Plurality of tree species responses to drought perturbation in Bornean tropical rain forest

D. M. Newbery · M. Lingenfelder

Abstract Drought perturbation driven by the El Niño Southern Oscillation (ENSO) is a principal stochastic variable determining the dynamics of lowland rain forest in S.E. Asia. Mortality, recruitment and stem growth rates at Danum in Sabah (Malaysian Borneo) were recorded in two 4-ha plots (trees $\geq$ 10 cm gbh) for two periods, 1986–1996 and 1996–2001. Mortality and growth were also recorded in a sample of subplots for small trees (10 to <50 cm gbh) in two sub-periods, 1996–1999 and 1999–2001. Dynamics variables were employed to build indices of drought response for each of the 34 most abundant plot-level species (22 at the subplot level), these being interval-weighted percentage changes between periods and sub-periods. A significant yet complex effect of the strong 1997/1998 drought at the forest community level was shown by randomization procedures followed by multiple hypothesis testing. Despite a general resistance of the forest to drought, large and significant differences in short-term responses were apparent for several species. Using a diagrammatic form of stability analysis, different species showed immediate or lagged effects, high or low degrees of resilience or even oscillatory dynamics. In the context of the local topographic gradient, species' responses define the newly termed perturbation response niche. The largest responses, particularly for recruitment and growth, were among the small trees, many of which are members of understorey taxa. The results bring with them a novel approach to understanding community dynamics: the kaleidoscopic complexity of idiosyncratic responses to stochastic perturbations suggests that *plurality*, rather than neutrality, of responses may be essential to understanding these tropical forests. The basis to the various responses lies with the mechanisms of tree-soil water relations which are physiologically predictable: the timing and intensity of the next drought, however, is not. To date, environmental stochasticity has been insufficiently incorporated into models of tropical forest dynamics, a step that might considerably improve the reality of theories about these globally important ecosystems.

Keywords Dynamics · Ecosystem · El Niño · Resilience · Stem growth · Tree mortality

D. M. Newbery (✉) · M. Lingenfelder
Institute of Plant Sciences, University of Bern,
Altenbergrain 21, CH 3013 Bern, Switzerland
e-mail: david.newbery@ips.unibe.ch

Introduction

Tropical rain forests are highly dynamic and responsive ecosystems. Their physical structure and processes may remain relatively stable over time, but species composition is thought to constantly fluctuate around a quasi-equilibrium or change slowly in the

long-term (Huston 1979, 1994). Perturbations drive these dynamics, and earlier ideas of equable tropical conditions have given way to the view that climate is indeed variable, particularly on the scale of decades to centuries (Newbery et al. 1999a). Droughts are the major cause of perturbation across much of South-East Asia, and are probably a main determinant of forest structure and tree species composition, in particular in Borneo. They are often associated with the El Niño Southern Oscillation (ENSO) cycle (Trenberth 1997; Trenberth and Hoar 1997; McPhaden 1999; Cane 2005). The last strong drought in Borneo was in 1997/1998 and prior to that 1982/1983 (Walsh 1996a, b; Walsh and Newbery 1999).

Global change scenarios for the tropics expect climate to become more unstable this century with more frequent and intense droughts (Hulme and Viner 1998; Timmermann et al. 1999). Not all models, however, predict more ENSO activity (Timmermann et al. 2004; Cane 2005; McPhaden et al. 2006; Meehl et al. 2007) although the risk of droughts is expected to increase during future El Niño events (Christensen et al. 2007), and this could have serious implications for forest management. Tropical rain forests appear to exist in variously complex and overlapping states of recovery from past perturbations, whether singular or multiply clustered, recent or from the distant past (Newbery et al. 1999a, b; Newbery and Lingenfelder 2004). Measuring how these forests respond to the perturbations could lead to valuable models of how changes in drought frequency and intensity affect their future. It might also allow a rethinking in tropical rain forest dynamics with broader considerations for rain forest conservation.

Forests in parts of Borneo are apparently still recovering from a very strong drought c. 130 years ago (Newbery et al. 1992; Walsh and Newbery 1999) with tree species appearing well adapted to the several less-severe intervening events (Gibbons 1998; Newbery et al. 1999b; Gibbons and Newbery 2003; Newbery and Lingenfelder 2004). Setbacks in forest biomass temporarily destabilize the ecosystem, but over centuries a form of dynamic equilibrium is presumably attained. Uncertain though is how far from this equilibrium are these forests due to the 1997/1998 and earlier droughts, and whether they have a high enough resilience to recover before the next one (Newbery and Lingenfelder 2004).

