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Developing tests of successional hypotheses with size-structured populations, and an assessment using long-term data from a Ugandan rain forest

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Abstract

In 1947, W. J. Eggeling published an account of forest succession at Budongo, Uganda. This interpretation was based on a large-scale comparative plot study, performed in the 1930s and 1940s. This account, with its implication that species richness declines in late succession, endures as a controversial corner-stone in theories and disputes about community diversity. Data have now been collected over six decades from five of Eggeling's original plots.

This paper evaluates Eggeling's successional interpretation of the Budongo vegetation. The first set of analyses assesses the consistency of the original data with the predictions of compositional progression and convergence implicit in Eggeling's model. The second analyses do the same for the time-series observations. A logical approach shows how temporal information may be derived from both between plot, and within plot, evaluations using size-structured data. A Detrended-Correspondence-Analysis (DCA) of canopy-tree composition, from the original data, ranks the plots in perfect correspondence to Eggeling's successional sequence. A 'development-scoring' procedure is developed using passive-ordination against this sequence; this is then applied to composition by plot and stem-size class.

Eggeling's original data are consistent with each prediction assessed. The analyses show compositional progression and apparent convergence *across* the plot series, and also progression and convergence *within* each plot. A monodominant-*Cynometra* forest is the natural end-point of this progression. The time-series results, though in apparent agreement for one early successional plot, do not generally accord with Eggeling's ideas. The analyses illustrate a general means for evaluating explicit and implicit compositional trends in communities with structured populations.

Introduction

W.J. Eggeling studied the vegetation of Budongo Forest, Uganda, during the 1930s and 1940s and published his main conclusions in 1947. Eggeling (1947) argued that expansion of forest cover into surrounding grasslands is the process that initiates and maintains a succession of forest communities. He described the vegetation types, using as examples descriptions and data from ten large plots numbered in the order of his implied succession (1–10). There is a clear rise and fall in species richness across the series. The successional interpretation appears consistent both with the historical distribution of vegetation-types (Eggeling 1947; Philip 1965), and with more recent observations of forest increase (e.g., aerial imagery, Sheil 1996a). Despite such circumstantial evidence C. E. Hewetson was sceptical of any such orderly forest development. He argued that Eggeling's interpretation was probably an illusion caused by naïve assumptions being imposed upon disordered communities (Hewetson 1956).

Eggeling's model remains a widely accepted account of how low-diversity tropical forest can develop (e.g., Connell & Lowman 1989; Hart et al. 1989).

Connell (1978, 1979) adopted the study as the main illustration of his *intermediate disturbance hypothesis* with its unimodal ('hump-backed') relationship of species-richness with successional development. This predicts an eventual decline in species richness in any system that develops in the absence of perturbations. Budongo's vegetation is thus viewed as a multi-aged system developing without significant extrinsic disturbance (cf, Eggeling 1947; Connell 1978, 1979). There is still no consensus on the role of disturbance and succession in explaining tropical forest diversity, but Eggeling's model, particularly the late-successional species decline, remains part of the controversy (cf, Sheil 1996b, 1997a; Phillips et al. 1997; Phillips & Sheil 1997).

Eggeling (1947) described the main forest types, subtypes, and ecotones, within his successional framework. This sequence emphasises the canopy composition and progresses from *colonising*, through *mixed*, to *ironwood* forest. In brief:

Colonising forest: moderately species rich, characteristic species include *Maesopsis eminii* Engl., *Albizia* spp., *Caloncoba crepiana* (De Wild. & T. Durand) Gilg. and *Olea welwitschii* (Knobl.) Knobl.

Mixed forest: species rich, typically including several mahogany and sapotaceous species amongst the largest stems, i.e., *Khaya anthotheca* (Welw.) C.DC., *Entandrophragma angolense* (Welw.) C.DC., *E. cylindricum* (Sprague) Sprague and *E. utile* (Dawe & Sprague) Sprague, and *Chrysophyllum perpulchrum* Mildbr. ex Hutch. & J. M. Dalz., *C. albidum* G. Don, *C. muerense* Engl., and *Bequartiodendron oblanceolatum* (S. Moore) Heine & Hemsley.

Ironwood (Cynometra) forest: species poor 'monodominant' forest dominated by *Cynometra alexandri* C. H. Wright, with an understorey of *Lasiodiscus mildbraedii* Engl.

Eggeling argued that, given sufficient time, forest composition follows a clear path and arrives at a defined end-point. In addition, if large-stems reflect the past composition of small-stems, useful temporal information is also contained in stem-size information. These concepts provide a formal approach to evaluating Eggeling's ideas.

This study aims firstly to develop methods for analysing successional change with size-classified composition data, secondly to evaluate Eggeling's data and interpretation, and thirdly to evaluate if the true time-series conform to this model.

Site and field methods

The forest

Budongo is located in western Uganda at 1°37′–2°03′ N and 31°22′–31°46′ E, on the eastern edge of the Albertine Rift Valley. The underlying Precambrian geology is heavily weathered and provides gentle topography with deep, relatively homogeneous, ferralitic-clay soils. Most forest occurs between 1000 and 1100 m a.s.l. Annual rainfall varies between 1200–1800 mm. Detailed rainfall data is summarised in Sheil (1997b). Most rain falls during September to November, and March to May, while in the January-March period rainfall can drop to below 50 mm a month. The canopy is predominantly deciduous, and emergents reach to 60 m.

