



Long-term observations of rain forest succession, tree diversity and responses to disturbance.

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Received 21 September 1999; accepted in revised form 20 April 2000

Key words: Budongo, Intermediate-disturbance-hypothesis, Monitoring, Monodominance, Permanent-sample-plot, Species richness

Abstract

The relationship between succession and tropical forest diversity has been much debated. A fundamental disagreement hinges on whether high local species richness is a transient successional property, albeit one that can be maintained by disturbance, or is rather a property of stable late successional communities. This paper addresses this controversy employing a series of long-term permanent sample plot data spanning seven decades. W.J. Egging studied the vegetation of Budongo Forest, Uganda during the 1930s and 1940s. He described a series of ten plots (1.4 and 1.86 ha) as a successional progression of forest types in which tree species numbers show a unimodal rise-and-fall over time – a pattern best known from Connell's illustration of his intermediate disturbance hypothesis. Tree communities in five of the original plots have been intermittently re-assessed over the subsequent decades. One data-series provides observations spanning 54-years from one intact 'undisturbed' old-growth forest plot. The remaining four plots were assessed before and after controlled disturbances (tree poisoning) executed in the late 1950s and early 1960s, and the resulting data-series span c. 20 years of pre-disturbance and c.35 years of post-disturbance changes. The unimodal pattern of species-richness in the original comparative plot-series is paralleled by a similar rise-and-fall in stem-densities, but rarefaction confirms that the unimodal pattern in richness also holds for fixed stem-counts. The proportion of species occurring in both large and small stem-size-classes increases across the series. As richness declines in later succession, low abundance species occur predominantly in larger stem-sizes. All time-series show a rise in species richness ranging from 12 to 177% ha⁻¹ (over 50–60 years). Each of the disturbed plots ultimately reaches greater richness than was recorded anywhere in Egging's original series. Contrary to expectation a small rise was also recorded in the undisturbed late successional plot (c.42 species \geq 10 cm diameter ha⁻¹, rising to c.47). The lowest species density observed in the study is a 1940s record of c. 10 species \geq 10 cm diameter ha⁻¹ in monodominant *Cynometra* [Caesalpinoideae] forest and the highest record is c. 61 ha⁻¹ recorded in 1992, in the youngest vegetation type monitored. These observations indicate both the volatile nature of tree-richness patterns and the limitations of simple models as aids to interpretation when confronted with real patterns of long-term change.

Introduction

The relationship between disturbance and tropical forest diversity remains a subject of considerable debate. Recent controversy has centred on succession and tree diversity. Some claim that high local richness is a transient successional property that can only be maintained by an appropriate disturbance regime (Huston 1994; Connell 1978), while others argue such

richness is actually characteristic of late successional 'equilibrium' communities (Brünig 1973; Peet 1978; Phillips et al. 1997). Controversy thus centres upon diversity patterns in relation to disturbance histories and forest age, and the stability and causal determinants of such patterns (Phillips and Sheil 1997). This argument has major implications for the interpretation of how species richness patterns relate to forest and landscape dynamics. Understanding low-diversity

and monodominant tropical forests (Gartlan et al. 1986; Newbery et al. 1988; Connell and Lowman 1989; Hart et al. 1989; Hart 1990; Martijena and Bullock 1994; Maisels and Gautier-Hion 1994; Sheil 1996a) is in itself an important counter-balance to the emphasis placed on richer formations. This paper considers tree diversity patterns observed at the 1–2 ha scale in a classic series of long-term plots in a Ugandan forest where both species rich tree-communities and monodominant tracts of the canopy species *Cynometra alexandri* C.H.Wright, Caesalpinoidae, occur.

W.J. Eggeling studied the vegetation of Budongo Forest, Uganda, during the 1930s and 1940s. He argued that long-term expansion of forest cover into surrounding grasslands had generated a successional sequence of distinctive forest communities. He described this putative successional series and showed that there is an initial rise in species numbers through early succession, reaching a maximum level at an intermediate phase, and a subsequent late successional decline to a monodominant forest with a canopy of over 70% of *Cynometra* (Eggeling 1947). This classic study gained renewed recognition after Connell (1978, 1979) used it as the principle illustration of his well known account of the Intermediate-Disturbance-Hypothesis. Eggeling's study has been widely cited in the context of succession and disturbance-diversity models (Connell and Lowman 1989; Hart et al. 1989; Huston 1994). Eggeling was the first to clearly describe the successional pattern and Connell was the first to specifically propose a disturbance-diversity relationship as applying to the Budongo vegetation, thus I refer to the fully elaborated concept as the 'Eggeling-Connell' model or interpretation. [One reviewer has objected to this designation on the ground that Connell was not the true origin of the Intermediate-Disturbance-Hypothesis, and many other authors had presented similar ideas – this is certainly the case (Grime 1973; Horn 1975; Wilkinson 1999), but the point here is that Connell developed this specific interpretation regarding the tree community in Eggeling's plots at Budongo, other authors did not. A comprehensive examination of the 'Eggeling-Connell' interpretation and Connell's more general form of the Intermediate-Disturbance-Hypothesis is provided by Sheil (1999a).]

Eggeling's (1947) account of forest succession uses data from ten plots numbered in the order of the implied succession (1–10). Two additional plots are a wet 'swamp' forest formation (Plot 11, in Eggeling

(1947)) and one (Plot 15) established originally in woodland at the forest edge and not named in Eggeling (1947) but monitored subsequently. Five of these plots (2, 5, 6, 7 and 15) were maintained as permanent sample plots (PSPs). One of these, Plot 7, has been free of all destructive interventions, but four were disturbed by silvicultural treatments some 20 years after their establishment. We thus have one comparative space-for-time ten plot sequence, dating from the 1930s and 1940s, that is claimed to show uninterrupted successional progression, and also two types of time-series: without (or before) and after major disturbances.

The 60-year period of this study is virtually unique, but such duration comes at a price – the data are the product of a complex context and history. The sceptical and the curious alike may justifiably claim the need for adequate information in order to evaluate data quality and interpretation. It is impossible to present the full richness, weaknesses, and historical context of this data set in a single research article. While a range of exploratory analyses and overviews are provided it is important that a broad range of data overviews and characterisations are available elsewhere (Eggeling 1947; Sheil 1995, 1996b, 1998, 1999b; Sheil et al. 2000).

The successional interpretation

The validity of Eggeling's (1947) interpretation is central to the analysis and interpretation of his data-series. Might it be an artefact of selection in a varied forest (Hewetson 1956)? Several lines of evidence convince me this is unlikely. According to Eggeling himself the plots were sited to illustrate the full range of forest types, and the proposed successional series arose naturally from these (Eggeling (1947, 1987) and pers. comm. 1992). Despite many visitors over the last 60 years there are no recorded concerns about unrepresentative locations (various.pers.comms, various unpublished correspondences, Uganda Forest Department records 1930 to 1993). The series indeed show many patterns consistent with a successional progression, e.g. guild classifications reveal increasing shade-tolerance across the series, and increasing height of canopy-species (Sheil 1996b). Multivariate evaluations of the series are highly consistent with four separate predictions of compositional development, i.e. compositional progression and apparent convergence across the plot series, and also progression and convergence *within* each plot (Sheil 1999b).

Table 1. Some implications of the *Eggeling-Connell* interpretation of successional patterns in tree species parameters at Budongo when coupled with a consistent and positive age-man-diameter-class relation for the majority of tree species (ignores seedling bank, i.e. includes only stems ≥ 10 cm drh).