In Central America, intensification of the 1982/1983 dry season by the ENSO that year, together with a regional trend of decreasing rainfall since 1965, have been shown to affect tree mortality and forest population change, and account for species' geographical distributions (Condit et al. 1995, 1996, 2004; Engelbrecht et al. 2007). This situation contrasts in interesting ways to that of Borneo with its regionally steady environment punctuated by occasional strong drought. Indeed when generally comparing drought effects worldwide, it is important to place these usual periods of large water deficit within the context of any long-term regular (annual or supra-annual) patterns characterizing the regional climate.

This paper reports on the impact of this 1997/1998 drought on lowland dipterocarp rain forest dynamics in the Danum Valley Conservation Area, Sabah, Malaysia (Marsh and Greer 1992), a site c. 70 km inland of the north-eastern coast of Borneo. With precise enumeration data over a 15-year period, collected before and after the drought on a large sample of trees, changes to the most abundant species and estimated ecosystem resilience are quantified. An omnibus test of the null model that there were no species-specific responses at the community level was performed. An attempt of this kind for tropical ecosystem dynamics has to our knowledge not hitherto been made. Finally, a new concept of rain forest dynamics emerging from this work is presented.

Climate

Meteorological data have been recorded at Danum Valley Field Centre (DVFC, 152 m a.s.l.) since July 1985. Monthly mean temperatures ranged 1.8°C about an annual mean temperature of 26.8°C, while the mean daily range was 8.6°C. The highest temperature was recorded in April 1992 with 36.5°C, the lowest in January 1993 with 16.5°C. Relative humidity varied between 95.3% at 08:00 and 78.3% at 14:00. These values are typical of equatorial rainforest locations (Walsh 1996b).

Mean annual rainfall (±SE) across complete years 1986–2003 was 2,825 ± 110 mm with a range from 1,918 mm in 1,997–3,539 mm in 2003. During the study period of 1986 to 2001 mean annual rainfall was

$2,787 \pm 115$ mm. Annual monthly rainfall ($\pm$SE) from July 1985 to December 2003 was 235 ± 13 mm ranging from 158 mm in April to 312 mm in January. For the study period the corresponding mean was 232 ± 13 mm. Mean rainfall in the month of April was significantly different from the annual monthly mean from 1985 to 2003 (Mann–Whitney U-test: $P = 0.006$), varying from 11 mm in 1998—the lowest monthly value on record—to 433 mm in 1999, the wettest month of that year. With 701.2 mm of rain, December 2003 was the wettest month on record at Danum. Although rainfall in the months of April and July/August on average was well below the annual monthly mean, rainfall fluctuated considerably between years as well as between months. There is no clear dry season indicating that Danum has a generally aseasonal tropical climate.

Since the start of meteorological data collection, Danum experienced 38 droughts, defined as periods with running 30-day rainfall total (R_{30}) < 100 mm for rain forests not short of water (Brünig 1969; Malhi and Wright 2004). These include two ENSO-related drought events in 1991/1992(–1994) and in 1997/1998. Before that, in 1982/1983, a strong ENSO-event affected Sabah (Beaman et al. 1985; Woods 1989) and may have had effects at Danum. Very strong droughts have been recorded in the late 19th and early 20th centuries at regional scales throughout Sabah (Walsh 1996a, b). In 1997/1998 drought effects on forest vegetation were reported to be stronger in Sarawak (Nakagawa et al. 2000; Potts 2003).

Methods

Antecedent rainfall history

For rain forest vegetation that is not short of water, water stress is assumed to set in when the monthly mean rainfall drops below 100 mm, the estimated value for evapotranspiration in the tropics (Brünig 1969, 1971; Walsh 1996b; Walsh and Newbery 1999; Malhi et al. 2002; Malhi and Wright 2004). For the daily rainfall data available, this threshold can be applied to R_{30}, the 30-day running total of rainfall. Droughts can be assessed by calculating an intensity index that takes into account the deficit (R_{30}–100) and the drought duration (Newbery and Lingenfelder 2004).