Plots and data

Two data sets are considered: the comparative-series and the time-series. Eggeling (1947) presents the comparative-series data as stem-counts by species and diameter-class for all species $\geq$10 cm diameter at reference height (drh: see below) from ten square plots of 1.486 ha. The plots were subjectively sited to represent a full range of typical forest vegetation types, (Eggeling 1992, pers. comm.). The time-series data relate to Plots 2, 5, 6, 7 (as in Eggeling 1947) and Plot 15, and derive from files at the Forest Department HQ in Kampala and the authors 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). These plots incorporate the full areas reported in Eggeling (1947). Plot locations, areas and additional information are provided in Table 1.

The time-series data can be divided into two types: a) records from pristine forest and, b) records after silvicultural interventions. 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 unmarketable tree species in many areas were poisoned, using the arboricides 2–4 D and 2–4–5 T. This treatment was intended to favour growth and regeneration of valued timber species and followed standard procedures at that time (see Dawkins 1954, 1955). This was often repeated due to high survival rates. Details relevant to each plot are included in Table 1.

Table 1. Details of the Budongo Plots listed in order of Eggeling's (1947) successional interpretation. Only Plots 15, 2, 6, and 7 were maintained as permanent sample plots.

Plot	Vegetation in 1940[a]	Vegetation in 1992	Interventions[b]	Basal Area Loss m^2ha^{-1} (min – max estimate)	Location (lat. Long.)	Elevation (m)	Area ha[c]
15	*Terminalia* grassland	Mixed (*Maesopsis*)	1955, 1956, 1958	8–15	1° 43′ N 31° 28′ E	1080	1.86
1	Colonising (Woodland)	*na*	*na*	*na*	*na*	*na*	1.49
2	Colonising (*Maesopsis*)	Mixed	1960, 1964	6–10	1° 45′N 31° 28′E	1050	1.86
3	Colonising (*Maesopsis*)	*na*	*na*	*na*	*na*	*na*	1.49
4	Ecotone to Mixed	*na*	*na*	*na*	*na*	*na*	1.49
5	Mixed	Mixed	1960, 1964	25–30	1° 44′ N 31° 28′ E	1050	1.86
6	Mixed	Mixed	1956, 1958, 1959	15–25	1° 44′ N 31° 28′ E	1070	2.12
7	Ecotone to Ironwood *Cynometra*	Ecotone	None	None	1° 43′N 31° 30′ E	1035	1.86
8	Ecotone to Ironwood *Cynometra*	*na*	*na*	*na*	*na*	*na*	1.49
9	Ironwood *Cynometra*	*na*	*na*	*na*	*na*	*na*	1.49
10	Ironwood *Cynometra*	*na*	*na*	*na*	*na*	*na*	1.49

[a]Terminology from Eggeling (1947).
[b]Silvicultural poisoning (Dawkins 1955; Philip 1965).
na ('not applicable') Not all Eggeling's plots were maintained as permanent plots, and the original details have been lost.
[c]As used in the time-series analysis. Eggeling's (1947) data derive from reduced plots of 1.486 ha.

Soil in all plots has similar properties (see Eggeling 1947; Sheil 1996a). Soil profiles are typically deep extending below 1 m with no (Plots 6, 7, 15) or few stones (Plot 5) in the deeper layers (>70 cm). Plot 2 occurs on similar but slightly shallower soil (stones recorded at 30 cm and large rocks at 70 cm), and Plot 6 includes a stream-gully (>3 m) with some exposed bed-rock, and slopes.

The plot census methods are described in Eggeling (1947) and Sheil (1995, 1996a). In this study the only censuses used are those where all species were recorded. Most stem diameters have been measured at 1.3 m, but when multiple measures have been taken (e.g., buttressed stems have commonly been measured at 3 m or even higher – see Sheil 1995) the higher measure (always the smaller record) has been used for classification, i.e. this is the 'diameter-at-reference-height' or drh. [The conventions relating to how buttressed stems are measured have varied somewhat over the history of these plots (Sheil 1995) but as such problems are confined to the very largest stems – here *within* the ≥60-cm drh size-class – this has no significance for these class-based data.] Indeed, the good quality of these PSP data is notable, e.g., multiple observations, initiated by the taxonomic authority on the local tree flora, and involving extensive herbarium collection and review (see Sheil 1995).

Eggeling (1947) and Sheil (1996a) provide the full data sets. Stem counts ≥10-cm drh, vary from 359 (Plot 10, Eggeling 1947) to 1090 (Plot 7 1992) and species vary from 11 (Plot 9, Eggeling 1947) to 74 (Plot 15 in 1992). Eggeling (1947) recorded a total of one hundred and twenty-five species ≥10-cm drh, and forty-three species ≥60-cm drh in the original ten

plots. The time-series data added forty-nine additional species ≥10-cm drh, and eleven species ≥60-cm drh. Various measures of abundance may be ecologically relevant (cf., Tokeshi 1993), but Eggeling's (1947) summaries do not provide individual stem sizes, and analysis is therefore based on stem-counts in the six size classes he used (five 10-cm interval classes between 10 and 60 cm, and one ≥60-cm diameter).

