Kolombangara was struck by four cyclones over the interval 1967-1970, i.e. 3-7 yr from the start of the study. Therefore we are also in a position to relate the tree species richness and diversity of forest types at the start of the study to the amounts of damage sustained by them in response to cyclone impact. Since damage and disturbance are the driving forces for the dynamics of populations and communities, we also investigate the relationships between initial tree species richness and diversity, and rates of mortality, recruitment and turnover over the following decade. Therefore this paper addresses the following questions.

1. What variation is there between forest types on Kolombangara in measures of tree diversity and stand dynamics (i.e. on a spatial scale of 100-20 000 m<sup>2</sup>)?
2. Is this tree diversity related to the amount of damage sustained by the forest canopy during a large-scale disturbance event?
3. Is tree diversity also related to measures of stand dynamics as was found, in a different context, by Phillips et al. (1994)?
4. Is the amount of disturbance intrinsic to each forest type and caused internally by treefall or death or does it result from extrinsic factors that can be regarded as stochastic?

### Study site and species

The study site is the island of Kolombangara (8° S, 157° E) in the Western Province of the Solomon Islands, Southwest Pacific. Kolombangara is an extinct Pleistocene volcano of nearly circular outline and rises from sea level to 1420-1580 m a.s.l. on the rim of the crater. Kolombangara has an aseasonal climate, with mean

annual rainfall at the coast ca. 3150 mm, probably increasing inland, and no month having a long-term mean of < 170 mm (Neumann 1986 and unpublished data). Mean daily temperature on the nearby island of New Georgia varied between 23.4 °C (in August) and 26.1 °C (in December) over the interval 1962-1985 (Neumann 1986). The rocks underlying most of the island and all of the plots discussed in this paper are olivine basalt breccias and lavas (Anon. 1984). The soils are described by Hansell & Wall (1975), with further data in van Baren (1961), Lee (1969) and Burslem & Whitmore (1996b). Topsoils are acidic (pH-H<sub>2</sub>O mostly 4.1-5.3 at 0-31 cm; n = 24) and have low total N concentrations.

The natural vegetation of lowland (< 300 m.a.s.l.) Kolombangara is tropical lowland evergreen rain forest *sensu* Whitmore (1984). Lowland evergreen rain forests in the western Solomon Islands have a lower tree species richness than equivalent tropical rain forests in Malaysia to the west (Whitmore 1974). Descriptions of the vegetation are given by Whitmore (1974, 1989). The 12 most common big tree species were selected for study following a preliminary census in 1964 (see below). They are:

- |  |                                |
|--|--------------------------------|
| <i>Calophyllum neo-ebudicum</i>                  | <i>Calophyllum peekelii</i>    |
| <i>Camposperma brevipetiolatum</i>               | <i>Dillenia salomonensis</i>   |
| <i>Elaeocarpus angustifolius</i>                 | <i>Endospermum medulosum</i>   |
| <i>Gmelina moluccana</i>                         | <i>Maranthes corymbosa</i>     |
| <i>Parinari papuana</i> ssp. <i>salomonensis</i> | <i>Pometia pinnata</i>         |
| <i>Schizomeria serrata</i>                       | <i>Terminalia calamansanai</i> |

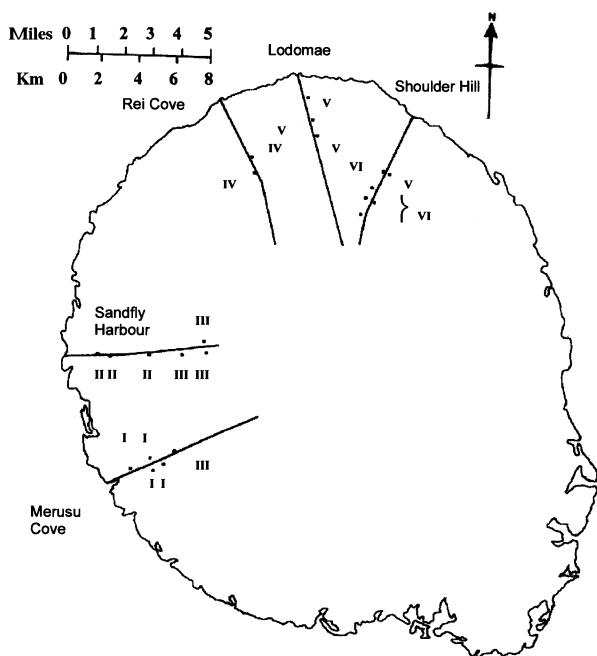
Their ecological and silvicultural characteristics are described in detail by Whitmore (1966, 1974, 1989) and Burslem & Whitmore (1996b).