Parameter	Prediction in early and mid succession	Prediction in late succession
A. Species number	Rises to a maximum at intermediate stage <i>Species counts are maximised when species restricted to both earlier and later succession overlap at an intermediate developmental stage.</i>	Decreases to low level <i>Only those few species that can regenerate and survive persist. Species numbers decline as relics of non-regenerating species die out.</i>
B. Species found in larger but not smaller stem classes	Increases early and persists <i>Such ephemeral species increase in number in early to mid succession as 'pioneer' and 'early' species fail to regenerate under increasing competition from species better adapted to later succession.</i>	Persists but finally decreases to low level <i>Most species that occur only in larger size classes are relics that finally die out.</i>
C. Species found in smaller but not larger stem classes	Increases to a maximum at intermediate stage <i>Tree species will fall into two types: 1) The understorey species which rarely or never achieve larger size under natural conditions; 2) those larger species which can achieve large sizes. These second group of species will be prevalent as long as succession involves continuing replacement by additional larger species.</i>	Decreases to steady level <i>Such species will ultimately be limited almost exclusively to species incapable of achieving large sizes.</i>
D. Proportion of species at large sizes which simultaneously occur in smaller stem classes	Low levels but rises <i>Few early canopy forming species will continue to regenerate under their own canopies.</i>	Rises to maximum <i>Ultimately, as a 'steady-state' is approached, all species will be regenerating within the same environment as the larger parent trees.</i>

The broader successional interpretation at Budongo is consistent with the historical distribution of vegetation-types (Eggeling 1947; Philip 1965), with the climatic records suggesting conditions suitable for forest expansion for the last few centuries (Hamilton 1982), and with more recent observations of forest increase making some age-gradient appear inevitable (e.g. aerial imagery from 1951, 1960 and 1988, Sheil (1996b)). Indeed the observations in Plot 15 show how rich forest can develop from open woodland.

Hypotheses and predictions

The original paper provided little quantitative analysis and no statistical characterisation, but the importance of Eggeling's (1947) account, and its subsequent use by Connell (1978, 1979) in the Intermediate Disturbance Hypothesis, justifies a careful re-ap-

praisal. Furthermore the time-series allows a new test of the applicability of these models.

The assumption of a general age-size correlation for each tree species (Boucher 1997) is implicit in both Eggeling (1947) and Connell (1978) and has allowed me to develop a series of predictions, Table 1. My simple null hypothesis is that there is no consistent pattern between the plots, or over time. An alternative, if crude, 'equilibrium' hypothesis can also be suggested that all forest will match the 'late successional' forest of Table 1, i.e. with all canopy species also being found at smaller sizes. In this paper I will focus upon three specific propositions, and also present some exploratory analyses that help interpretation.

1. Species-number rises and falls as a unimodal relationship with successional development

(Table 1, line A).

2. There is a decrease in the proportion of species which, though physically capable of achieving large size, are found only in smaller size-classes, while the proportion of species occurring in a broad range of size-classes increases (Table 1, lines B-D).
3. Disturbance can increase tree diversity. Here we will propose that the treatments of plots 2, 5, 6 and 15 can be considered as discrete disturbance events, i.e. they 'release and reallocate community resources' (Clark 1990).

Site, data and methods

The forest

The Budongo group of reserves includes over 400 km² of closed forest located in western Uganda at 1°37'–2°03'N and 31°22'–46'E, on the eastern edge of the Albertine Rift Valley. The underlying Precambrian geology has weathered to provide gentle topography with deep, relatively homogeneous, ferralitic-clay soils. Most forest occurs between 1000 and 1100 m a.s.l. Annual rainfall varies between 1,200–1,800 mm. Most rain falls from September to November and March to May, while between January and March rainfall can drop to below 50 mm a month (Sheil 1997). The canopy is predominantly deciduous, and emergent trees reach to 60 m. Despite the limited physical and edaphic variation, Budongo has a relatively rich tree flora with over 220 forest (and 40 woodland) species reaching stem diameters of 10 cm or more (Synnott 1985; Howard 1991; Sheil 1996b). No major sources of extrinsic natural disturbance such as hurricanes, droughts, or forest fire have been recorded at Budongo within the closed forest, although fire occurs in surrounding woodlands, and large herbivores have had a definite influence on regeneration (Laws et al. 1975; Sheil 1996b).

Plots and data

I consider both the comparative-series and time-series data. Eggeling (1947) presented the comparative-series data as stem-counts by species and diameter-class for all species ≥ 10 cm diameter at reference height (drh – defined below) from ten square plots of 1.486

Table 2. Dates of silvicultural treatment and estimated subsequent basal-area loss. The treatment involved a poisoning (using 2–4D and 2–4–5T) of non-commercial species. Surviving data are not sufficient to make more accurate assessments.

Plot	Intervention	Net Basal Area Loss m ² ha ⁻¹ (min – max estimate)
15	1955, 56, 58	8–15
2	1960, 64	6–10
5	1960, 64	25–30
6	1956, 58, 59	15–25
7	None	None

ha. The plots were selected to represent a full range of typical forest types and labelled one to ten in order of their putative successional stage. There is no information concerning the true age of the forest in any of these plots. Soil in all plots is generally deep and uniform.

Time-series data are available for plots 2, 5, 6, 7 and 15, and derive from files at the Forest Department Headquarters in Kampala and my own surveys (1992–1993). Plot 15 was not detailed in Eggeling (1947) but was established during the same period in wooded grassland that has since turned to forest (it could be considered a plot '0' within the putative successional series, and may have provided Eggeling's (1947), description of 'woodland'). These 1.86 ha incorporate those detailed in Eggeling (1947) which were reduced to 1.486 ha to be comparable with other studies (ignoring data from a 100 by 400 foot strip, approx. 30 × 120 m).

The time-series data can be divided into two types: records from pristine forest and records after disturbances. Records from pristine forest include early observations from all plots (also Eggeling (1947)) and Plot 7 throughout the entire period. Between the late 1950s and early 1960s, non-marketable tree species were poisoned in many areas using the arboricides 2–4D and 2–4–5T. This treatment was intended to favour growth and regeneration of valued timber species and followed established procedures (Dawkins 1954, 1955), but was often repeated due to high survival rates (Table 2). The plots have never been formally harvested.

The minimum stem sizes and species recorded have varied. Those censuses where all species were recorded have been used here. Most stems have been measured at a height of 1.3 m, but when multiple measures have been taken (e.g. buttressed stems) the higher measure (always the smaller record) has been

used, and this is called the 'diameter-at-reference-height', or drh. The good quality of these data is notable, involving multiple observations, extensive herbarium collection and review (Eggeling 1940; Sheil 1995). The variety of populations used provide choices for evaluation and presentation (e.g. if smaller stems are considered fewer census dates provide adequate records), and only a range of illustrative results are provided here (Sheil 1996b). Stem size classes are labelled with a shorthand where the lower bound is inclusive and the upper bound exclusive, e.g. stems in a 'd₁-d₂ cm class' are $\geq d_1$ cm and $< d_2$ cm drh. Fuller accounts of the census methods are provided in Eggeling (1947) and Sheil (1995, 1998).

Rank-abundance and species richness

Tokeshi's (1993) form of the rank-abundance presentation is used, but with logarithms in base-two (allowing comparisons with the 'octaves' approach, e.g. Whittaker (1965)). There are many approaches to trying to assess species richness independently of sample size, but virtually all suffer biases and none can eliminate the noise inherent in small samples (e.g. Fisher et al. (1943); Hurlbert (1971); Kempton (1979); Bunge and Fitzpatrick (1993); Colwell and Coddington (1994); Hayek and Buzas (1998)). Here species numbers are estimated for fixed stem-counts by Hurlbert's (1971) rarefaction method (see Appendix 1 for an account of the computation used). This is an unbiased method (Peet 1974; Smith and Grassle 1977; Kempton 1979) for assessing mean richness (Sn_r) for a given number of individuals or stems (n_r) drawn (with replacement) from a larger sample. Rarefaction allows comparisons of richness that are independent of stem densities. However, the chosen sample size (n_r) does influence some aspects of relative stem richness. This procedure was selected as, unlike many quantities (Bunge and Fitzpatrick 1993; Colwell and Coddington 1994), the conceptual interpretation of the measure is clear, the value is unbiased, and plotting Sn_r versus n_r allows the potential influence of n_r on evaluations to be considered directly. Thus while low n_r values cannot always be avoided here ('younger' plots contain few large diameter stems), all reported patterns are relatively consistent with higher n_r values when these are obtainable (Sheil, unpublished analyses).

