

Drought in a Bornean everwet rain forest

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Abstract

1 In 1998, the forests of Lambir Hills National Park experienced a severe drought. Between late January and mid-April, less than one-fifth of the normal expected rainfall was received. To investigate the effects of the drought, survival among 6993 trees (≥ 1 cm d.b.h.) in the drought period (1997–98) was compared with survival among 7270 trees in the same area before the drought (1993–97).

2 Mortality rates for the pre-drought and drought periods were calculated using maximum likelihood techniques. Forest wide mortality rates during the drought were 7.63% year⁻¹ as compared to 2.40% year⁻¹ during the pre-drought period. Logistic regression was used to investigate habitat effects. During the pre-drought period, soil type was the most important predictor of tree survival, while during the drought period, slope was the most important.

3 The mortality rate of large (≥ 10 cm d.b.h.) rare trees (< 2 individuals ≥ 1 cm d.b.h. ha⁻¹) did not differ between pre-drought and drought periods, while that of large common trees (> 35 individuals ≥ 1 cm d.b.h. ha⁻¹) increased 6.5 fold in response to the drought suggesting a possible compensatory mechanism maintaining the persistence of rare species. Mortality of large common and rare species however, did not differ significantly during the drought due to small sample sizes.

4 The results of a comparative analysis of the impacts of droughts in four tropical forest sites provide evidence in support of the Intermediate Disturbance hypothesis.

Key-words: compensatory mechanisms, diversity, drought, rain forest, Intermediate Disturbance hypothesis

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Introduction

Catastrophic disturbances, such as drought, fire, typhoons and land slides, although infrequent in their occurrence, may have a major impact on the ecology of equatorial forests (Whitmore 1984; Ashton 1993). Connell's Intermediate Disturbance hypothesis predicts that, depending on their severity and frequency, these disturbances have the potential to be either diversity enhancing or diminishing (Connell 1978). Disturbances such as drought may also induce changes in species phenology (Corlett & LaFrankie 1998), forest size structure and water and light availability, leading to differential impacts on tree species performance.

Numerous studies have investigated the effects of drought on the function, structure and diversity of tropical tree communities. Leighton & Wirawan (1986), Condit *et al.* (1995) and Nakagawa *et al.* (2000)

investigate and quantify the effects of single drought events on tree species performance, while other studies (Condit 1998; Newbery *et al.* 1999; Walsh 1999) have broadly focused on the qualitative relationship between drought frequency and changes in forest composition and diversity. No recent study has synthesized the existing quantitative information on drought effects in order to better understand the role that disturbances (particularly droughts) play in maintaining tropical tree species diversity.

Thus, the occurrence of a severe drought in early 1998 over a region including an existing long-term forest dynamics plot in the Lambir Hills National Park in Malaysia provided a unique opportunity to gather further quantitative data on the differential impact of a drought and to perform a comparative analysis of drought effects in tropical forests. Harrison (2000, 2001) has reported on the breakdown of the fig (*Ficus* spp.) and fig wasps (Agaonidae) mutualism as a result of this drought. Nakagawa *et al.* (2000) focused on the effect of the drought on tree species performance, studying large tree (≥ 10 cm d.b.h.) mortality and growth in relation to tree size, topographic landform and taxonomic group

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in an 8-ha permanent sample plot located in a different part of Lambir Hills National Park.

The larger plot size (52 ha) and availability of soils data for the forest dynamics plot allowed me to report on tree mortality rates over a much wider range of sizes (≥ 1 cm d.b.h.), as well as to investigate the effects of both topography and soil type. The large sample size and species level data also allowed me to investigate drought-induced changes in species diversity, in particular, effects on rare and common species. Little is known about how rare species, which make up a large portion of total diversity, persist in tree communities (Hubbell & Foster 1986; Condit *et al.* 1996). All things being equal, rare species face a greater chance of extinction than common species due to stochastic effects of small population sizes and greater tolerance to drought may help to explain their continued persistence.