Analytical methods

A general conceptual framework

In Eggeling's model, each canopy-species is understood to follow a unimodal or monotonic relationship of abundance against time, i.e.,

$$A_i = f_i(t, s_{i1}, \ldots s_{in}), \tag{1}$$

where A_i is a measure of the abundance of species i, t is time since the start of forest development (i.e., when the area was first crossed by a forest edge expanding into grassland, $t = 0$), and s_{i1} to s_{in} are parameters that measure non-biotic (e.g., edaphic) variation between sites at a defined time (e.g., $t = 0$). f_i is a unimodal or monotonic function of t and each factor s_{i1} to s_{in}. If sites are homogeneous, or if the differences are ignored, Equation (1) can be simplified to:

$$A_i \approx f_i(t). \tag{2}$$

Abundance thus provides information on possible values for t. In real samples many species occur only at low abundance and are thus difficult to characterise with any confidence. However, if the relationships can be approximated in any way, these may be appropriately weighted and combined to provide a statistical 'best-bet' model of compositional turnover. If $\mathbf{A}_t$ is the unit composition vector composed of elements $A_i / \Sigma A_i$, and if $f_i(t)$ are unimodal (or monotonic) functions for all positive t, we can postulate the existence of some procedure, to be defined later, $\Theta(\cdot)$ such that:

$$\Theta \mathbf{A}_t \cong t, \tag{3}$$

where t lies between 0 and some upper limit when a self-replacing community is achieved. For unique solutions it is sufficient that each successional stage has a distinct mean-composition.

Eggeling's comparative-series does not allow the explicit use of time, as forest ages are not known, but the ordered developmental series allows that a related function can nonetheless be derived and examined. It is sufficient to develop an operation, or 'development-scoring' procedure, $\theta(.)$, such that ($\theta(\mathbf{A}_t)$ has a monotonic relationship to t, i.e., if $t_1 < t_2$ then $\theta(\mathbf{A}_1) < \theta(\mathbf{A}_2)$, and has a smooth and continuous relation to variation in composition. (Note: 'Θ' denotes the calibrated procedure that estimates t, and θ, indicates the uncalibrated procedure). These ideas are developed further below. Related issues are returned to in the discussion and a fuller account of all aspects has been provided in Sheil (1996a).

Hypotheses

From Eggeling's ideas, and a development scoring procedure that reflects his view of compositional changes in succession, four hypotheses can be explicitly proposed. These are detailed here and illustrated in Figure 1.

Requirement 1. Sequential-progression. If $t_1 < t_2$ then $\theta(\mathbf{A}_1) < \theta(\mathbf{A}_2)$. This monotonic relation is also the requirement of our procedure, θ, in order to demonstrate logical consistency as a 'development score' (see above).

Requirement 2. Sequential-convergent-trend. As t increases $\theta(\mathbf{A}_1)$ tends to a constant value $\theta(\mathbf{A}_\infty)$, i.e., $\mathrm{d}\theta(\mathbf{A}_t)/\mathrm{d}t$ tends to zero (generally if $t_1 < t_2$; $\mathrm{d}\theta(\mathbf{A}_1)/\mathrm{d}t > \mathrm{d}\theta(\mathbf{A}_2)/\mathrm{d}t$), i.e., composition tends towards an equilibrium. Tests require an explicit knowledge of time (i.e., age or census observations).

The following steps rely on the proposition that large-tree composition is generally reflected in the composition of smaller-trees at an earlier time. If $\mathbf{A}_{\text{canopy}}$ and $\mathbf{A}_{\text{saplings}}$ are composition vectors based on large canopy trees and smaller (potential) canopy species respectively, the requirements 1 and 2 (above) will still apply to each. If composition is defined to include only species that can occur in both classes then the following requirements or hypotheses are developed.

Requirement 3. Intrinsic-progression. At a given site $\theta(\mathbf{A}_{\text{canopy}}) \leq \theta(\mathbf{A}_{\text{saplings}})$ for all t.

Requirement 4. Intrinsic-convergent-trend. As t increases $\theta(\mathbf{A}_{\text{canopy}})$ and $\theta(\mathbf{A}_{\text{saplings}})$ i.e., $\theta(\mathbf{A}_{\text{canopy}}) - \theta(\mathbf{A}_{\text{saplings}})$ tends to some small value (see Figure 1). In practice this convergence may be approximate, as species may not have equivalent stand profile dynamics.