Results

An exploratory analysis of Eggeling's series

Species-counts for stems of 10 cm drh and over follow a unimodal pattern with an approximately five-fold range in total richness across Eggeling's (1947) original data series (Figure 1). The highest species-numbers occur in plots 4 and 5 with 58 species each. Plot 2 has the lowest diversity for a putatively early successional vegetation with 34 species (59% of the maximum recorded), and Plot 9 has the lowest overall count with only 11 species (19% of the maximum). Stem-number shows a similar trend (Kendall's rank correlation of stems versus species number $\tau = 0.539$, $p = 0.03$, [$n = 10$]), but over a smaller relative range, with less than half as many stems in Plot 10 as in Plot 4 (45%). Species-richness per fixed stem-count (n_r) also shows a unimodal pattern indicating that the pattern is not an artefact of stem densities alone. For example, with $n_r = 200$ stems, richness rises from 66% of maximum in Plot 2 to the highest values in Plots 5 and 6 both with 36 species, and finally declining to 25% of this maximum in Plot 9 (Table 3). As might be expected genus and family richness follow the same general patterns as species number (Table 3), and are positively correlated with both species number (genera versus species $\tau = 0.955$, $p = 0.0002$, and families versus species $\tau = 0.501$, $p = 0.05$), and stem-densities (genera versus stem-counts $\tau = 0.584$, $p = 0.02$, and families versus stem-counts $\tau = 0.471$, $p = 0.07$).

Examination of Eggeling's (1947) data suggests that Plots 4, 5, 7 and 10 have relatively many low-abundance species. For example Plots 9 and 10 indicate some variation in the species richness associated with putatively late successional forest types with 11 and 25 species respectively. These differences are caused by low abundance species with over half the 'extra' species in Plot 10 being represented by a single individual (13 of 25 total, and 18 with six or less [i.e. $n_i \leq 6$]) while Plot 9 has few such low abundance species (3 singles of 11 total, and 3 $n_i \leq 6$).

The fits of the rank abundance curves to lognormal distributions are summarised in Table 4 (the Kolmogorov-Smirnov [K-S] test is most appropriate when distributions from single samples are examined, Tokeshi (1993)). Several of the plots fit the distribution adequately at the 95% confidence level but three of the four significantly non-log-normal distributions arise in the more species-rich mixed forest (Plots 4, 5

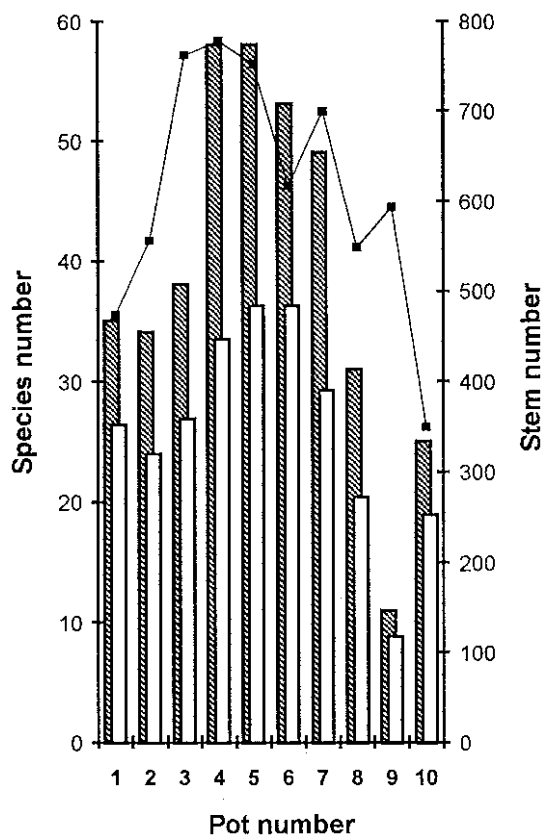


Figure 1. Species and stem-numbers ranked in the order of Eggeling's putative successional series. Species-number (dark bars), expected species counts for 200-stem samples (white bars) and stem-number (line) for stems (≥ 10 cm drh from Eggeling's (1947) plot data.

and 7). The distributions were also examined by eye (not shown), but no peculiarities or additional patterns of fit were noted.

The rarefaction of Eggeling's data is presented in Figure 2. It is seen that, apart from Plot 9, the species-numbers show little sign of levelling-off with increasing stem-counts (Figure 2a). For the relative ranking of richness to be independent of stem-number requires that the cumulative species-count versus sample-size curves do not cross ($n_r > 1$). This is best examined using the near linear relationships provided in the log-scaled presentation (Figure 2b). Differences in richness decrease with smaller n_r in both absolute and relative terms. Only plots 1 and 3 show Sn_r relations which cross those of other plots and having higher relative stem diversity at small reference-sizes due to greater relative evenness in species abundance.

Patterns of diversity through time

All the plots had increased in richness by 1992 (Table 3). In Figure 3, a more inclusive range of populations (higher minimum diameters) are included allowing more observations to be examined. The estimated changes in tree-richness, per ha, between Eggeling's records and the 1992 evaluations (after Plots 2, 5, 6 and 15 had been disturbed) show that Plot 2 increased by 77%, Plot 5 by 12%, Plot 6 by 21%, Plot 15 by 177% (22 to 61), and Plot 7 by 12% (42 to 47). Changes in species and stem numbers are again positively associated.

Community structures (i.e. species abundance distributions), are shown by the rank-abundance curves in Figure 4. All the changes are significant by two-sample K-S tests at $p < 0.001$ (this is true even for Plot 7 Eggeling's data versus 1992, $p = 0.0006$, and the 1992 form is also not log-normal, $p = 0.011$). A careful assessment of the trends in Plot 7 shows this is due to a relative reduction of moderately abundant species and more low abundance species.

Size-class diversity relationship

The raw species-numbers for Eggeling's (1947) data by stem size-class are shown graphically in Figure 5. A rise and fall for each size-class is credible, although larger diameter classes, with lower counts, are less consistent. Apart from the ≥ 60 cm drh class which rises with plot number ($\tau=0.778$, $n=10$, $p=0.0017$) stem-numbers show less clear patterns Figure 5. The relative stem diversity for Eggeling's (1947) data at 3 stem size-classes is shown in Figure 6 (A low n_r , [$n_r = 10$] was unavoidable as 'younger' plots contains few large diameter stems). The greatest diversity for the smallest size-class occurs in Plot 1, (Plot 3 and 4), for the intermediate size in Plot 3 (and Plot 5) and for the largest size-class is Plot 5 (Plot 6 and 4). Data are sufficient for limited time-series observations in Plot 15, the youngest vegetation, and in Plot 7, the putatively most mature vegetation followed. These data show the rise in Plot 15 (including rapid change prior to treatment) and the less marked changes in Plot 7 (Figure 7).

Relations between size-classes

The within plot ratio of larger stems (≥ 60 cm drh) as a proportion of all stems (≥ 10 cm drh) is shown in Figure 8. There is a significant rank-correlation be-

Table 3. Plot, species and stem statistics for stems (≥ 10 cm drh).

Plot	Total area (ha)	Total stems	Stems/ha	Total species	Total genera	Total families	Estimated species-counts ^a			
							\sim sp/ha ^b	$n_r=20$	$n_r=100$	$n_r=200$
1 ^c	1.48	473	320	35	32	22	31	11	21	26
2 ^c	1.48	556	376	34	33	23	30 ^d	8	18	24
3 ^c	1.48	762	515	38	35	23	35	11	21	27
4 ^c	1.48	778	526	58	50	25	51	10	24	33
5 ^c	1.48	752	508	58	50	20	52	10	26	36
6 ^c	1.48	617	417	53	45	20	47 ^d	10	27	36
7 ^c	1.48	699	472	49	40	23	42 ^d	9	21	29
8 ^c	1.48	548	370	31	25	16	26 ^d	7	15	20
9 ^c	1.48	593	401	11	10	8	10 ^d	5	8	9
10 ^c	1.48	349	236	25	22	16	21 ^d	7	14	19
11 ^c (swamp)	1.48	562	380	80	71	29	68	14	37	52
2, in 1992	1.86	982	528	63	57	30	53	13	29	38
5, in 1992	1.86	808	434	69	57	22	58	13	33	44
6, in 1992	2.12	846	399	70	58	24	57	13	32	44
7, in 1976	1.86	981	527	57	47	27	45	9	21	29
7, in 1978	1.86	975	524	57	47	27	44	9	21	29
7, in 1992	1.86	1090	586	60	49	28	47	9	21	29
7, in 1993	1.86	1087	584	60	49	28	47	9	21	29
15, in 1944	1.86	382	205	25	21	18	22 ^d	8	17	22 ^d
15, in 1950	1.86	699	376	35	30	14	32	11	23	28
15, in 1992	1.86	921	495	74	61	19	61	13	33	45

^a Estimated according to Hurlbert's (1971) method which assumes random mixing of stems. ^b Based on Hurlbert's method and using the stems ha^{-1} as n_r . ^c Data from Eggeing (1947). ^d In these cases as stems $\text{ha}^{-1} \geq (N - N_{\text{max}})$ the estimate is provided by a Log[S] versus Log[N] 'linear' interpolation between the highest rarefaction estimate and the total measured plot value.