I addressed the following specific questions. (i) Did the drought affect tree survival and, if so, how strongly? (ii) Did taxonomic groups respond differently to the drought? (iii) Did tree size and habitat (soil type and slope) have differential effects on tree survival before and during the drought? (iv) Are rare species less susceptible to drought than common species? By correlating the results with broad biogeographical patterns of species richness, rainfall availability and drought frequency and intensity in tropical forests (Richards 1996), I then assessed the applicability of Connell's Intermediate Disturbance hypothesis for the maintenance of diversity in this system.

Materials and methods

ENVIRONMENTAL SETTING

Lambir Hills National Park (Lambir NP) is located in Sarawak, East Malaysia (4°20' N, 113°50' E). It comprises 6800 ha of primarily lowland mixed dipterocarp forest (MDF) on sandy-clay rich soils (Watson 1985). The forest is extremely heterogeneous and is characterized by undulating topography and small scale variations in soil type (Palmiotto 1995; Yamakura *et al.* 1995; Lee *et al.* 2002).

In 1991, a 52-ha forest dynamics plot (500 m \times 1140 m) was established in Lambir NP following a standardized protocol (Condit *et al.* 1997). Within the plot, every woody stem ≥ 1 cm d.b.h. was tagged, measured for girth, identified to species and mapped to the nearest 0.01 m. An initial census was completed in the middle of 1993 and a second census undertaken in 1997, at which time 339 266 stems were found (representing 1171 species, Lee *et al.* 2000).

Lambir NP receives *c.* 3000 mm of rainfall a year, with all months averaging > 100 mm (Watson 1985; Vose *et al.* 1992). Temperatures range from a mean daily minimum of *c.* 24 °C to a mean daily maximum of *c.* 32 °C and show no significant seasonal variation. The drought in 1998 was particularly severe (Fig. 1). For an 89-day period, beginning in late January and

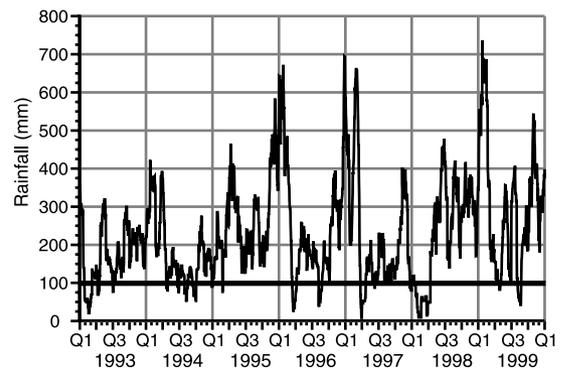


Fig. 1 Thirty day running (average) rainfall for Lambir NP (1993–2000). For 89 days during the 1998 drought, the running average rainfall was < 100 mm.

lasting until mid-April, the 30 day running average rainfall was below 100 mm. Only one-fifth of the normal expected rain fall fell over this period. The 1998 drought was much more severe than the 12 previous 3-month droughts recorded between 1917 and 1980 (Vose *et al.* 1992). Walsh (1999) and Harrison (2001) both provide more detailed information on rainfall patterns and frequency of drought events in North-west Borneo.

FIELD SAMPLING

Three 10 m \times 700 m transects, separated by 80 m, were laid out in the Lambir forest dynamics plot during the last week in June and the first week in July 1998, approximately 4 months after the end of the drought (Fig. 2). The transects were laid out parallel to the long axis of the plot so as to capture the maximum variation in soil types and topography. All stems ≥ 10 cm d.b.h. were re-censused, together with all stems ≥ 1 cm d.b.h. within the left-hand half. Because very few species in this forest are deciduous, mortality was judged by a lack of leaves as well as a dried inner cambium. Stems not located after a systematic search were also recorded as dead. Slashing was performed on trees greater than approximately 5 cm d.b.h. at or above 1.3 m. Pre-drought tree census data for the identical survey transects was extracted from the 52-ha plot data set.