**Methods**

In 1964, 22 plots of 5 × 3 chains (ca. 100 m × 60 m) were established along five access lines striking inland from the north and west coasts of Kolombangara, making a total area of 13.2 ha (Fig. 1). Plots were located either on flat land (plateaux or ridges: nine plots), on slopes (seven plots), in valleys (three plots) or on mixed topography (three plots). Each plot was divided into 15 subplots of 1 × 1 chain (ca. 20 m × 20 m), and in mid-1964 all trees > 9.7 cm DBH were censused on the resulting 110 subplots. These data were classified using a combination of association analysis and ordination by Principal Components Analysis (Greig-Smith et al. 1967), which identified a major distinction between a group of mainly west-coast subplots containing *Teysmanniodendron ahernianum* and *Dillenia salomonensis* and the remaining north coast subplots lacking these species. The association analysis identified six spatially-segregated forest types which are defined on floristic grounds, and ordination exposed differentiation within them with respect to altitude and topography (Greig-Smith et al. 1967). The analyses presented in this paper were conducted using the same 22 plots examined by Greig-Smith et al. (1967), and the six forest types we recognise are those identified by these earlier analyses.

The 12 most common big tree species on these plots were identified from the one-foot-girth census, and it is the populations of these species which were selected for study over the following 30 yr. Their mean densities in the six forest types in 1964 are indicated in Table 1. In August 1964 the populations of all stems > 4.9 cm DBH of these 12 species were measured and permanently tagged on all plots. Re-censuses were conducted in October 1965, March and August 1966, February and August 1967, February and August 1968, February 1971, September/October 1975 and on five additional occasions up to 1994. On each occasion, surviving stems were re-measured, dead individuals noted and new recruits recorded. One plot could not be relocated after a cyclone in November 1967; otherwise, the number of surviving plots did not change between 1964 and 1975 (the focus of this paper), although a further 12 plots were logged or abandoned between 1975 and 1994.

On five occasions between August 1966 and February 1994 all surviving plots were mapped according to phase of the forest growth cycle, on a three point scale named as gap, building and mature phases by Whitmore (1984). A subsample of plots were scored for forest



**Fig. 1.** Kolombangara: location of plots and forest types of the Kolombangara Ecological Survey (after Whitmore 1974).

**Table 1.** Mean abundance (stems/ha > 9.7 cm DBH) of the 12 common big tree species in six different forest types on Kolombangara with their location on west (W) or north (N) coasts, altitudinal range (m a.s.l.), and topographies of individual plots (R = ridge; P = flat plateau; S = sloping hillside; V = valley bottom; S/V and P/S = mixed topography; R-V = catena from ridge to valley). Source: Greig-Smith et al. (1967); Whitmore (1974).

Coast	Forest type					
	I W	II W	III W	IV N	V N	VI N
Altitude (m)	60 - 220	60 - 170	250 - 360	160 - 200	50 - 160	310 - 420
Topography	S/V, P, P, P	S, P, S	S, P, P/S, V	R-V, S, P	V, P, P, P	S, S, S, V
<i>Calophyllum neo-ebudicum</i>	0.5	2.3	0.8	13.8	3.0	9.0
<i>Calophyllum peekelii</i>	7.0	8.3	3.0	13.8	8.8	0.0
<i>Campnosperma brevipetiolatum</i>	10.3	21.8	15.0	11.3	0.0	4.5
<i>Dillenia salomonensis</i>	30.0	6.8	8.3	0.0	0.0	0.0
<i>Elaeocarpus angustifolius</i>	0.0	0.5	0.0	7.5	2.3	0.8
<i>Endospermum medullosum</i>	0.0	0.5	0.0	2.3	5.8	5.3
<i>Gmelina moluccana</i>	2.3	0.5	2.0	4.5	1.0	4.5
<i>Maranthes corymbosa</i>	0.0	3.3	0.5	6.0	1.3	1.3
<i>Parinari papuana</i>	7.0	11.3	4.3	9.0	9.8	5.8
<i>Pometia pinnata</i>	0.5	0.0	0.0	4.5	2.8	2.5
<i>Schizomeria serrata</i>	2.3	1.0	3.8	4.5	0.5	6.5
<i>Terminalia calamansanai</i>	0.0	3.3	0.5	6.0	12.3	16.0

phase in August 1968 or March 1969, but these incomplete records are not treated in this paper. The data we present here are derived from the forest phase maps of all 21 plots made in early April 1970 and in February 1971, which spans the impact of cyclone Isa on 17 April 1970. On these occasions, one assessment was made per 20 m × 20 m subplot (15 per plot). Disturbance is defined as 'percent reversion through the forest growth cycle between April 1970 and February 1971', i.e. subplots recorded as mature or building phase in 1970 and as gap phase in 1971 or as mature phase in 1970 and either building or gap phase in 1971 are classified as having been disturbed during that interval.

### Analytical procedures

Species richness and mean annual rates of mortality ( $mt$ ) and recruitment ( $rc$ ) were estimated according to the equations presented by Sheil et al. (1995) and Sheil (1998) respectively.

$$mt = 1 - (1 - (N_0 - N_1)/N_0)^{1/t} \quad (1)$$

and

$$rc = 1 - (1 - n_{rc}/N_1)^{1/t} \quad (2)$$

where  $N_0$  and  $N_1$  are the total numbers of stems at the beginning and end of interval  $t$ , and  $n_{rc}$  the number of new recruits during that interval. Turnover is defined as the mean of  $mt$  and  $rc$  over a given interval. An analogous formulation was used for estimating mean annual

rates of canopy disturbance,  $ds$ , during interval  $t$ :

$$ds = 1 - (1 - (N_0^* - N_1^*)/N_1^*)^{1/t} \quad (3)$$

where  $N_0^*$  is the number of sample units per plot and  $N_1^*$  the number of sample units which were not disturbed during the interval. These equations assume constant probabilities of stem loss, stem gain or disturbance during the interval.