Table 4. Evaluation of Eggeing's (1947) plot data, stems ≥ 10 cm drh, against the log-normal distribution. Fit is evaluated using the Kolmogorov-Smirnov (K-S) test (Statgraphics Plus 1993) following Tokeshi's (1993) advice on single sample distributions.

Plot	1	2	3	4	5	6	7	8	9	10
D-N ^a	.226	.161	.129	.192	.193	.142	.198	.204	.168	.294
$p =$.056	.34	.55	.027 ^b	.026 ^b	.24	.043 ^b	.15	.92	.027 ^b

^a D-N is the absolute maximum vertical distance between the cumulative distribution function (CDF) of the data and the CDF of the best fit log-normal distribution, with the significance level adjusted for the 2 df used in fitting the distribution. ^b Denotes significant deviation from a log-normal distribution ($p < 0.05$).

tween putative successional order and larger stems taking up increasing proportions of all stems ($\tau=0.867$ $p=0.0005$). By 1992 Plots 15, 2 and 5 reveal a similar development with more large stems but Plots 6 and 7 have increased the proportions of stems at small sizes.

There is an apparent decrease in the proportion of species unique to smaller size-classes across Eggeing's series (Figure 9). Species unique to larger size-classes reveals a clear unimodal pattern and zero counts for Plots 2, 9 and 10 (Figure 10a-c). Examining the proportion of species present in both smaller and larger stem sizes (Figure 10d) show that there is an increase across Eggeing's series. The Kendall's rank correlation of these values versus plot number is

significant: *i.e.* for species with stems ≥ 30 cm/[stems ≥ 20 cm], $\tau = 0.63$, $p = 0.012$, and for stems ≥ 60 cm/[stems ≥ 20 cm], $\tau = 0.60$, $p = 0.016$. Over time, Plot 15 also shows such an increase, but Plot 7 does not (Figure 10e, Figure 10f).

Discussion

Overview and interpretations

Eggeing's (1947) data series conform to the first two propositions. The series reveals, 1) a unimodal pattern for many measures of tree richness, and 2) a de-

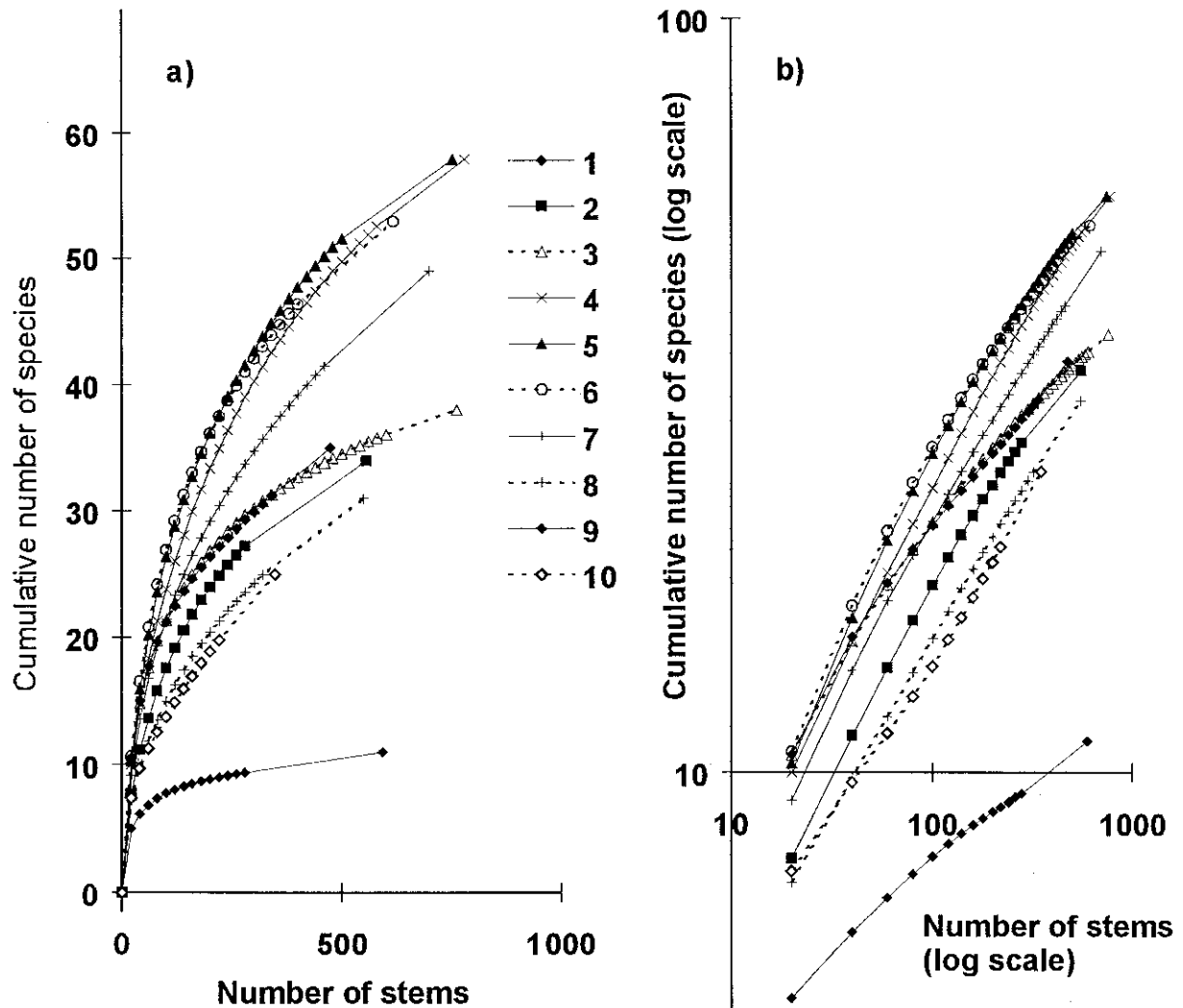


Figure 2. Species versus stem-number for Eggeling's (1947) data (stems ≥ 10 cm drh, plots 1 to 10) by Hurlbert's (1971) method. a) Linear-scaled presentation. b) Log-scaled presentation.

crease in the proportion of species found only in smaller size-classes, while the proportion of species occurring in a broad range of size-classes increases. The time series observations are less consistent. Plot 7 indicates that tree diversity in late-successional forest does not inevitably decline with time. But the magnitude of change in the remaining plots supports 'proposition 3' showing that tree diversity can markedly increase following disturbances three decades previously. Auxiliary examinations of tree densities, stem-counts per class and community abundance distributions, suggest relationships which in some cases accentuate the observed diversity patterns but offer no

artefactual or 'non-successional' explanations in themselves.

The accordance of Eggeling's original series with the model is expected. This was after all the illustration used to develop the model. However, the above evaluations are more detailed than anything reported by Eggeling or others, and include new time-series information. The results are open to a range of *post-hoc* interpretations. The importance of reviewing these is that they can be used to generate testable predictions.