This approach, however, neglects the rainfall preceding the 30-day periods. A period of rainfall below 100 mm that had low rainfall in the months before would, assuming that the soil water reservoir was already depleted, likely be more severe for the trees than such a period with high rainfall preceding it, in which case water would probably be still available from storage in the soil (Malhi and Wright 2004; R. P. D. Walsh, pers. comm.). Water stress caused by a deficit in soil water tends to affect the forest immediately (in <15 days), but some time is required (c. 60 days in a central Amazonian rain forest) for the soil to be recharged with water after a dry season (Malhi et al. 2002).

Antecedent rainfall history was brought into the calculation of drought intensity in the following way. Across the 18.5 years for which data were available, Julian-day rainfall was averaged to give mean values of what the vegetation might 'expect'—the annual distribution of rainfall to which its species have generally been subjected. This was termed the mean daily rainfall, MDR (Fig. 1). The difference between the actual and mean daily rainfall (ADR–MDR), the daily rainfall anomaly (DRA), was accumulated across 90, 180 and 365 days prior to each day (the accumulated rainfall anomaly, ARA). For any one day ARA gave the sum of rainfall across the selected period that was a deficit or a surplus to the expected average for that period.

Plots and enumerations

Two permanent plots were set up and first enumerated in 1985–1986. They lie 0.8 km NW of Danum Valley Field Centre, 0.3 km apart on gently undulating terrain at c. 200–250 m asl. Each plot has dimensions 100 m $\times$ 400 m (total area = 8 ha). Eight 40 m $\times$ 40 m subplots were selected in a stratified random manner within each plot in 1998 (area = 2.56 ha), half on lower slopes (<12 m elevation) and half on ridges ($\geq$25 m). For further information about the site and the plots see Newbery et al. (1992, 1996) and Newbery and Lingenfelder (2004).

Plots were enumerated in (1) August 1985–December 1986, (2) November 1995–February 1997 and (3) February 2001–February 2002; and subplots alone in December 1998–March 1999. All trees
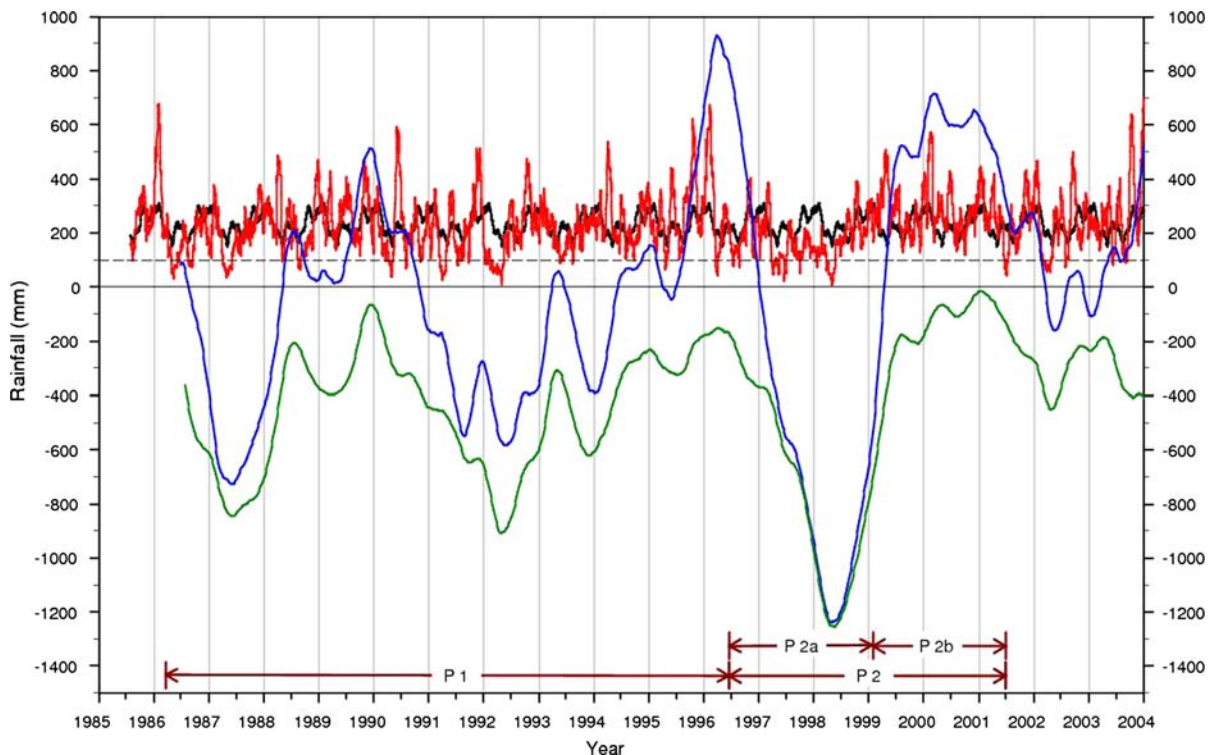
Fig. 1 Accumulated rainfall anomalies (*ARA*) with conditions applied at Danum, 1985–2003: R_{30} of mean daily (*MDR*; black line) and actual (*ADR*; red) rainfall, ARA_{365} (blue) and accumulation only when $R_{30} < 232$ mm (*CARA*$_{232}$; dark green); dashed reference at 100 mm (see text for explanations). Smoothing algorithm used a negative exponential function with sampling proportion equal to 0.02 (smoothing showed not all of the individual shorter and milder drought events as defined but was nevertheless preferred over the raw data for clarity). Intervals between plot measurements are shown as periods P1 and P2, and sub-periods P2a and P2b