Species diversity per plot was expressed as values of Fisher's  $\alpha$  (Fisher et al. 1943). In a recent evaluation of tropical forest data sets this diversity index has been shown to be less sensitive to sample size than other commonly-used indices (Condit et al. 1996, 1998). It is defined by:

$$S = \alpha \ln(1 + N/\alpha) \quad (4)$$

where  $S$  is the number of species and  $N$  the total number of stems on the plot. Values of  $\alpha$  were estimated from  $N$  and  $S$  using the programme presented by Condit et al. (1998). Across the range of values of  $N$  in this study (193-352 stems per plot) there was no significant relationship between  $N$  and  $\alpha$  ( $F = 0.67$ ,  $P = 0.422$ ,  $n = 22$  plots) or between  $\log N$  and  $\log \alpha$  ( $F = 0.70$ ,  $P = 0.412$ ,  $n = 22$ ), so we have not corrected values of  $\alpha$  to a common sample size as recommended by Condit et al. (1998) for samples of this size.

Values of  $mt$ ,  $rc$ ,  $ds$  and  $\alpha$  were computed for each plot over various intervals or censuses as described below, and mean values compared between the six forest types identified for these 22 plots (three or four

plots per forest type). All correlation coefficients reported are Pearson product-moment correlation coefficients.

## Results

### Floristic variation

Greig-Smith et al. (1967) identified six forest types on Kolombangara. Three of these were distributed on the north coast and three on the west coast (Fig. 1). The mean stem density per ha of stems > 9.7 cm DBH of the 12 most common big tree species on the six forest types is shown in Table 1. The main factor which distinguishes the west coast from the north coast forest types is the presence of *Dillenia salomonensis* in the former, sometimes at very high abundance, and its complete absence from the latter. *Camposperma brevipedunculatum* was also very abundant on the west coast, with a mean density there which varied inversely with that of *Dillenia salomonensis* at the level of forest type. Forest types I and II represented the extremes of the floristic variation on the west coast with an average of 50 % and 11 % of all stems > 9.7 cm DBH made up by *Dillenia*, and 17 % and 37 % by *Camposperma* respectively. Most species were on average much more common in north-coast forests (*C. neo-ebudicum*, *C. peekelii*, *Elaeocarpus*, *Endospermum*, *Maranthes*, *Parinari*, *Pometia*, *Schizomeria*, *Terminalia*) and, when present on the west coast, most abundant in forest type II. There is physical evidence of the presence of former human settlements close to the plots of forest type VI, and floristic evidence that this forest type is part of an old secondary forest which has established on agricultural land abandoned ca. 100 yr ago (Whitmore 1974; Burslem & Whitmore 1996b).

### Species richness and diversity of big trees in 1964

For stems > 9.7 cm DBH at the 1964 census there were a mean of 51 species (range 31 - 68) and 275 stems (range 193 - 352) per 0.6 ha plot on Kolombangara.  $\alpha$  had a mean value of 19.0 (range 8.4 - 32.5) on these plots. North and west coast plots did not differ significantly for either species number ( $F = 2.23$ ;  $P = 0.151$ ) or  $\alpha$  ( $F = 0.24$ ;  $P = 0.632$ ). However, both diversity measures differed significantly between forest types (Table 2). Plots of forest types I and III (both west coast) had a significantly lower mean species number and  $\alpha$  than plots of forest type II (also west coast). Forest type II did not differ significantly from any of the three north coast forest types in these two diversity measures.

**Table 2.** Mean (and standard error) number and diversity (Fisher's  $\alpha$ ) of tree species > 9.7 cm dbh on 0.6 ha plots in 1964, and rates of canopy disturbance (% plot area yr<sup>-1</sup>) between April 1970 and February 1971, for six forest types on Kolombangara, Solomon Islands. The number of replicate plots within each forest type is indicated by n, and degree of significance (variance ratios following analysis of variance) as follows: \* =  $P < 0.05$ ; \*\*\* =  $P < 0.001$ .

Forest type	n	Species number	Fisher's $\alpha$	Canopy disturbance
I	4	42.5 (0.96)	14.9 (0.28)	53.4 (5.04)
II	3	61.7 (0.88)	27.9 (2.39)	91.2 (6.02)
III	4	43.3 (4.09)	14.6 (2.11)	53.6 (17.9)
IV	3	55.3 (5.81)	19.8 (2.93)	79.5 (9.39)
V	3	51.0 (2.80)	18.3 (1.24)	80.9 (7.49)
VI	4	55.8 (5.65)	20.5 (2.78)	51.4 (5.36)
F		3.63 *	5.04 ***	2.80 ( $P = 0.056$ )