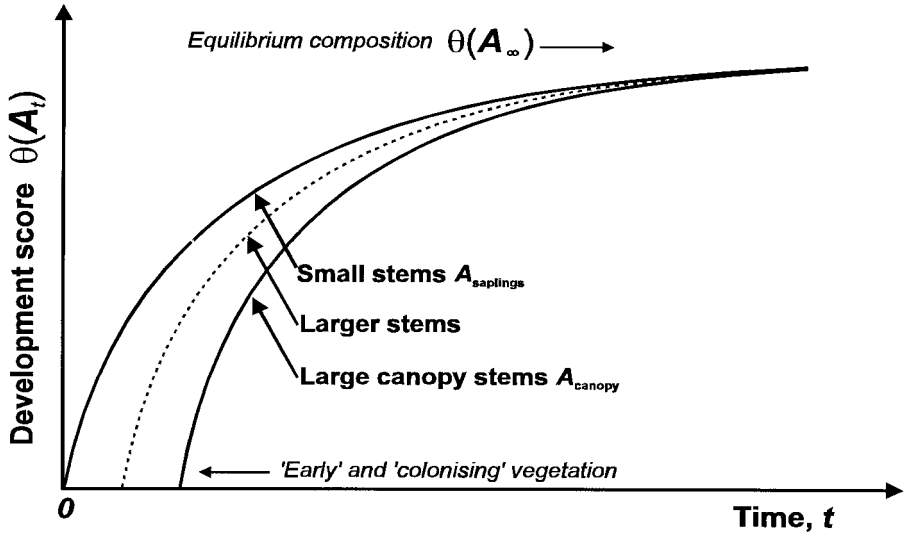


Figure 1. Diagram showings the expected relationship of stem composition along a theoretical successional gradient in which equilibrium is approached. $\theta(\mathbf{A}_t)$ is a development-scoring measure based on relative composition at time t, $\mathbf{A}_t$. The composition of small-stems in younger plots will represent larger-stems in older plots. The composition of each stem-size class, within each plot, is found in a vertical locus between the upper and lower curve. Ultimately at equilibrium the composition values converge on $\theta(\mathbf{A}_\infty)$ for all size classes.

Multivariate approach

Detrended-correspondence-analysis (DCA) methods provide an explicit and well-understood approach to developing a 'best-fit' model of composition turnover (Hill 1979; Hill & Gauch 1980; Gauch 1982; Minchin 1987a, b; Ter Braak 1985; Ter Braak & Prentice 1988). DCA is suited to rich communities with long primary-gradients, particularly when secondary gradients, though likely to be present, are of less interest. Passive ordination allows compositions to be assessed against a fixed turnover-model and provides an independently determined 'best-fit' value of where each assemblage might occur against this reference (Purata 1986; Cramer & Hytterborn 1987; Ter Braak 1988, 1990). In the DCAs used no species are weighted *a-priori*, detrending is by segments (following Minchin 1987a; Ter Braak 1990), and the axes are scaled by SD units (Hill 1979).

A development-scoring procedure

Any order or compositional reference could be developed as a model for evaluation, either through artificial data sets, or through alternative ordination procedures. This provides considerable power and flexibility. The 'development-scoring' procedure applied here uses a DCA (Axis I) of Eggeling's data for relative counts of stems ≥60-cm drh (43 species in Plots 1–10) as the reference of comparison. This conveniently fulfils two *a priori* requirements, *i.e.* (1) the analysis considers only species known to be able to reach all size-classes, and (2) species turnover corresponds exactly to Eggeling's interpretation (there is perfect rank-correspondence between this DCA and Eggeling's 1–10 numbering – see below). Tree composition is evaluated against this turnover through passive ordination against Axis I. This position provides a simple single-value 'developmental-score' for further evaluation.

This study involves both multiple comparisons and tests to repeated measures. For simplicity and clarity each rank-order evaluation is reported as an independent test (no corrections have been made to p values). As a convention each correlation is reported as positive or negative according to whether they are in-line with, or contrary to, Eggeling's model. Attention is drawn to significant results following standard notation, i.e., $^{*} = p \leq 0.05$, $^{**} = p \leq 0.01$, and $^{***} = p \leq 0.001$.

Results

Exploratory evaluations

Initial analysis examined the compositional variation in Eggeling's (1947) data. Typical ordination patterns are illustrated by the 10–20-cm and ≥60-cm drh

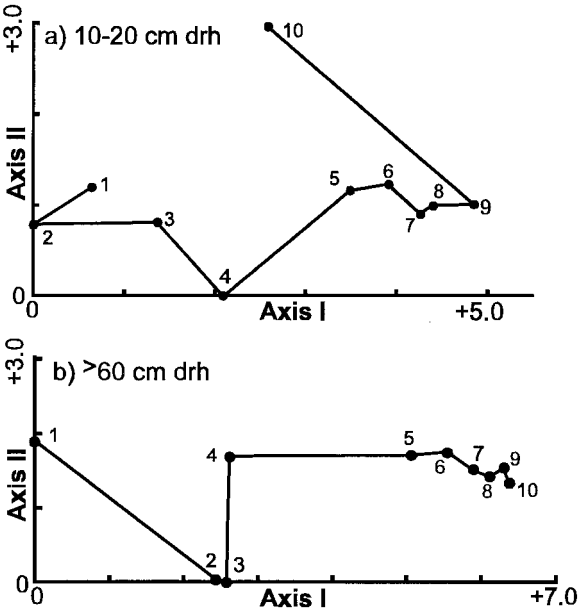


Figure 2. (a) DCA of Eggeling's (1947) data for stems between 10 and 20 cm drh (first two axes). Axis I accounts for 25% of variation in abundances (subsequent axes 5%, 2%, 0.4%). (b) As in 2a, but for stems ≥60-cm drh. Axis I accounts for 30% of variation (subsequent three axes account for 6% 3% and 2%).