≥10.0 cm stem *gbh* (girth at breast height) or 3.18 cm *dbh* (diameter), were measured for *gbh* (above buttresses where these occurred), mapped and identified at each plot census; deaths were recorded, and recruits enumerated, in 1996 and 2001. In subplots trees 10 to <50 cm *gbh* (small trees) were remeasured, and deaths recorded: in 1999 limited resources did not permit the measurement and identification of recruits. In 1996–2001 a system of identifying suitable trees for valid growth rate estimates was introduced. Plots 1 and 2 had 17,942, 17,265 and 16,623 trees ≥10 stem *gbh* in 1986, 1996 and 2001, respectively, of correspondingly 450, 466 and 489 species. With 98% of trees identified to named species, 2% stayed at unnamed but distinct taxa. Voucher material is held at the Rijksherbarium (Leiden) and the Sabah Forest Department Herbarium (Sepilok, near Sandakan).

At the plot level all measured trees were considered. The intervals 1986–1996 and 1996–2001 were designated periods P1 (10.0 years) and P2 (5.0 years), respectively. At the subplot level only small trees were considered at the four dates: recruits in 1996 and 2001 were omitted. Period P2 was subdivided into sub-periods P2a (1996–1999, 2.6 years) and P2b (1999–2001, 2.4 years; see Fig. 1). Further, for all trees three size classes were defined: small, 10 to <50; medium, 50 to <100 and large ≥ 100 cm *gbh*; and for small trees four 10 cm *gbh* classes.

Species selection

As many species had too few individuals to permit reliable analysis, those 34 with $n \geq 100$ trees, in both plots together, in either 1986, 1996 or 2001 were selected. This gave $n \geq 60$ valid trees per species for

growth estimates. Newbery et al. (1999) give the basis for these sample sizes. These abundant species represented on average 60% of all trees enumerated in 1986–1996–2001. For the subplots, the 22 species each with $n \geq 50$ small trees in 1986 were selected: they represented on average 53% of the populations.

Dynamics rates

Annualized rates (% year^{-1}) of mortality (m_a) and recruitment (r_a) were based on the numbers of trees that died (n_d) or recruited (n_r) relative to those at the start of intervals (n_{start}) and mean time intervals (t) per species:

$$m_a = \left(1 - \left(1 - \frac{n_d}{n_{start}}\right)^{\frac{1}{t}}\right) \cdot 100$$

$$r_a = \left(\left(1 + \frac{n_r}{n_{start}}\right)^{\frac{1}{t}} - 1\right) \cdot 100$$

were derived (Sheil et al. 1995; Alder 1996). Calculations of mortality and recruitment rates on the plot or subplot level, or for different species and size classes, used the mean time intervals of each individual group. Regressors, trees that decreased in size to < 10 cm gbh but remained alive (Lingenfelder 2005), were not considered in the present analysis. Confidence limits of means (95%) of m_a were found using an approximation based on the F-distribution (Alder 1996; Nelson 1982). Recruitment was based on the size of each period's starting population because the dynamics of the forest was in a state of strong disequilibrium over the 15 years recorded. Using final population sizes (i.e. the numbers of survivors), as have Phillips et al. (1994), would have led to the estimate of r_a being confounded by the effect of the drought on m_a.