Palmiotto (1998) constructed a soil texture map (Fig. 2, Table 1) for the entire 52-ha plot by sampling the centre of each of the 1300 20 m \times 20 m quadrats in the plot. Soil 5–15 cm deep was assigned to one of four texture classes based on sand content, stickiness and slipperiness (Kimmins 1987). Soil samples ($n = 145$) representing all four texture classes were analysed (Table 1) using a LaMotte Soil Texture Unit (LaMotte Co., Chestertown, MD). Although statistically significant differences exist between all four soil types, soils classes 2 and 3 are not functionally distinct and have been grouped together for all subsequent analyses. Additionally, the mean slope in each of the 1300 20 m \times 20 m quadrats in the 52-ha plot was recorded (Palmiotto 1998). The mean slope was 21° with a standard deviation of 10°.

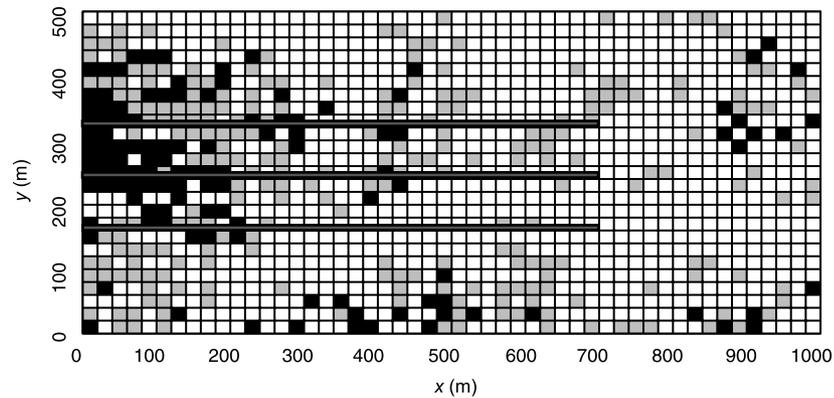


Fig. 2 Soil texture map of Lambir NP 52-ha forest dynamics plot (FDP) with dark grey lines indicating sampled transects. Black indicates udult (Type 1) soils; grey, intermediate (Type 2 and 3) soils; and white, humult (Type 4) soils (see Table 1 and text).

Table 1 Soil texture variation in the 52-ha plot at Lambir Hills National Park, Sarawak, Malaysia. Mean (± 1 SE) percentage sand, silt and clay contents determined for four field texture classes. Sample sizes given in parentheses. Different letters following rows indicate significant differences among soil texture classes (*G*-tests; $P < 0.05$)

Soil texture class	Sand (%)	Silt (%)	Clay (%)	
1	39 \pm 0.8 (56)	25 \pm 0.8 (51)	36 \pm 0.7 (51)	a
2	45 \pm 1.0 (23)	37 \pm 1.5 (22)	19 \pm 1.3 (22)	b
3	51 \pm 0.8 (35)	22 \pm 0.7 (33)	27 \pm 0.8 (33)	ba
4	64 \pm 1.4 (31)	23 \pm 1.1 (29)	13 \pm 1.0 (29)	c

DATA ANALYSIS

Mortality rate estimation

Mortality rates (λ) were calculated using a maximum likelihood technique (Kobe *et al.* 1995; Kobe & Coates 1997; Kubo *et al.* 2000). Confidence limits on λ were calculated using the likelihood ratio test. (Hilborn & Mangel 1997). The λ calculated is properly referred to as the exponential mortality coefficient (Sheil *et al.* 1995).

Mortality rates were calculated for different size classes (all sizes, 1–3 cm d.b.h., > 10 cm d.b.h.) and for stems of all size classes growing on different soil types. Mortality rates for all rare and all common species were also calculated, defining rare species as one having an average density of < 2 individuals \geq 1 cm d.b.h. per ha across the whole 52-ha plot, and common species as one having an average density of > 35 individuals \geq 1 cm d.b.h. per ha.

Habitat effects

To investigate the effects of soil type, slope and size on tree survival during and before the drought, a modified version of logistic regression was performed. I used the logistic equation in the following form:

$$P = [1/(1 + \exp(-z))]^t \quad (\text{eqn 1})$$

where P is the probability of survival, t is the length of the census interval in years and z is a linear function of size, slope and soil type:

$$z = b_0 + b_1x_1 + b_2x_2 + b_3x_3 \quad (\text{eqn 2})$$

where x_1 is the size of individual, x_2 is the slope, and x_3 is the soil type. Maximum likelihood techniques were used to estimate the model parameters. The ability of different model parameters (i.e. slope, soil type and size) to explain species survival was determined as follows. First, an analysis of deviance for the sequential addition of each variable was performed. A chi-square test was then used to test for differences between models. It should be noted that the P -values reported were robust to permutation of parameter addition order.