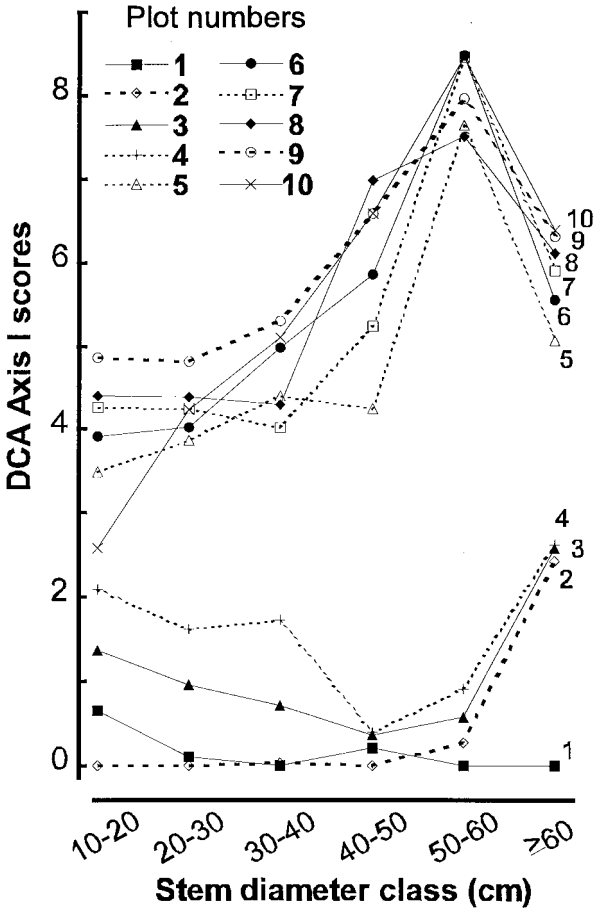


Figure 3. DCA first axis position by stem size-class for Eggeling's series. Lines assist the identification of plot by size-class.

classes (Figure 2). Many additional ordinations were performed but provided similar results (Sheil 1996a). The relationships of first axis-gradient lengths and comparative plot positions by stem-size are demonstrated for the full data in Figure 3. The ≥60-cm drh class has perfect ordering with Eggeling's model (exact probability, $p = 1/10!$ or $2.8 \times 10^{-7***}$).

Comparative-series

The development scoring procedure was applied to each stem-class for each plot. Results are plotted in Figure 4, and can be compared with the 'expectation' of Figure 1. Each 'requirement' 1 to 4 provides a testable hypothesis:

Requirement 1. Sequential-progression. The ranking of the plots along the species turnover model is positive for all stem-classes (Table 2).

Requirement 2. Sequential-convergent-trend. Figure 4, suggests that composition does indeed stabilise both against the model (Figure 4a) and more generally (e.g., Figure 4b). Nevertheless, this cannot be formally assessed in a series where age-differences are unknown. The *Cynometra* forest plots (Plot 9 & 10) are the end-point of this progression.

Requirement 3. Intrinsic-progression. The relative rankings of the size-classes within plots demonstrate the expected order in eight of the ten plots (see Table 3, 8:2 has a one-sided binomial probability of 0.05*). Plots 5 and 6 both show perfect correspondence (exact probability $p = 1/6!$, $= 0.004^{**}$ for each). Plot 10 provides a significant negative result.

Requirement 4. Intrinsic-convergent-trend. Convergence of composition is clear in Figure 4. The difference in Axis I score for 10–20 and ≥60-cm diameter-classes by plot gives $\tau = 0.56$, $p = 0.025^{*}$, $n = 10$, or [as this includes negative values] a rank based upon absolute scores provides τ as 0.422 $p = 0.089$. This convergent pattern is even more pronounced when all classes are examined together – either as maximum to minimum spread, or standard deviation, of scores by plot ($\tau = 0.689 p = 0.0056^{**}$, $n = 10$, for both). Compositional convergence is also seen more generally, e.g., Figure 4b.

Table 2. Plot number against relative position on DCA axis one of stems over 60 cm diameter (see Figure 4a) Kendall's rank correlations by size class (diameter class in cm) ($n = 10$).

drh class cm	10–20	20–30	30–40	40–50	50–60
Kendall's τ	0.42	0.69	0.69	0.69	0.87
p	*0.089*	*0.0056***	0.0056**	0.0056**	0.0005***

The standard asterisk-shorthand is used to draw attention to notable p values, All p values relate to two-sided null-hypotheses.