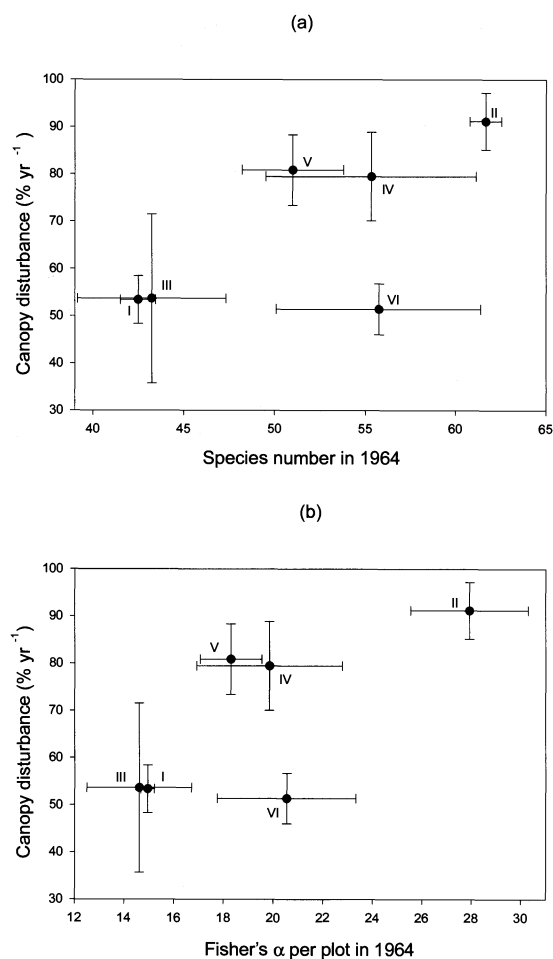
### Relationship between diversity and disturbance

The fourth cyclone to influence Kolombangara during the study period (cyclone Isa in April 1970) caused the greatest amounts of canopy damage to forests on the plots and will be used here as an index of susceptibility to disturbance between geographic locations and forest types. Canopy damage records spanning the three earlier cyclones are less complete (see Methods).

The mean percentage of plot area which reverted through the forest growth cycle between April 1970 and February 1971 did not vary significantly ( $F = 0.22$ ;  $P = 0.64$ ) between north coasts (mean 69 % of plot area/yr) and west coasts (mean 64 % of plot area/yr), but the differences between forest types (Table 2) were only marginally non-significant ( $F = 2.80$ ,  $P = 0.056$ ). Forest-type mean values for the rates of canopy disturbance to forest types over this interval varied across the range 51 - 91 % plot area/yr (Fig. 2). If all six forest types are compared, mean rates of canopy disturbance were not significantly correlated with mean species number ( $r = 0.685$ ;  $P > 0.05$ ) or  $\alpha$  among stems > 9.7 cm DBH at the 1964 census ( $r = 0.714$ ;  $P > 0.05$ ). However, the values for the secondary forest, type VI, are clear outliers on these plots, and if this point is ignored the positive correlations between disturbance and both species richness ( $r = 0.959$ ;  $P < 0.01$ ) and  $\alpha$  ( $r = 0.881$ ;  $P < 0.05$ ) are highly significant (Fig. 2).

### Relationship between diversity and dynamics

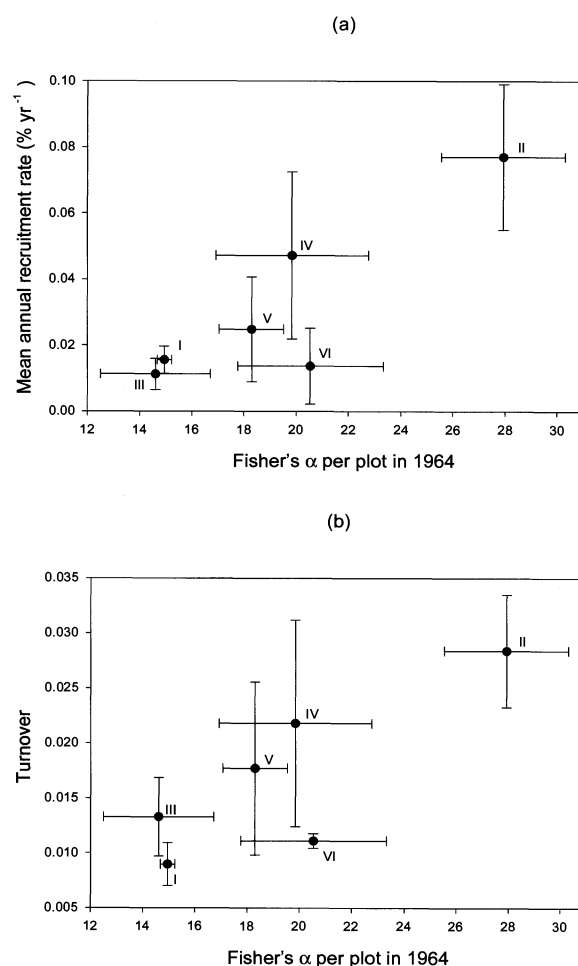
Percentage mortality of the 12 most common big tree species varied significantly between forest types both over the interval 1964-1975 and the interval span-



**Fig. 2.** Scatterplot of mean and standard error rate of (a) canopy disturbance (% plot area/yr) between April 1970 and February 1971 against number of tree species > 9.7 cm DBH in 1964 and (b) rate of canopy disturbance (% plot area/yr) between April 1970 and February 1971 against Fisher's  $\alpha$  for tree species > 9.7 cm DBH in 1964 for six forest types on Kolombangara. Roman numerals correspond to forest types I - VI in Table 1.

ning cyclone Annie in November 1967 (Table 3). The percentage of new recruits between 1971 and 1975 also differed significantly between forest types.