Annualized mortality rate, m_a, in period P1 was adjusted to a 5.0-year basis (to equate period P2) following the correction procedure of Newbery and Lingenfelder (2004). The approach was based on the earlier theoretical analysis of Sheil and May (1996). Correction factors (i.e. the numbers by which the original values of m_a must be multiplied) for the rates of all trees in the plots, and for their size classes (small, medium and large) were correspondingly 1.04 (1.03, 1.08 and 1.10). In an analogous way, for small trees in subplots, the correction factors for period P1 and sub-periods 2a and 2b were 1.11, 0.83 and 0.85, respectively. These last values were also applied to

the 10-cm gbh size classes of small trees without differentiation. The correction procedure assumes that the major source of heterogeneity within tree populations lies with species-specific differences in m_a. A similar correction procedure for r_a is unknown.

Relative (rgr; mm m^{-1} year^{-1}) stem growth rates were calculated from gbh at the start and the end of an interval for valid trees, based on time intervals of each tree.

$$rgr = \frac{(\ln(gbh_{end}) - \ln(gbh_{start}))}{t} \cdot 10^3$$

For a growth rate to be valid between enumerations the previous point of measurement on the stem should not have moved (due a problem at the old point) or been lost (e.g. due to tree breakage), and the stem was in an optimal condition (i.e. no new buttress growth; no cracks, splits or embedded lianas in, or excrescences or termites on, the bark; absence of deformations such as strong fluting or hollowness, a pronounced oval cross-section or spiral form; and not based on relascopic measurement—a few very large trees). A bootstrapping procedure using $N = 2,000$ runs found the means and 95% confidence limits to rgr (with GenStat 7/8, Payne 2000).

Drought response index

Percentage response to drought (R_D) of a dynamic rate variable, v, was calculated as the difference in v between periods P1 and P2 (v_1, v_2) relative to the weighted mean of the rates in these periods. The rate in P1 received double the weight of that in P2 to reflect the relative interval lengths of 10.0 and 5.0 years:

$$R_{D\_1,2} = ((v_2 - v_1) \cdot 300)/(2v_1 + v_2)$$

R_D had a minimum of -150% when v_2 was 0, and a maximum of 300% when v_1 was 0. The R_D for m_a was multiplied by -1 so that decreases in m_a indicated positive responses, in a similar manner to increases in r_a and rgr. A new composite index cmp was constructed using squares of loadings on the first axis of a principal component analysis as linear coefficients (m_a -0.587, r_a -0.451 and rgr -0.672):

$$R_{D\_cmp} = 0.345 \cdot R_{D\_m_a} + 0.203.R_{D\_r_a} + 0.452.R_{D\_rgr}$$

(correlation-based; $\lambda = \{0.42, 0.32, 0.26\}$).

Percentage response to drought was found for P1–P2a ($R_{D\_1,2a}$), P2a–P2b ($R_{D\_2a,2b}$), and P1–P2b ($R_{D\_1,2b}$), using m_a or rgr as variable v. Sub-periods P2a and P2b were each taken to be c. 2.5 years in duration so that the relative weights for P1 and either P2a or P2b would be 4 to 1:

$$R_{D\_1,2a} = ((v_{2a} - v_1) \cdot 500)/(4v_1 + v_{2a})$$

$$R_{D\_1,2b} = ((v_{2b} - v_1) \cdot 500)/(4v_1 + v_{2b})$$

$$R_{D\_2a,2b} = ((v_{2b} - v_{2a}) \cdot 200)/(v_{2a} + v_{2b})$$

Of the 22 species, *Reinwardtiodendron humile* was outlying because of its highly negative growth rates which strongly biased the weighted mean across species. In one case, m_a for *Lophopetalum becarrianum*, both v_1 and v_2 were 0 and $R_{D\_2a,2b}$ was also set to 0. With results for r_a lacking, a composite index was not calculated for the subplot-recorded species.