Results

FOREST-WIDE PATTERNS OF MORTALITY

For all stems, regardless of size and soil type (Table 2a), the mortality rate during the drought period was three times higher than during the pre-drought period. The statistical significance of this result was confirmed by looking both at the confidence intervals calculated from a likelihood ratio test and at a Wilcoxon paired-sample (signed rank) test on a species by species basis ($P < 0.001$). In terms of raw numbers, 493 out of 6983 stems in the sampled area died over a period of approximately 1 year including the 3-month drought while 853 out of 7270 stems died in a 5-year period prior to the drought.

SIZE EFFECTS

Substantial size effects were evident both prior to and during the drought (Table 2a). Not unexpectedly, small trees suffered significantly ($P < 0.01$) higher mortality

Table 2 Mortality rates by size for (a) all species; (b) rare species; (c) common species (95% confidence limits given in parenthesis)

(a) Size Class	Pre-drought		Drought	
	Stems	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
All	7270	2.40 (2.29–2.52)	6983	7.63 (7.17–8.12)
< 3	4042	2.98 (2.81–3.15)	3820	8.98 (8.30–9.70)
> 10	226	1.56 (1.34–1.79)	1240	5.43 (4.54–6.44)

(b) Size Class	Pre-drought		Drought	
	Stems	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
All	580	2.63 (2.23–3.07)	534	6.55 (5.11–8.23)
< 3	259	3.05 (2.42–3.78)	236	9.67 (7.09–12.82)
> 10	158	1.49 (0.97–2.17)	164	2.48 (1.13–4.62)

(c) Size Class	Pre-drought		Drought	
	Stems	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
All	1725	1.69 (1.50–1.90)	1704	7.67 (6.73–8.69)
< 3	1041	2.16 (1.88–2.46)	1013	8.55 (7.28–9.97)
> 10	241	0.58 (0.33–0.94)	248	4.02 (2.44–6.17)

rates in both the pre-drought and drought periods but the drought had a slightly greater impact on large trees. During the drought, large trees (> 10 cm d.b.h.) died at a rate 3.5 times that of the pre-drought period vs. a figure of 3.0 for small trees (< 3 cm d.b.h.).

SOIL AND SLOPE EFFECTS

Soil effects differed between pre-drought and drought periods (Table 3a). Pre-drought trees on adult soils (type 1) had higher mortality than the overall average (2.40% year⁻¹), while mortality of trees on humult (type 4) soils was lower (differences significant at $P < 0.05$). This trend disappeared during the drought period with trees on both soils having above average mortality. The results of the logistic regression amplify these findings, since soil type was a significant predictor ($P < 0.01$) of tree survival during the pre-drought period, but not in the drought period (Table 4). Neither the pre-drought and drought periods showed pronounced effects of slope. However, in the drought period, slope was a marginally significant predictor of survival ($P = c. 0.07$) probably due to the highly significant effect on humult (type 4) soils (Table 4). On these soils, every one degree increase in slope decreased the probability of survival by 2%.

TAXONOMIC EFFECTS

While the sample size of the census was too small to compare the effects of the drought on individual species or genera, it was possible to explore differential effects on different families. Families represented by a least 100 stems in both the pre-drought and drought census were analysed.