The forest-type mean number and diversity of tree species on a plot did not correlate significantly with mean annual mortality rates of the 12 most common big tree species over the interval 1964-1975 or during the peak of mortality which accompanied the impact of cyclone Annie in November 1967 (Table 4). However, forest-type mean annual recruitment rates of these 12 species were positively correlated with the number and diversity of all trees in 1964, particularly when the



**Fig. 3.** Scatterplot of mean and standard error (a) mean annual recruitment rate (%/yr) between 1971 and 1975, and (b) turnover (mean of mortality and recruitment rates) between 1964 and 1975, against Fisher's  $\alpha$  for tree species > 9.7 cm DBH in 1964 for six forest types on Kolombangara. Roman numerals correspond to forest types I - VI in Table 1.

**Table 3.** Mean (and standard error) annual rates (%/yr) of mortality (*mt*) 1964-1975 and during the interval spanning the impact of cyclone Annie in November 1967 (August 1967-February 1968), and recruitment (*rc*) 1971-1975 for 12 tree species in six forest types on Kolombangara. *n* = number of replicate plots within each forest type; significance levels (*G* statistic): \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ .

Forest type	<i>n</i>	<i>mt</i> (1964 - 1975)	<i>mt</i> (cyclone Annie)	<i>rc</i> (1971 - 1975)
I	4	1.14 (0.25)	5.12 (2.83)	1.56 (0.41)
II	3	2.32 (0.04)	24.10 (6.85)	7.70 (2.20)
III	4	1.98 (0.51)	15.68 (2.99)	1.12 (0.47)
IV	3	2.26 (0.75)	12.60 (9.43)	4.72 (2.53)
V	3	2.38 (0.84)	1.90 (10.10)	2.48 (1.58)
VI	4	1.58 (0.40)	4.77 (1.65)	1.37 (1.15)
<i>G</i> <sub>adj</sub>		13.0 *	20.5 **	71.5 ***

outlying values for forest type VI are excluded from the data-set (Table 4, Fig. 3a). Mean turnover rates (the mean of mortality and recruitment) between 1964 and 1975 were also positively correlated with richness and diversity of trees in 1964 (Fig. 3b).

## Discussion

### *Limitations of the data*

These data were not collected originally to answer the questions we have posed in this paper. One major difficulty lies with the use of measures of ‘diversity’ and ‘dynamics’ drawn from non-coincident populations of trees on the plots. Diversity was measured by the original census of all trees greater than 9.7 cm DBH in 1964, while estimates of dynamics during 1964-1975 (mortality, recruitment and turnover) were drawn from the populations of stems > 4.9 cm DBH of only the 12 most abundant big tree species. Our interpretation assumes that community-level estimates of dynamic processes are highly correlated with our estimates for the 12 most abundant species. The validity of this assumption rests on the proportion of all stems which are represented by the 12 study species and the absence of a systematic bias between representation of these species and either diversity or dynamic rates. At the 1964 census, the 12 species represented 12.7 - 69.3 % (mean 42.0 %) of the basal area of trees > 9.7 cm DBH and 22.8 - 100 % (mean 72.2 %) of trees greater than 70 cm diameter. Although the proportion of total basal area of stems greater than one foot girth in 1964 represented by the 12 most common big tree species did differ significantly between forest types ( $F = 2.95, P = 0.047$ ), there was no relationship between that proportion and

any of the diversity or dynamics variables examined in this paper ( $P \gg 0.05$ ). We conclude that differences between forest types in representation of the 12 common species does not introduce a systematic bias into our comparison of diversity and turnover measures.

### *Relationships between diversity, disturbance and dynamics*

Tree diversity in 1964, amounts of canopy disturbance during a cyclone in 1970, and rates of community dynamics during 1964-1975 were all positively correlated among ‘primary’ forest types on Kolombangara (Table 4, Figs. 2 and 3). Mean values for turnover rates (‘dynamism’ of Phillips et al. 1994) varied almost as much between the six forest types on Kolombangara over the study interval (0.9 - 2.8 %/yr, Fig. 3b) as in the pantropical collection of sites compared by Phillips et al. (0.5 - 2.8 %/yr), and, as in their study, correlated positively with a measure of tree species diversity. This demonstrates that a positive relationship between turnover rate and species diversity may be manifested in comparisons across a wide range of spatial scales in tropical forest communities.