1. **Interpretation I:** The model is and was fundamentally incorrect, and the proposed 'succes-

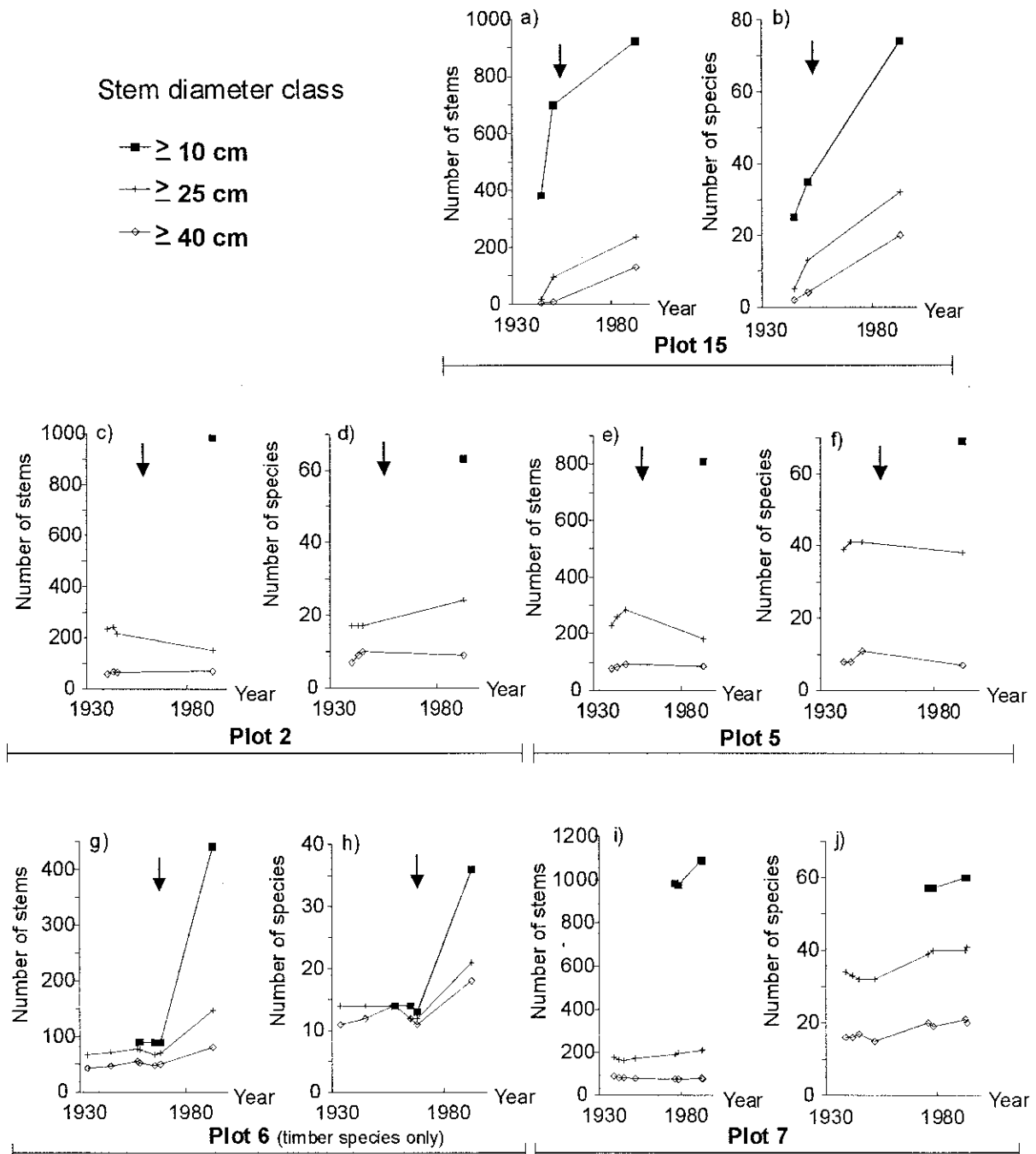


Figure 3. Changes in stem and species-numbers by plot. Populations used are ≥ 10 , 25 and 40 cm drh and are taken from all available full species records (except for Plot 6), so some missing data points arise in the ≥ 10 cm class. For Plot 6 only timber species were available before 1992, and this limited but fixed list is used here (See Sheil et al. (2000), for a full list). Arrows show approximate dates of disturbance by silvicultural treatment.

sional sequence' is an artefact. **Prediction:** Factors incompatible with the successional viewpoint may be exposed by continued and detailed examination of the Budongo forest, and

related data sets. **Comment:** None of the indirect assessments of successional status that have been devised have challenged Eggleing's original interpretation of his data (Sheil (1996b,

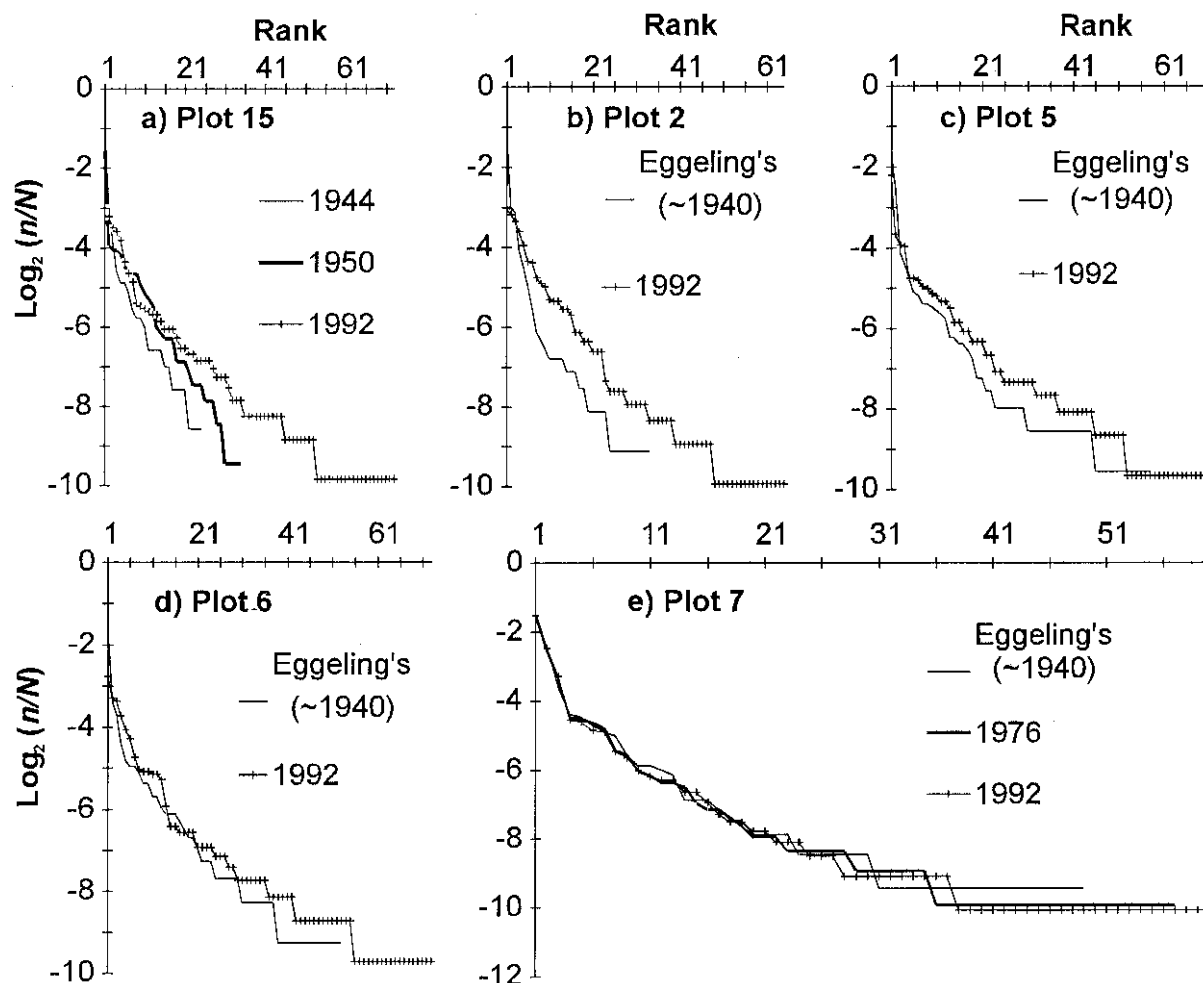


Figure 4. Rank-abundance plots showing the changes in relative community structure over time. a) Plot 15. b) Plot 2. c) Plot 5. d) Plot 6. e) Plot 7 (expansion of the X axis fails to reveal any clear change in structure).

1999b), this study). Spatial patterns within the forest are also compatible. The changes in Plot 15, where woodland has become mixed-forest, show that the early stages of the putative succession conform with direct observations.