Table 3 Mortality rates by soil type for (a) all species; (b) rare species; (c) common species. (95% confidence limits given in parenthesis)

(a)	Pre-drought		Drought	
	Soil Type	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
1	1297	3.67 (3.35–4.01)	1174	7.87 (6.80–9.06)
2–3	1669	2.84 (2.59–3.11)	1592	5.42 (4.64–6.29)
4	4304	1.84 (1.71–1.97)	4217	8.46 (7.82–9.14)

(b)	Pre-drought		Drought	
	Soil Type	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
1	164	3.69 (2.83–4.70)	143	8.25 (5.37–12.00)
2–3	202	2.68 (2.03–3.47)	191	5.24 (3.26–7.88)
4	214	1.78 (1.27–2.41)	200	6.57 (4.28–9.56)

(c)	Pre-drought		Drought	
	Soil Type	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
1	174	3.85 (3.00–4.86)	160	7.40 (4.82–10.76)
2–3	326	1.67 (1.27–2.16)	317	3.32 (2.07–5.00)
4	1225	1.39 (1.19–1.61)	1227	8.93 (7.73–10.26)

Table 4 Results of logistic regression analysis: (a) P -values for model parameters from logistic regression analysis; (b) value of model parameters for different soil types. ** indicates $P < 0.01$ and NS indicates not statistically significant

(a)	Size	Soil	Slope
Pre-drought	**	**	NS
Drought	**	NS	0.07

(b)	Pre Drought		Drought	
	Type	Slope	Type	Slope
All	0.028**	0.0	0.042**	-0.007
1	0.105**	0.003	0.034	0.005
2–3	0.027**	0.004	0.089**	0.027
4	0.025**	-0.004	0.046**	-0.019**

Individuals in all families experienced higher mortality during the drought (Table 5), statistically so for nine of the families analysed. Only in the family Annonaceae was there no significant change in mortality rate. Differences between family mortality rates were statistically significant.

Pre-drought mortality rates ranged from 0.57% in the Myristicaceae to 4.40% in the Moraceae, while drought mortality rates ranged from 3.72% in the Annonaceae to 15.09% in the Rubiaceae. Mortality rates were on average five times higher during the drought period.

SPECIES ABUNDANCE

By pooling individuals in rare and common species, it was possible to explore the effects of the drought on species of different abundance.

Table 5 Mortality rates by family (95% confidence limits given in parenthesis)

Family	Pre-drought		Drought	
	Stems	Rate (% year ⁻¹)	Stems	Rate (% year ⁻¹)
Anacardiaceae	357	1.06 (0.76–1.44)	365	8.18 (6.19–10.56)
Annonaceae	308	2.10 (1.62–2.65)	308	3.72 (2.37–5.50)
Burseraceae	463	1.28 (0.98–1.63)	459	4.35 (3.08–5.92)
Dipterocarpaceae	1094	2.03 (1.78–2.32)	1092	7.17 (6.06–8.41)
Euphorbiaceae	1014	1.60 (1.36–1.86)	1016	8.71 (7.45–10.12)
Lauraceae	230	2.31 (1.74–3.00)	225	5.22 (3.33–7.72)
Moraceae	116	4.40 (3.27–5.77)	113	13.60 (9.17–19.29)
Myristicaceae	171	0.57 (0.28–1.00)	175	8.00 (5.31–11.49)
Myrtaceae	179	1.82 (1.26–2.53)	167	7.88 (5.13–11.46)
Rubiaceae	364	2.39 (1.92–2.93)	340	15.09 (12.21–18.39)

During the pre-drought period, rare species regardless of size suffered higher mortality rates than common species, regardless of size (Table 2b & c). The effect was most pronounced in large stems (> 10 cm d.b.h.) with common trees having a mortality rate one-third that of rare species. Soil type had similar effects to those of size. Except for those growing on adult (type 1) soils, rare species suffered higher mortality rates than common species (Table 3b & c).

Although both rare and common species suffered higher mortality during the drought, the effects of abundance differed because of size dependence. Rare large trees exhibited no significant change in mortality while large common trees exhibited a 6.5-fold increase in mortality that was highly significant (Table 2b & c). While common large trees had higher mortality than large rare trees during the drought, the result was not statistically significant due to the small number of mortality events.

Soil type again had differential effects during the drought (Table 3a & b). Rare trees suffered lower mortality rates on sandy soils while common trees survived better on clay and intermediate soils.

Discussion

DROUGHT IN LAMBIR HILLS NATIONAL PARK

Drought or near drought (30-day rainfall totalling < 100 mm) events occur on an almost yearly basis in this area (Brünig 1969; Baillie 1976; Whitmore 1984), suggesting that the forests of Lambir NP may be acclimated to periodic water stress. However, analysis of rainfall data by Nakagawa *et al.* (2000) suggests that droughts of the severity of early 1998 occur at frequencies of less than once per century, although recent evidence (Harrison 2001) indicates the frequency of severe droughts is increasing.