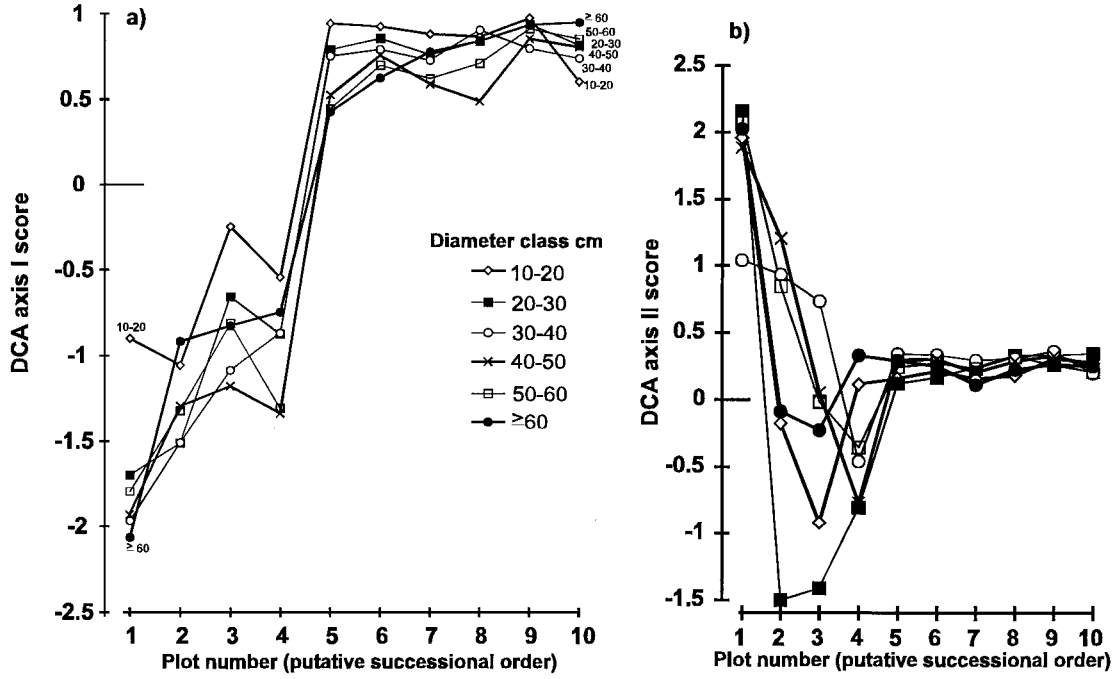


Figure 4. (a) First-axis positions of Eggeling's series by stem size-class passively arranged over the ≥60-cm drh DCA (Figure 2b). The interpretation of this figure is assisted by reference to Figure 1. The passive ordination accounts for 30% of total variance on the constrained axis (cf, Figure 2b), but additional variation is accounted for in the remaining three unconstrained axes, i.e., 28%, 19% and 7.5%. (b) shows the first unconstrained axis values from this same analysis.

Time-series

The time-series results can be viewed in Figure 5. Plot 15 (originally woodland) has progressed in all six size-classes over the three observations. Plot 2, shows little change prior to interventions, and subsequently shows a positive net development in the smaller stem sizes while progress in large-stem composition is unclear. Plot 5 shows no clear trend prior to interventions, and subsequently indicates a net regression for smaller stem sizes and a less clear pattern in large sizes. Plot 6 has regressed. The undisturbed Plot 7 shows a mixed and complex behaviour, with the ≥60-cm class showing positive succession over time ($p = 0.0015^{**}$, Kendall's τ, $n = 8$), and the 50–60-cm class showing a distinct negative trend ($p = 0.0018^{**}$, Kendall's τ, $n = 8$). There are no clear trends in compositional convergence (*Requirements 2* and *4*) in any plot.

Relative size-class orders were evaluated as indicators of composition trend across the time-series for each plot following '*Requirement 3. Intrinsic progression*' (all by Kendall's τ rank correlation of the 6 size-classes). Plot 15 maintains a positive (theory affirming) relationship ($p = 0.038^{*}$). Plot 2 has rearranged over time into a positive form ($p = 0.038^{*}$), having started out as negative from 1940 to 45 ($p = 0.0143^{*}$). Plot 5 started as positive ($p = 0.05^{*}$ in 1940, $p = 0.0048^{**}$ in 1948) but has become disordered by 1992 (Kendall's τ, negative, $p > 0.5$). Plot 7 reveals no consistent intrinsic trend.

Table 3. Size class (diameter classes in cm) rank correlations of DCA position against relative size ($n = 6$). All p values relate to two-sided null-hypotheses.

Plot	1	2	3	4	5	6	7	8	9	10
Kendall's τ	0.60	−0.33	0.47	0.20	1.00	1.00	0.33	0.33	0.20	−0.73
p	0.091	0.35	0.19	0.57	0.005**	0.005**	0.35	0.35	0.57	0.039*