Two general classes of mechanisms might account for these patterns, which reflect different perspectives on the importance of historical versus contemporary factors in the determination of tree species richness, and would have different implications for the equilibrium status of forests which manifest a positive relationship between turnover rates and species diversity. One hypothesis is that differences in species richness are maintained by small-scale disturbance events, whereby local differences in soils, altitude or topography generate faster turnover rates in some forest types than others and enable a greater number of species to coexist in the ‘more dynamic’ forest types (Phillips et al. 1994). This is equivalent to the hypothesis that “species-rich forests can experience lengthy phases during which they are at equilibrium with respect to species-richness” (Phillips et al. 1997), although the context is different to that for which this statement was framed.

An alternative hypothesis is that the suite of forest types are recovering from large-scale disturbance and represent stands at different successional stages, whereby the most diverse are approximately mid-successional forests destined to lose species diversity over time as the late-successional species (e.g. on Kolombangara *Dillenia salomonensis*) become increasingly dominant (Connell 1978; Sheil 1996). This is equivalent to invoking the intermediate disturbance hypothesis and a non-equilibrium view of the maintenance of species diversity.

Which of these hypotheses is supported by this study? The positive relationship found between tree species

**Table 4.** Pearson product-moment correlation coefficients comparing forest-type mean annual rates of canopy disturbance (*ds*), mortality (*mt*), recruitment (*rc*) or turnover (*to*) over various intervals with forest-type mean species number and Fisher’s  $\alpha$  for trees on plots in 1964 (correlations excluding forest type VI in parentheses). Sample size is six forest types (five forest types for values in parentheses). Significance levels: + =  $P < 0.1$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

	Number of species per plot in 1964	$\alpha$ per plot in 1964
<i>ds</i> (cyclone Isa, 1970)	0.685 (0.959 **)	0.714 (0.881 *)
<i>mt</i> (1964-1975)	0.549 (0.720)	0.489 (0.575)
<i>mt</i> (cyclone Annie, 1967)	0.389 (0.674)	0.491 (0.675)
<i>rc</i> (1971-1975)	0.779 + (0.961 **)	0.875 * (0.980 **)
<i>to</i> (1964-1975)	0.768 + (0.984 **)	0.819 * (0.945 *)



diversity in 1964 and the amount of canopy disturbance during the April 1970 cyclone (Fig. 2) is a prediction of the intermediate disturbance hypothesis. The most diverse forest types on Kolombangara contain a greater abundance of individuals and species with a disturbance-dependent assemblage of life-history characteristics, such as a fast growth rate and low timber density. Among the 12 common big tree species on Kolombangara there is a significant negative relationship between wood density and diameter growth rates (Burslem & Whitmore unpubl.), and similar trends have been found in other tropical forests (Swaine & Whitmore 1988). If low-density timber is a risk factor for windstorm damage and mortality (as has been found for forest trees in Panama and Puerto Rico, Putz et al. 1983; Zimmerman et al. 1994), then we would expect a forest containing a higher proportion of these species to suffer greater amounts of damage during a cyclone.

On Kolombangara the most diverse forest types (II and IV) contained the greatest abundance of species and individuals with low-density timber, such as *Campnosperma*, *Elaeocarpus* and *Endospermum* (Table 1). By contrast, the least-affected and least diverse forest type (I) was very heavily dominated by the heavy hardwood timber species *Dillenia salomonensis*.

Therefore the diversity-disturbance relationship (Fig. 2) provides a potential mechanism for the diversity-dynamics relationship (Fig. 3). Forests which are more heavily disturbed suffer greater rates of mortality in the short-term and then higher recruitment rates during the recovery phase. These relationships arise because mortality and recruitment rates are correlated across plots and across species (Burslem & Whitmore unpubl.). A positive relationship between mortality and recruitment rates across canopy tree species has also been found at the Pasoh forest reserve, Peninsular Malaysia, during a period when large-scale disturbance events did not occur (Okuda et al. 1997; cf. He et al. 1997 on tree diversity in this forest).

However, the intermediate disturbance hypothesis is not supported uniformly by the Kolombangara data. Forest type VI is a clear outlier in its susceptibility to disturbance and the dynamics of tree populations: canopy disturbance rates in 1970, and recruitment and turnover rates of trees, were much lower for its mean species richness and diversity than in the other forest types (Figs. 2 and 3). We have suggested elsewhere that this forest type has regrown on land formerly settled and possibly cultivated until ca. 100 yr ago (Whitmore 1974; Burslem & Whitmore 1996b), in which case it must be regarded as an old secondary forest. Part of the evidence supporting this conclusion is that a group of species known to be characteristic of highly disturbed or secondary forests (*Caryota rumphiana*, *Cyathea alta*,