Although this drought had the potential to cause dramatic changes in forest structure and dynamics, it did not have an immediate catastrophic effect. In addition to the quantitative data reported here, observations of the forest both immediately after the drought and 1 and 2 years later suggested that little additional tree mor-

tality or re-sprouting occurred. Similarly, no significant effects were found on seedling mortality among individual species (Delisio 2000) and vertebrate seed dispersers were not severely affected by the drought (M. Shanahan, personal communication). Finally, although Harrison (2000) found local extinctions of some species of fig wasps immediately after the drought, the majority of those species have now recolonized (Harrison 2001).

Differential effects of the drought relative to species identity and abundance, as well as habitat factors, did however occur and have the potential to alter community structure and dynamics.

Taxonomic effects

Large trees, even those below the age of reproductive maturity, form the basis of the next generation of canopy trees and are crucial for successful replacement of a species. Thus, the lower mortality rates of large rare trees as compared to large common trees during the drought may affect species abundance relationships. Caution must be taken in the interpretation of this result due to its lack of statistical significance, but assuming the underlying trend is real, the relative performance of rare species may be favoured by droughts particularly if they are increasing in frequency.

Lifespan can be roughly calculated by taking the inverse of the mortality rate. In the absence of drought, large rare trees have a mortality rate of 1.49% and therefore have an expected life-span of 67 years, vs. 0.58% and 172 years for large common trees. If a drought of the severity of that in 1998 occurs once every 100 years, then the life-span of common trees decreases by 6% while the life-span of rare trees is reduced by only 1.5%. Furthermore, a drought of this severity occurring every 20 years would reduce the life-span of common trees by 27% vs. 3% for rare trees. Thus, it appears that greater resistance to drought by rare trees may in part explain their continued persistence and the increasing frequency of droughts might actually allow them to increase in relative abundance.

While it is clear that drought may have a differential impact on the survival of rare vs. common species, the ecological basis of this difference is not known.

However, some insight can be gained by analysing the spatial distribution of rare and common species. Over half of all species in the Lambir forest show some degree of habitat association (M. Potts, unpublished data). Due to their higher abundance, common species are more often found in suboptimal habitats. Thus, it is not surprising that the drought may have had a stronger relative effect on them. For example, the high mortality rate of individuals of common species on the type 4 sandy soil may be attributed to the death of species that prefer soil type 1 and that had established themselves on the sandy soil during non-drought conditions. More research on a species by species basis is needed to determine the exact ecological traits of drought tolerance, and how they are related to species abundance (Debski *et al.* 2002).

During the drought, different families responded differently in terms of relative increases in mortality. These results parallel Nakagawa *et al.* (2000) who also found that sensitivity and tolerance to drought varied among taxonomic groups. As a general trend, the families that had the lowest mortality during the pre-drought period (Anacardiaceae, Euphorbiaceae and Myristicaceae) had the largest relative increase in mortality rate, while families that had the highest pre-drought mortality (Annonaceae, Lauraceae, and Moraceae) had the smallest relative increase in mortality rates. These results suggest that the drought may induce changes in community diversity and composition. Unfortunately, because of the tremendous variation in life history traits for species within families and especially their variation in response to water shortage (Condit *et al.* 1995), it is impossible to make detailed inferences about the underlying ecological traits of drought tolerance.

Soil and slope effects

Our results indicate that a complex relationship exists between tree mortality rates and soil type and slope. The lowest drought mortality rates were observed on the type 2–3 (intermediate) soils which are found along the main drainage basin within the plot. These areas are likely to experience less water stress as they receive water from upslope. This conclusion is supported by Daws *et al.* (2002) who found that downslope sites on Barro Colorado Island, Panama were supplied with water from upslope and experienced a water regime more similar to forests with much higher rainfall. In contrast, the highest mortality during the drought was found on type 4 sandy soils, which is the soil type with the lowest water retention.