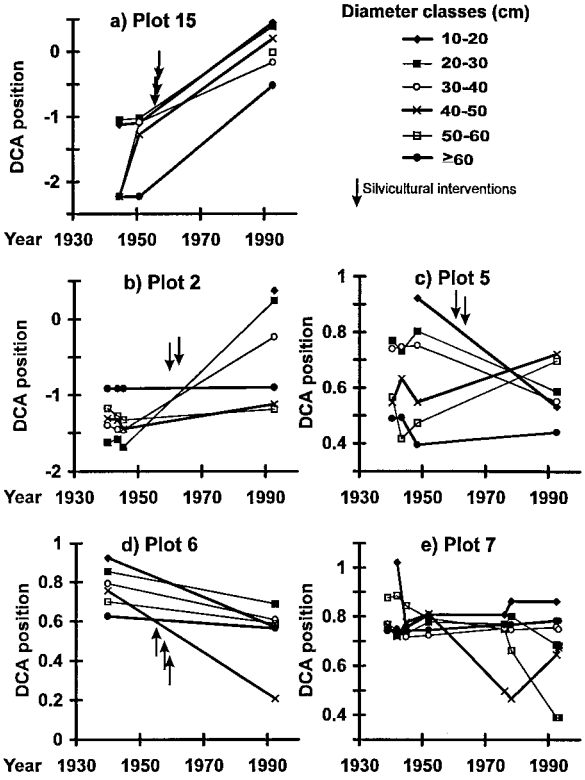


Figure 5. First axis positions of the time-series by stem size-class passively arranged over the ≥60-cm drh DCA model. Note that the scaling of the Y-axis differs between graphs. A positive succession, *i.e.* in accord with expectation, is demonstrated by positive change on the Y-axis. For Plot 6, Eggeling's (1947) data is used for the initial '1940' observation, as there is no other early 'all-species' data for this plot.

Discussion

What can these tests imply?

Eggeling's compositional turnover is composed of steps (community A becomes community B, etc.), and of many species. Each of these elements could be addressed as separate hypothesis. Such a reductionist analysis was not the purpose of this study. The overall consistency of the model has implications for other holistic properties of the sequence, i.e., the associated rise and fall in species-richness.

The approach presented here appears logical, includes a minimum of necessary assumptions, and many of the test-statistics reach high levels of significance. It is however, also true that the 'generality' of the results are somewhat compromised. Eggeling's plots were chosen to illustrate his model, and do not objectively represent the whole forest (though he was attempting to illustrate all major types and sub-types). The statistical tests evaluate the consistency of Eggeling's data with Eggeling's model. The null-model is an extreme version of Hewetson's (1956) claim of disorder, i.e., that Eggeling's data are randomly assembled. Non-conformation of the model with the original data would have undermined Eggeling's model, i.e., falsification, or lack of corroboration, *were* logical possibilities. On the other hand, confirmation of the model with the original data provides credibility to the original hypotheses, and to the model.

How consistent are the model and data?

The comparative-data show consistency with Eggeling's model. This contradicts Hewetson's (1956) accusation that their was no evidence for Eggeling's structured views. The plots have been selected in such a way that (1) sequential composition progression, (2) apparent trend towards stability, (3) internal progression, and (4) compositional convergence, are all evident. Though Eggeling was undoubtedly a meticulous observer such results appear difficult to generate by selection alone in a non-successional system (none of the notable, and in some cases sceptical, individuals visiting or working on these plots has ever reported any selection biases, e.g., W. J. Eggeling, H. C. Dawkins, M. S. Philip, A. Katende, A. Aubreville, T. Synnott – Sheil 1996a, and unpublished correspondance). Observations of forest expansion, the implication of age-gradients, and the (pre-management) spatial patterns of the forest types further bolster Eggeling's interpre-

tation. In addition there are clear trends of increasing shade-tolerance across Eggeling's series (by species based guild-classes and counted both by stems and species, this is true for all size-classes, Sheil 1996a). The consistency of the model has been demonstrated. The time-series data offer a more powerful evaluation of Eggeling's hypotheses.

Plot 15 was not used in model development and the positive (theory affirming) development, *woodland* to *mixed-forest*, is clear although never in doubt. The positive size-structured patterns in the 1992 vegetation of both Plot 15 and Plot 2, are less expected. If progression of the time-series data had been general, then calibration would have allowed forest-age to be estimated from composition (i.e., derive Θ from θ). This may be possible in other studies

The interventions, in all but Plot 7, confound ready interpretation of subsequent behaviours. Silvicultural treatments might either accelerate or reverse an implied successional change depending upon the species removed and the stems replacing them. Such modified vegetation may eventually recover and show the same trends as more pristine forest. Younger forests generally have higher stem-turnover (Sheil 1996b), so it is notable that it is Plots 15 and 2, the youngest time-series plots, that have regained positive composition structure since treatment, an observation seemingly consistent with rapid recovery.

The overall time-series results suggest the model does not provide a good prediction of short-term development in mid-succession or of longer-term development in later succession within these plots. Various explanations can be suggested. Firstly, the model is and was incorrect – if this is the case, it is unclear how Eggeling could have selected his original plots with such specificity (see previous discussions). Secondly, the model may be correct but suffer from a poor signal-to-noise-ratio in the time-series, i.e., the data sets are too short-term, too limited in size, and affected by random events, such that general trends are obscured. This argument implies that larger samples or longer time periods would ultimately conform to expectation – it should be noted that these plots are almost 2 ha each, and represent some of the longest tropical-forest time-series in existence. Thirdly, the model may have been valid prior to Eggeling's time but, since then, successional determinants have changed. Many environmental factors have indeed changed (Sheil 1998). Research itself may have a detectable impact (Sheil 1995's type 2 artefacts). Elephant populations, and their decline, have been identified as amongst the likely major influences (Laws et al. 1975; Sheil 1996a, 1998). Many factors affect vegetation, and these are not addressed by Eggeling's non-mechanistic model. The following sections do not pursue these issues but examine the model and results in more detail.