2. **Interpretation II:** The model is correct but data suffer from statistical noise. **Prediction:** Larger samples or longer periods would ultimately conform to expectation. **Comment:** These PSPs are almost 2 ha each, and include uniquely extended time-periods. However, single plots (e.g. Plot 7), however large and old, are inadequate for generalisation.
3. **Interpretation III:** The model was valid under the limited environmental variations occurring in the earlier part of the century, but successional determinants have changed. **Prediction:** Specific auxil-

iary phenomenon can be proposed which will be associated with each causal factor. Factors to consider include climate change, management interventions, the impact of research on the PSPs themselves, harvesting and disturbance in many areas of the forest and subsequent changes in seed rain (Sheil 1995, 1998; Plumptre 1995), and the decline in elephants *Loxodonta africana* (Laws et al. 1975; Sheil 1996b, 1998). **Comment:** These ideas deserve further examination given the changes that have occurred over the last century. Many factors influence vegetation, and these are not addressed by the Egging-Connell model, which assumes a stable environmental context and is, apart from the

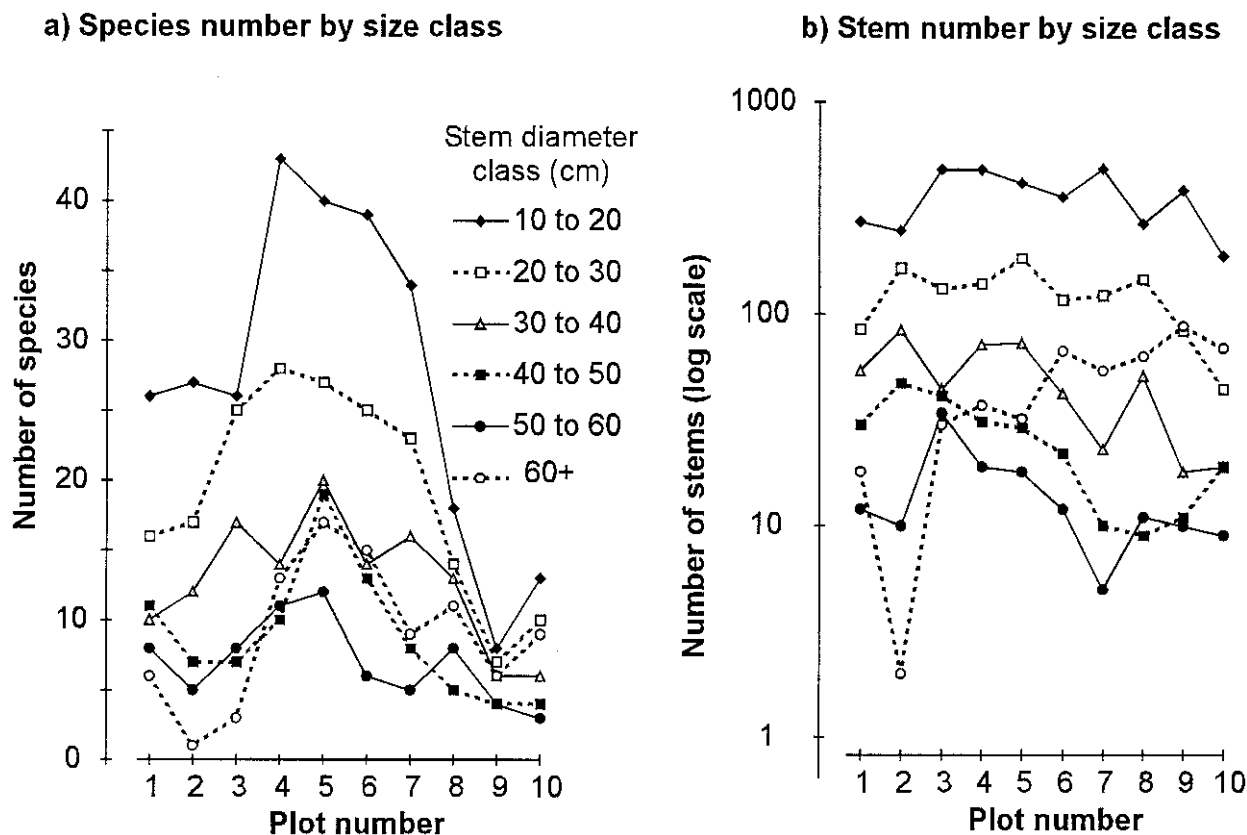


Figure 5. a) Species number by stem-size-class in Eggeing's (1947) data. b) Stem counts by size class (note log scale on Y axis). The plots are in numerical order, representing Eggeing's putative successional series.

factor called 'disturbance', deterministic and 'mechanism free' (Sheil 1999a).

It remains unclear whether any evaluation that considers all species equally can offer sufficient insight to determine the important mechanisms and processes in real communities. The next challenge is thus to develop a more integrated model of expected behaviour based less on generalities and more on the local context and species. I suggest that the decline in large herbivores at Budongo has had a marked influence on the forest regeneration manifested both in the 'release' of sensitive species, and in the greater overall density of the long-lived understorey species. Gathering better evidence for or against this view must be the subject of future studies. The following discussion will not address this but considers the results in more detail.

Species-number through succession

Eggeing's series shows a unimodal pattern in species number, and also in stem densities. The two-fold difference in stem densities could not explain the five-fold variation in richness. The species-per-fixed-area relation is accentuated by this co-variation, but rarefaction shows that the unimodal richness pattern holds for fixed stem-counts. Though not an element of the Eggeing-Connell interpretation in itself, the pattern of stem densities is readily explained as a successional phenomenon. Stem numbers increase through tree colonisation until canopy space (basal area) is filled, and then decreases as larger trees subsume ever increasing proportions of the limited space (Figure 8). Stem-number, like species-number, changes with the putative development, and their correlation appears to reflect shared underlying successional processes rather than any other cause-effect relationship (Sheil 1996a). Species richness patterns can be methodological artefacts. For example the humped pattern of diversity versus biomass recorded

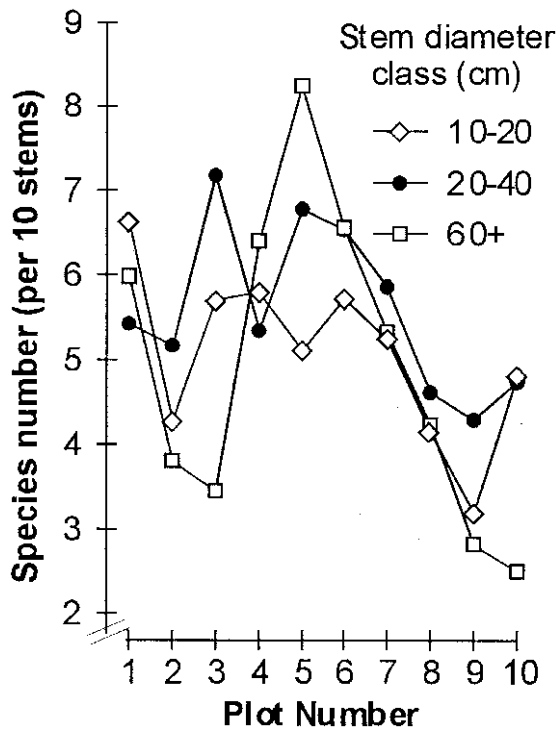


Figure 6. Rarefaction of species numbers to $n_r=10$ in Eggeling's (1947) data by size class (classes were selected to provide sufficient numbers for analysis).

in some herbaceous communities (Al-Mufti et al. 1977) has been interpreted both as ecologically meaningful (Grime 1973) and as a sampling artefact related to co-variation in plant density, size and other community parameters (Oksanen 1996; Stevens and Carson 1999). Here, by using rarefaction and specifically examining the relationship of richness with stem-size such potential artefacts are identified and assessed.