DROUGHT AND SPECIES RICHNESS IN TROPICAL FORESTS

Tropical forests have diverse rainfall patterns as well as different frequencies and intensities of droughts (Walsh 1996; Walsh 1999). Therefore, comparing the relative frequency of severe droughts across sites in the

context of their different climatic regimes may help to clarify the role that droughts play in maintaining high tropical tree species diversity and would provide a test of the Intermediate Disturbance hypothesis (IDH) (Connell 1978). Simply stated, the IDH postulates that intermediate levels and frequencies of disturbance should lead to maximal levels of diversity.

I compared my results with three published studies that have focused on an extreme drought event, were based on a large data set which sampled from the whole tree community and did not have fire as a confounding effect (Table 6). Each was located in a different geographical and climatic region. The impact of different census interval lengths on observed mortality rates must be taken into account but, fortunately, except for Condit *et al.* (1995), all drought or post-drought censuses were conducted at an interval of approximately 1 year. For the Condit *et al.* (1995) study, the 1-year drought mortality rate needed to reach the mortality observed over the 3-year census interval that included the drought was approximately 4.75%.

In the two studies of seasonal neo-tropical forest sites in the Amazon (Williamson *et al.* 2000) and Barro Colorado Island (BCI), Panama (Condit *et al.* 1995), droughts had a small effect on tree mortality rates (Table 6). Both of these sites experience annual dry seasons, and droughts of the intensities reported by the authors occur quite frequently (Table 6). Droughts might be expected to have a small impact as these forests are exposed to dry-season induced water shortages on an annual basis.

In contrast, the studies of Lambir NP and in Kutai National Park, East Kalimantan (Leighton & Wirawan 1986), do provide evidence for the possibility of droughts affecting dominance–diversity relationships. Lambir Hills National Park is everwet (perhumidity index A (Walsh 1996)) while Kutai National Park (perhumidity index A/B) is everwet or nearly everwet and extreme droughts are much less frequent at both these sites than at the neotropical sites. Extreme droughts at Lambir could enhance diversity through the greater increase in mortality for large trees, taxonomic differences in mortality rates and the relatively better performance of rare trees. At Kutai National Park, an extreme drought occurs at most once in a generation of canopy of trees. The severity of the 1982–83 drought led to extremely high rates of mortality of canopy trees (14–24% year⁻¹) and to potentially dramatic changes in the dominance–diversity relationship. In addition, a large number of seedlings of rarer trees species were observed to have germinated soon after the drought (Leighton & Wirawan 1986).

In summary, these studies illustrate the various potential impacts of drought. The drought at Kutai, although potentially diversity-enhancing, was so severe that it may actually have diminished diversity in the long run, while the droughts at Manaus and BCI had little effect on species dominance–diversity relationships. In contrast, the drought at Lambir Hills NP

Table 6 Drought severity and intensity in different forests. Perhumidity index is adapted from Walsh (1996). A — Tropical Superwet, B — Tropical Wet, C — Tropical Wet Seasonal. Frequency is number of droughts of that severity occurring every 20 years from Walsh (1999). a is based on baseline mortality rates from Phillips *et al.* (1994). b from Leighton & Wirawan (1986). c is the annual mortality rate calculated for a 1-year census interval (see text for more information)

Location	No. species ha ⁻¹ (approx.)	Mortality (% year ⁻¹)		Non-drought	Perhumidity index	Frequency	Reference
		Year	Drought				
Manaus, Brazil	280	1997/98	1.12	1.91	B	15	Williamson <i>et al.</i> (2000)
BCI, Panama	175	1982/83	1.98	4.75 ^c	B/C	3	Condit <i>et al.</i> (1995)
Kutai NP, Indonesia	500	1982/83	1–3 ^a	14–24	A/B	< 1 ^b	Leighton & Wirawan (1986)
Lambir NP, Malaysia	600	1997/98	1.56	5.43	A	1	Present study

was of a frequency and intensity that it enhanced rather than diminished diversity. This comparative analysis therefore provides evidence for the validity of the Intermediate Disturbance hypothesis as a mechanism maintaining high tropical tree species diversity.

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