*Elaeocarpus floridanus*, *E. angustifolius*, *Euodia* spec., *Fagraea racemosa*, *Gmelina moluccana*, *Macaranga polyadenia* and *Mallotus floribundus*) were most abundant in forest type VI (Greig-Smith et al. 1967; Whitmore 1974). It is therefore paradoxical that these forests were not more susceptible to cyclone disturbance. We suggest that the answer lies in the characteristics of *Terminalia calamansanai*, which is the most abundant big tree species on plots of this forest type (Table 1). This species is not regenerating *in situ*, and is presumed to have established following a very large-scale disturbance event, such as cultivation (Whitmore 1974). It has large buttresses as an adult tree, medium density timber and is very resistant to cyclones (Burslem & Whitmore 1996b), which might account for the apparent resistance of the forest type to cyclones (Fig. 2). Therefore, not all strongly light-demanding or pioneer species, and not all (relatively) early-successional forests, respond to disturbance in the manner predicted by our current understanding of life-history differences among tropical forest trees. These observations support the suggestion that the characteristics of dominant individual species, as well as species diversity, might be an important determinant of community-level processes (Wardle et al. 1997). It is also clear from these analyses that the two 'large-scale disturbance factors' to which the forests on Kolombangara have been exposed (anthropogenic effects and cyclones) have very different effects on the composition and dynamics of disturbed forests.

These data highlight the need to distinguish between processes generating differences in species diversity and those which maintain them, as pointed out by others (e.g. Whitmore 1984; Denslow 1987). For example, it is certainly possible that subtle differences in altitude, topography, soils and human impact, acting on ecological time-scales, were sufficient to generate the range of floristic and diversity differences observed among the forests on Kolombangara in 1964. Whether or not these forests were at an 'equilibrium' with respect to their environmental conditions at that time (the evidence for forest type VI at least is that it was not), the effect of cyclones would have been to *maintain* the floristic differences rather than re-set the succession across the entire island.

Two conclusions arise from our interpretation of the Kolombangara data. The first is that differential exposure to cyclones is unlikely to have been the factor which *created* the initial differences in floristic composition across the island. The implications of this finding for our understanding of cyclone-impacts elsewhere, and the significance of other large-scale disturbance factors, need to be examined. Secondly, the high diversity primary forests were inherently less resistant to disturbance (Fig. 2), but potentially more resilient (Fig. 3). It may be that, in the presence of cyclones, diversity

maintains diversity, while the dominant species of some low-diversity forests create the conditions which permit their continued dominance. Thus, in summary, on Kolombangara, major external disturbance maintains differences in species diversity between forest types, by favouring the maintenance of the status quo.

**Acknowledgements.** The Kolombangara Ecological Survey has been maintained as a research project of the Solomon Islands Forest Division for 30 years. We thank the Commissioner for Forests, the Meteorological Bureau, Brisbane, and the Solomon Islands Meteorological Service for access to unpublished data; the late Aiden Beveni, Simeon Iputu and Nixon Denmark for facilitating fieldwork in 1994; Sonter Chite, David Babala, Nixon Denmark, Rojer Fogert, Timothy Ohawere and Francis Paekolo for field assistance in 1994; and numerous individuals for contributions to previous phases of the project. Funding for the 1994 enumeration was provided by a grant to ABW Associates Ltd from the Forestry Research Programme of the UK Department for International Development, and for previous enumerations by the National Geographic Society and the Solomon Islands Government. We are grateful to Prof. Tohru Nakashizuka and two anonymous referees for comments on a previous draft of this manuscript, and to Dr. Douglas Sheil for permission to cite his unpublished work.