The time series data are less consistent. Prior to the silvicultural disturbance, the four treated plots show richness consistent with the rising portion of the Eggeling-Connell relationship (most clearly in Plots 15 and 5). Plot 7 is positioned beyond the diversity maximum in Eggeling's series (Figure 1) (and this placement is not inconsistent under any of the many analyses that the series has been subjected to, e.g. Sheil (1996b, 1999b) so under the Eggeling-Connell interpretation a decline is the expected trend. However, over the 54 years an increase is recorded. The increase in species-number in Plot 7's 10–20 cm drh class is unusual, being due to increased stem densities alone and there is a concurrent decrease in relative stem richness (Figure 9d). There is no evidence of increased gap formation or recruitment of light de-

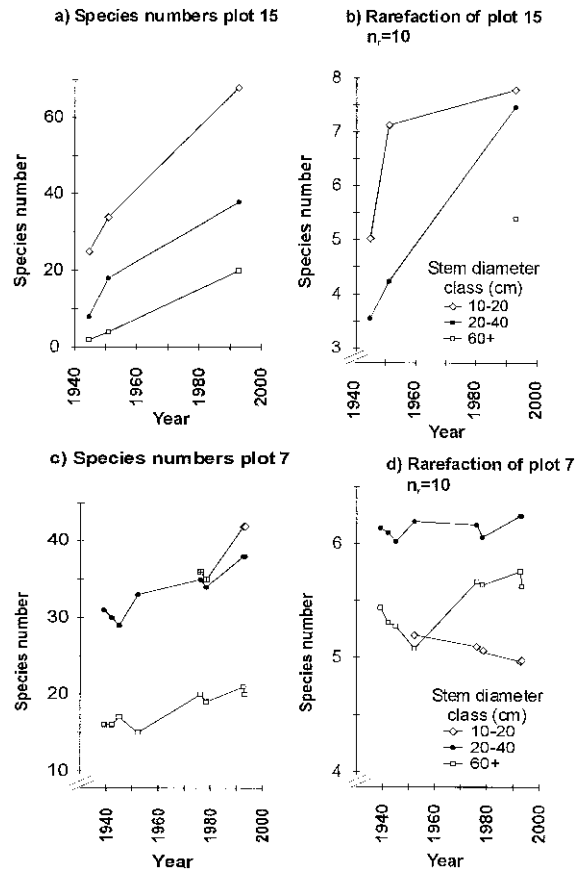


Figure 7. Species numbers and rarefaction over time by stem size-class. a) Total species counts in Plot 15. b) Plot 15 rarefaction ($n_r=10$), note there are insufficient stems in the ≥ 60 cm stem-class for the earlier observations to allow rarefaction. c) Total species counts in Plot 7. d) Plot 7 rarefaction ($n_r=10$).

manding species (stem by stem there is an increase in the proportion of more shade tolerant species, Sheil (1996b)). There are no strong trends in the abundance or stand structure of *Cynometra* itself: in 1939 Plot 7 had 17 and 28 stems in the 20–60 and over 60 cm drh classes, by 1993 this had changed to 12 and 30 respectively, and regeneration is still observed (Sheil 1996b). Plot 7 appears typical of the surrounding vegetation, and the observed changes show low stem and basal-area mortality (Sheil 1996b).

Rarefaction and rank abundance

There is a general tendency for most plot rarefaction lines to curve with decreasing gradients with relation to a power model (Figure 2b) at larger stem counts, and overall differences in richness increase in both absolute and relative terms as stem counts (n_r) in-

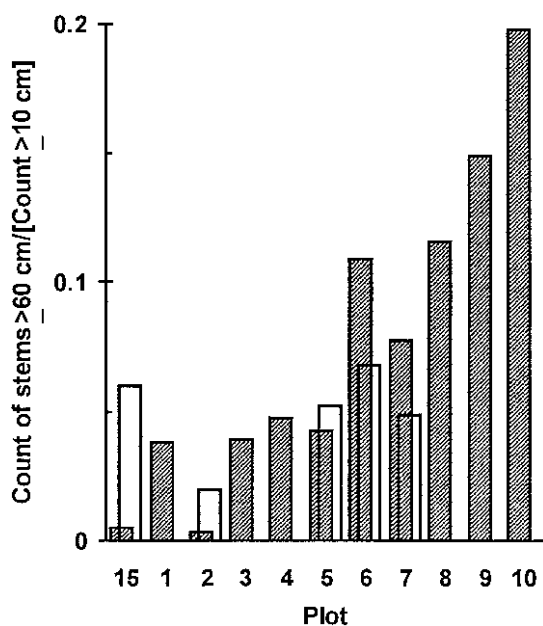


Figure 8. The relative number of stems ≥ 60 cm drh, as a proportion of all stems (10 cm drh, for Eggeling (1947) plot series and Plot 15 in 1944 (dark bars) and for the time-series plots in 1992 (empty bars). The plots are in numerical order, representing Eggeling's putative successional series.

crease. While some authors have drawn attention to similar results (Condit et al. 1996) it is a mathematical requirement, or truism, as all rarefaction lines must meet at $n_r=1$; the point where one stem gives one species. The examinations based on assessing the lognormal distributions yielded no clear trends. Three of the four significantly non-log-normal distributions arise in richer forest, but this is probably due to the power of the test (i.e. type II error is reduced with higher species counts). Nonetheless, it is clear that abundance distributions have profound influences on net richness. Plots 9 and 10 have a net difference in richness of fourteen species (11 versus 25) but this difference is due to low abundance species, i.e. three versus 18, with six or less stems, and three versus 13 with only one stem recorded).

Species and stem sizes through succession

The overall species counts for smaller stem-sizes indicate a decline in later stages in Eggeling's series (Figure 6). Three main factors can be postulated to influence species counts within and across stem size-classes: 1) a limited number of species can dominate under any given competitive situation and this selective force should reduce richness with size (time); 2)

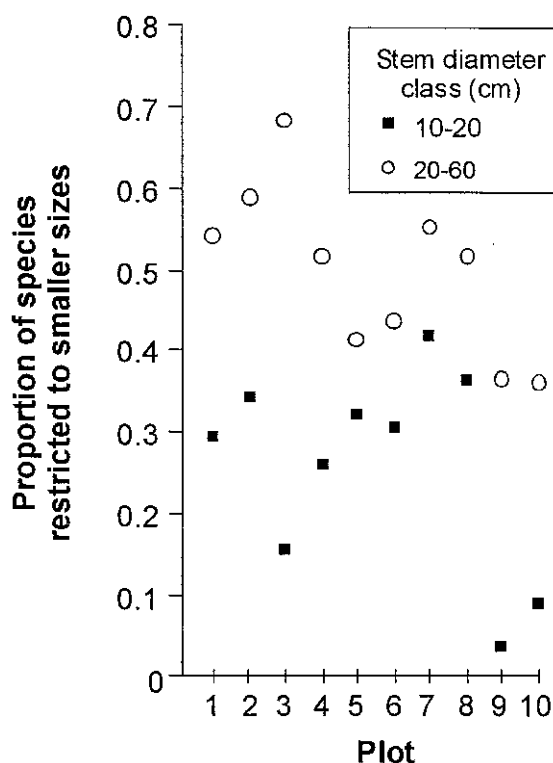


Figure 9. The proportion of species unique to smaller stem-diameter classes in Eggeling's (1947) plots in numerical order, representing his putative successional progression. The number is calculated independently for each plot and represents the number of species in each size class but not at larger sizes, divided by the total number of species in the plot. A rank correlation analysis reveals that the analysis based on the 20–60 cm class is significantly related to plot number ($\tau = -0.56$, $p = 0.025$, and for the 10–20 cm class $\tau = -0.0667$, and $p = 0.79$).

If regeneration is irregular more age variation in a class can potentially include more species, thus potential richness may increase with both wider diameter classes; and, 3) with older and larger stems. In Figure 6, the second and third explanations can speculatively be applied as explanations at intermediate stages but the first prevails in late succession, as expected if direct competition is the major selective force in succession (Eggeling 1947; Connell 1978).