The size-structured analyses

The consistency of the size-structured evaluations is impressive, but requires appraisal. The analyses here have used rank-methods to generate significance values; these are justified if the observations are independent in relation to the hypothesis under evaluation. The null hypothesis of 'random' communities appears extreme. Neighbouring size-classes within a plot will certainly include overlap in stem-ages, yet it is the structure of this relationship, and the inherent compositional trends that have been predicted by the model that are being assessed here – though on a plot by plot basis. These within-plot results are certainly more convincing in their generality amongst plots (8 out of 10). A greater concern is that the developmental scores may be inherently biased by size-class due to influences of different species-stand-structures. This would affect the assessment of intrinsic-progression (*requirement 3*) in particular. Any size-bias would be visible in a mature 'fully converged' community (i.e. without bias these scores would be equal). Thus the odd, and significant, reverse order seen for Plot 10's stem-classes is of interest, and suggests that the '$\theta(\mathbf{A}_{\text{canopy}}) - \theta(\mathbf{A}_{\text{saplings}})$' may ultimately be negative (see *requirement 4*). A negative bias would oppose the rankings predicted by Eggeling's model and is not an explanation for the general positive results (8 out of 10 plots). Community-specific correction terms could be estimated if sufficient data were available (e.g., a transition matrix approach could determine mean stable age-stage distributions for each species).

What else do the results suggest?

It has often been concluded that canopy-species are the most consistent floristic consideration for the ecological classification of tropical forest (Webb et al. 1967, 1970; Austin & Greig-Smith 1968; Greig-Smith 1971; Orloci & Mukkattu 1973; Knight 1975; Newbery et al. 1986). Here again the largest size-class best conforms to a perceived typology. The larger stems also reveal greater overall Axis I lengths than the small stems, with few shared species between Plots 1, 2–4 and 5–10 which cluster into three groups on the Axis while the composition in the smaller size-classes appears more

continuous in nature. It is important to recognise that Eggeling's model has been developed and stated at an explicit scale, i.e., 1–2 ha, and does not address heterogeneity at smaller scales. The size-class DCA evaluations, and in particular the behaviour off the smallest stems, may reflect a 'mosaic-nature' in late succession in which the oldest plots include short-lived areas of small stems with a 'younger composition' (cf., Aubreville 1938; Swaine & Hall 1988). This may also be relevant for the reverse composition-by-size structure found for Plot 10.

The pattern of Figure 4a, implies a general agreement with the hypotheses illustrated in Figure 1. The difference between Plots 4 and 5 implies a poorly represented transition, but the time-series data provide many scores in this -0.5 to 0.5 range (Figure 5) showing that the model is not compromised in this zone. The meaning of the second axis in the model (Figure 4b, the first unconstrained axis) is unknown but may reflect residual variation related to the *Maesopsis* and woodland-colonising-forest sub-types (Eggeling 1947). There is compositional convergence on Eggeling's *Cynometra* dominated *Ironwood* forest.

Various distortions can arise in DCA, particularly when species are not well dispersed along the primary gradient (Ter Braak & Barendregt 1986; Ter Braak 1985; Ter Braak & Prentice 1988). It appears that, as observed, compositional resolution will deteriorate in late-succession as no additional species are gained. Other techniques such as Nonmetric-Multi-Dimensional-Scaling (Kruskal 1964a, b; Kenkel & Orloci 1986) warrant evaluation as alternative approaches.

Outstanding issues

Succession and multivariate analysis are both characterised by controversy – it is inevitable that a succinct account will leave 'loose-ends', but it is noted that:

– A general age-size relation has been assumed but not demonstrated. Boucher (1997) provides a review that justifies the generality of such relations, but multimodal size-age distributions are theoretically possible (e.g., Huston 1986, and refs.).

– The model assumes that small-stem composition predicts future canopy composition, and thus requires that composition be largely defined before the $\geq$10-cm drh size is reached. This does not seem unreasonable as an approximation, but contrasts with the details of some persuasive mechanistic models (e.g., Kohyama 1993).

Conclusions

This paper has demonstrated how an objective measure of development can be formulated with respect to a given successional model. This clarifies hypotheses and eases testing. The approach, and the derivation of compositional scoring procedures, has both intuitive clarity and a potential for wider adaptation and application.

Eggeling's (1947) data series show consistency with his successional interpretation. The analyses confirm compositional progression and apparent convergence across the plot series, and also progression and convergence within each plot. A low-diversity *Cynometra* forest is confirmed as an end-point in the succession. The time-series results, though in apparent agreement for one early successional plot, do not generally accord with Eggeling's ideas. The most likely explanation is that successional processes have changed. We must now seek an improved understanding of such changes and their consequences.

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