## References

- Anon. 1984. *Kolombangara, Kohinggo and Parara Islands*. New Georgia Geological Map Sheet NG3 1:100000, Geological Survey Division, Ministry of Land, Energy and Natural Resources, Honiara, Solomon Islands.
- Burslem, D.F.R.P. & Whitmore, T.C. 1996a. *Silvics and wood properties of the common timber tree species on Kolombangara*. Tropical Forestry Papers 34 and Solomon Islands Forest Record 7, Oxford Forestry Institute, Oxford.
- Burslem, D.F.R.P. & Whitmore, T.C. 1996b. A long-term record of forest dynamics from the Solomon Islands. In: Turner, I.M., Diong, C.H., Lim, S.S.L. & Ng, P.K.L. (eds.) *Biodiversity and the dynamics of ecosystems*, pp. 121-131. DIWPA Series Vol. 1. DIWPA, Kyoto.
- Burslem, D.F.R.P., Whitmore, T.C. & Denmark, N. 1998. A thirty-year record of forest dynamics from Kolombangara, Solomon Islands. In: Dallmeier, F. & Comiskey, J.A. (eds.) *Forest biodiversity research, monitoring and modelling. Conceptual background and Old World case studies*, pp. 633-645. UNESCO and Parthenon, Paris and Carnforth.
- Condit, R., Hubbell, S.P., LaFrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B. & Ashton, P.S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *J. Ecol.* 84: 549-562.
- Condit, R., Foster, R.B., Hubbell, S.P., Sukumar, R., Leigh, E.G., Manokaran, N., Loo de Lao, S., LaFrankie, J.V. & Ashton, P.S. 1998. Assessing forest diversity on small plots: calibration using species-individual curves from 50-ha plots. In: Dallmeier, F. & Comiskey, J.A. (eds.) *Forest biodiversity research, monitoring and modelling. Conceptual background and Old World case studies*, pp. 247-268. UNESCO and Parthenon, Paris and Carnforth.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Connell, J.H. & Lowman, M.D. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. *Am. Nat.* 134: 88-119.
- Denslow, J.S. 1987. Tropical rain forest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431-451.
- Eggeling, W.J. 1947. Observations on the ecology of the Budongo rain forest, Uganda. *J. Ecol.* 34: 20-87.
- Fisher, R.A., Corbet, A.S. & Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12: 42-58.
- Greig-Smith, P., Austin, M.P. & Whitmore, T.C. 1967. The application of quantitative methods to vegetation survey. I. Association analysis and principal component ordination of rain forest. *J. Ecol.* 55: 483-503.
- Hansell, J.R.F. & Wall, J.R.D. 1975. *Land resources of the Solomon Islands 4. New Georgia Group and the Russell Islands* (one text vol., one map vol.). Land Resources Study 18. Ministry of Overseas Development, Surbiton.
- Hart, T.B., Hart, J.A. & Murphy, P.G. 1989. Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *Am. Nat.* 133: 613-633.
- He, F., Legendre, P. & LaFrankie, J.V. 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. *J. Veg. Sci.* 8: 105-114.
- Lee, K.E. 1969. Some soils of the British Solomon Islands Protectorate. *Phil. Trans. R. Soc. Lond. B* 255: 211-257.
- Manokaran, N. & Kochummen, K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol.* 3: 315-330.
- Neumann, A.J. 1986. *Rainfall and other climatic data for forestry stations to September 1986*. Forestry Research Note 13-13/86. Ministry of Natural Resources, Forestry Division, Honiara, Solomon Islands.
- Okuda, T., Kachi, N., Yap, S.K. & Manokaran, N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rain forest - implications for regeneration and maintenance of species diversity. *Plant Ecol.* 131: 155-171.
- Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Vásquez, R. 1994. Dynamics and species richness of tropical rain forests. *Proc. Natl. Acad. Sci. U. S. A.* 91: 2805-2809.
- Phillips, O.L., Hall, P., Sawyer, S.A. & Vásquez, R. 1997. Species richness, tropical forest dynamics, and sampling: response to Sheil. *Oikos* 79: 183-187.
- Prance, G.T. 1987. Noutulae de Chrysobalanaceis Malesianis Praecursoriae. *Brittonia* 39: 364-370.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. & Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011-1020.

- Sheil, D. 1996. Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* 76: 587-590.
- Sheil, D. 1997. Further notes on species richness, tropical forest dynamics and sampling - a reply to Phillips et al. *Oikos* 79: 188-190.
- Sheil, D. 1998. A half-century of permanent plot observation in Budongo forest, Uganda: histories, highlights and hypotheses. In: Dallemeier, F. & Comiskey, J.A. (eds.) *Forest biodiversity research, monitoring and modelling. Conceptual background and Old World case studies*, pp. 399-428. UNESCO and Parthenon, Paris and Carnforth.
- Sheil, D. 1999a. Tropical forest diversity, environmental change and species augmentation: the intermediate disturbance hypothesis. *J. Veg. Sci.* 10: 851-860. (This issue.)
- Sheil, D. 1999b. Developing tests of successional hypotheses with size-structured populations, and an assessment using long-term data from a Ugandan rain forest. *Plant Ecol.* 140: 117-127.
- Sheil, D., Burslem, D.F.R.P. & Alder, D. 1995. The interpretation and misinterpretation of mortality rate measures. *J. Ecol.* 83: 331-333.
- Stevens, P.F. 1980. A revision of the old world species of *Calophyllum* (Guttiferae). *J. Arnold Arbor.* 61: 117-424.
- Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.
- Swaine, M.D., Lieberman, D. & Putz, F.E. 1987. The dynamics of tree populations in tropical forest: a review. *J. Trop. Ecol.* 3: 359-366.
- van Baren, F.A. 1961. The pedological aspects of the reclamation of tropical, and particularly volcanic soils in humid regions. In: *Tropical soils and vegetation: Proceedings of the Abidjan Symposium*, pp 65-67. UNESCO, Paris.
- Wardle, D.A., Zackrisson, O., Hörnberg, G. & Gallet, C. 1997. The influence of island area on ecosystem properties. *Science* 277: 1296-1299.
- Whitmore, T.C. 1966. *Guide to the forests of the British Solomon Islands*. British Solomon Islands Protectorate Forestry Department. Forest Record 2. Oxford University Press, Oxford.
- Whitmore, T.C. 1974. *Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands*. Commonwealth Forestry Institute Paper 46, University of Oxford.
- Whitmore, T.C. 1984. *Tropical rain forests of the Far East*. 2nd ed. Clarendon Press, Oxford.
- Whitmore, T.C. 1989. Changes over twenty-one years in the Kolombangara rain forests. *J. Ecol.* 77: 469-483.
- Whitmore, T.C. & Burslem, D.F.R.P. 1998. Large scale disturbances in tropical rain forest. In: Newbery, D.McC., Prins, H.H.T. & Brown, N.D. (eds.) *Dynamics of tropical communities*, pp. 549-565. Blackwell, Oxford.
- Zimmerman, J.K., Everham, E.M. III, Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *J. Ecol.* 82: 911-922.

Received 6 May 1998;

Revision received 14 October 1998;

Accepted 30 November 1998.