In agreement with the Eggeling-Connell interpretation there is a decrease in the proportion of species unique to smaller size-classes across Eggeling's data series (Figure 9). Similar results are obtained by analysis of those species unique to larger size-classes, and species present in both smaller and larger stem sizes (Figure 10). The Plot 15 time-series data follow the predicted trends, while those from the undisturbed Plot 7 do not. Although Plot 15 was disturbed, it was

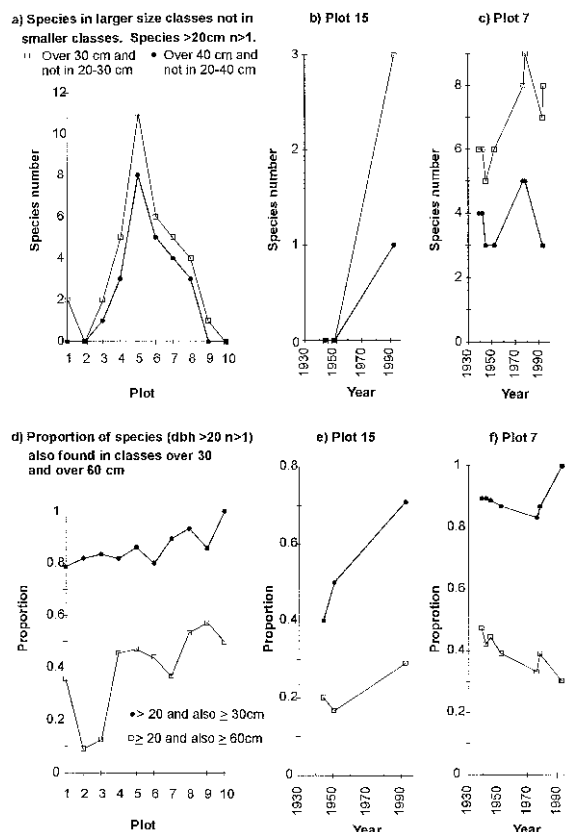


Figure 10. Examination of species with more than one stem over 20 cm drh. a) Number of species exclusive to larger stem-sizes in Eggeling's (1947) data. b) Plot 15, the number of species exclusive to larger stem sizes in over time. c) Plot 7, the number of species exclusive to larger stem sizes in over time. d) Proportion of all species found in the ≥ 30 cm and also in the ≥ 60 cm diameter class for Eggeling's (1947) data. e) Plot 15, proportions as d. f) Plot 7, proportions as d.

already at an early successional stage, and evidence suggests it had recovered rapidly (Sheil 1996b; Sheil et al. 2000).

Disturbance and change in diversity

Plots 2, 5, 6 and 15 were treated at known dates using arboricide. In the 1990s each of these treated PSPs achieved species densities greater than Eggeling (1947) recorded anywhere outside of 'swamp forest' (Plot 11). This supports the prediction that disturbance can increase diversity. The Eggeling-Connell interpretation does not address the relative stem diversity achievable in a disturbed forest as opposed to during an uninterrupted successional progression. Connell (1978) graphical account uses the same uncalibrated Y-axis and relation for three separate X-

axis labels ('time since', 'frequency of', and 'size of disturbance'). However, by returning to the basic principles we can recognise that in a progressive succession, species co-existence occurs only when the periods of species persistence overlap. However, no such temporal limits apply to successional heterogeneity in the one treated sample area. This intimate mixing of distinct successional communities does not necessarily explain the extent of the rises seen in the disturbed PSPs. Plot 15 lacked late successional species both when it was being silviculturally treated (in the 1950s), and in 1992 (Sheil 1996b) but still reached exceptional richness. The stem-size-based evaluations, (illustrated above by Plots 7 and 15) appear most consistent with the recruitment of an expanded suite of species in all the time series.

Succession or transition? A note on woodland species

The typology of the proposed succession is unclear as it is neither a primary or secondary succession as the putatively 'younger' vegetation contains species-records that may be best interpreted as residual, large-stemmed woodland remnants. Should these species be eliminated from the analyses? The presentation of species richness by size-class across Eggeling's series, particularly when a fixed stem count is used are 'noisy' at best (Figure 6) and if 'woodland species' are eliminated some patterns conform better to expectation, e.g. the predicted unimodal pattern in the ≥ 60 cm drh class is apparent (Sheil unpublished analyses). On the other hand such selective elimination is counter to the holistic approach adopted thus far and has the appearance of 'rigging the data'. This unease is compounded by three additional factors: that the 'woodland species' actually increase in density within the forest margin and are clearly part of the succession rather than pre-dating it (Sheil et al. 2000); old aerial imagery (1930s and 1951) confirms that there was previously almost no tree cover outside of the forest; and that these 'woodland' species can be seen to behave as classic 'light-demanding pioneers' after any sizeable area is opened within the forest (pers. obs.). Successions representing transition between vegetation types, appear common (e.g. when herbivores are excluded, or as climate changes) and the classical primary-secondary dichotomy is inappropriate.

Diagnosis of forest history and developmental status

Successional models (e.g. Egging (1947)) provide opportunities for devising simple indices of vegetation development (e.g. Figures 9 and 10). Such combined stem-size and species based approaches have potential value for assessing forest status although the sampling properties of such quantities remain uncharacterised. The stem-count ratios across size classes (Figure 8) provide a simple measure of 'successional structure', that would not be biased by sample sizes. However, measures based on species counts are, by contrast, greatly influenced by sample size. These potential indicators warrant further study with simulation and bootstrapping approaches on larger data sets.

Conclusions

Tree diversity has increased over the last half century in all five plots examined. The disturbed plots achieved notably higher levels of tree diversity than was encountered in even the richest sites in the first half of the century. These observations underline how local tree-diversity can vary over both space and time, and emphasises the local and ephemeral nature of species richness patterns.

The comparative-series shows all the trends predicted by the Egging-Connell model. The species densities reached in the treated time-series plots support the prediction that disturbance can increase richness. The Plot 7 time-series, by contrast, shows unexpected deviations and increases in richness despite a decline being predicted. Size-based analyses appear robust enough to conform to expectation in the original series, but prove equivocal when applied to the time series. The environmental changes that have taken place over the last half-century provide the plausible explanations that should be evaluated further through additional assessments.

Successional models for species richness have important implications. The Egging-Connell view, if generalised, implies that any pattern of richness is short-lived or disturbance dependent, while the contrary arguments imply that current local species 'hot-spots' are more stable (Sheil 1996a, 1996b; Phillips and Sheil 1997; Phillips et al. 1997; Sheil et al. 1999). Both views, when stated in such simple form, ignore the complexity of real systems. It has long been known that a large number of factors affect diversity, and many are themselves subject to outside influ-

ences. We require less naïve models (Sheil 1999a). A better integration of processes and mechanisms is needed to predict the diverse relationships between tropical forest diversity, inherent dynamics and external influences.

Acknowledgements

I dedicate this account to the memory of W.J. Egging and H.C. Dawkins – though both are now deceased their enthusiasm for this study provided vital inspiration. This study was funded by the Overseas Development Administration as project R4737 under the Forestry Research Programme component of the Renewable Natural Resources Research Strategy. A comprehensive list of acknowledgements for the Budoongo study is provided in Sheil (1998). I am particularly grateful to the Uganda Forest Department for providing access to the data and for their generous collaboration in re-measuring and maintaining the plots. Special thanks also to Joseph Connell, S.J. Wright, David Newbery, Michael Huston, Jonathan Moss, Peter Savill, Tim Synnott, Robert Whittaker, Nigel Asquith, Rick Condit, Steve Jennings, Jules Siedenburb and anonymous referees for comments and discussion on previous drafts and related texts, and to Rosita Go and Meilinda Wan for help preparing the manuscript.

Appendix 1

Hurlbert's (1971) technique estimates the mean number of species (Sn_r) that would be encountered if n_r individuals were randomly drawn with replacement from the full sample of N individuals. The formula is:

$$Sn_r = \sum_i \left(\frac{(N-N_i)!(N-n_r)!}{(N-N_i-n_r)!N!} \right)$$

where Sn_r is the mean expected number of species in n_r individuals, from N observations, and N_i is the recorded full-sample number of individuals for the i th species. Calculation is limited to $n_r < (N - N_{max})$, where N_{max} is the number of individuals of the most abundant species. Factorial formulae are computationally clumsy due to large intermediate values and

the rounding errors that can accrue. I therefore provide the logical-arithmetic elements of the *Quick Basic* (Microsoft Corporation 1990) computer routine I have used (based on Ludwig and Reynolds (1988)):

$$\text{Defining}[a] = \frac{1}{2}\text{Log}_e(2\pi a) + a\text{Log}_e[a/e]$$

a is the value of the expression being operated on by $f[\cdot]$.

E_i , S^* and all outputs of $f[\cdot]$ are double precision variables.

Earlier steps read in N_i for each species, calculates their sum N , and receives the requested estimate parameter n_r .

- FOR $x = 1$ TO S
 - IF $N - N_i(x) \leq 0$ OR $N - N_i(x) - n_r \leq 0$ OR $N - n_r \leq 0$ THEN to failure routine
 - $E_i = f[N - N_i(x)] + f[N - n_r] - f[N - N_i(x) - n_r] - f[N]$
 - $S^* = S^* + (1 - \exp(-E_i))$
- NEXT
- PRINT "For a sample of"; n_r ; " individuals "; S^* ; " species are expected"

i.e., when x reaches S then S^* is the estimated ' S_n ' for the factorial formula.

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