Randomization and multiple testing

To test whether species differed from one another significantly, more than would be expected had their dynamics variables been completely randomly distributed across trees of all species, a Monte Carlo approach was taken. Randomization simply removed species identity. For P1 and P2, deaths were re-assigned across all trees at random, to the same extent as was recorded. Samples equal in size to those of the 34 species' populations (with a further all-other-species sample) were randomly selected without replacement (FORTRAN77 program with NAG20 algorithms), and m_a and R_D calculated. The procedure was repeated a recommended $N = 5,000$ times (Manly 1997), and exact probabilities found as twice the percentile of the tail of the ranked values more extreme than that observed. Values of r_a were simulated in the same way, but for rgr all values were re-allocated at random across valid samples sizes. Individual randomized values of cmp were found as for the recorded data, and because they were weighted means of $j = 3$ variables it was necessary to re-scale them by multiplying by $\sqrt{j}$, and to re-adjust means to their original values.

To derive an overall test for the whole community individual species' tests needed to be combined as a 'family'. Family-wise error rate (FWER) tests of significance were achieved with the sequentially rejective procedure of Holm (1979) applying Sidák's adjustment to the Bonferroni α-level, and by finding the Benjamini–Hochberg false discovery rate (FDR) (Westfall and Young 1993; Benjamini and Hochberg 1995). The Holm procedure was applied to the values of rgr, but not m_a, of the 22 species of small trees in the subplots. For both 34- and 22-species data sets, the Bernoulli formula was applied to find the minimum numbers of species required to reject the null hypothesis of no family response at $\alpha = 0.05$, these being based on the lowest Bonferroni critical P-values allowed by the FDR for the four variables separately (Moran 2003).

Sidak's adjustment to the level of individual hypothesis rejection ($\alpha' = 1 - (1 - \alpha)^{1/k} = 0.001508$; $\alpha = 0.05$, $k = 34$) was used because it more powerful than that of Bonferroni ($\alpha' = 0.05/k = 0.001471$) yet it maintains a strong family-wise error rate (Westfall and Young 1993). The $N = 5,000$ randomizations allowed a lowest P-value of 0.0002 to be detected, which is well below α' in either case above. As a consequence, ranking could result in ties at this lowest level or simple multiples of it. In these cases, whilst the family-wise P-value at each step was the maximum of the previous and currently considered step, adjusted α'-values were averaged across ties (Appendix 3).

Stability analysis

Building upon the concepts of classical stability thinking, a diagrammatic approach was developed to highlight the different species' modes of response. Graphing R_{D1-2b} against R_{D1-2a} permitted an evaluation of each species' trajectory. The four quadrants (numbered clockwise) showed which species remained positive (1) or negative (3), and which switched from being positive to negative (2) or vice versa (4), between P2a and P2b. Diagonal lines, where Δ ($= R_{D1-2b}/R_{D1-2a}$) was either 1 or -1 represented no change between sub-periods, or a change in the opposite direction of the same magnitude, respectively. Subdividing, octants defined regions of stability and instability; numbered again clockwise they represented four types of response behaviour: destabilizing non-recovery (1', 5'; either increasingly positive or negative; $\Delta > 1$), stabilizing

recovery (2′, 6′; reduced positive and negative; $0 < \Delta > 1$), stabilizing oscillation (3′, 7′; positive switching to negative of less magnitude and the converse; $-1 < \Delta > 0$) and destabilizing oscillation (4′, 8′; positive switching to negative of greater magnitude and the converse $\Delta < -1$).

Results

Antecedent rainfall history

Values of *accumulated rainfall anomalies* across 90, 180 (not shown—see Lingenfelder 2005) and 365 days (ARA_{365}) ran roughly in parallel, with the 1 year curve having the strongest amplitudes both in rainfall deficit and surplus (Fig. 1). Accumulation of anomalies across 1 year is assumed to adequately reflect the water conditions and to reveal the severity of drought events by reflecting depletion or saturation of soil water content quantitatively rather than simply stating whether it was below or above a certain threshold value. With this approach, immediate strong rainfall deficits ($R_{30} < 100$ mm) as well as the ecologically more meaningful long-term (365-day) deficits are being picked up.

Definition of events

Forest on soil that was already water-saturated would not be able to make use of more rainfall, the excess running off or draining away. Whilst accumulating rainfall as *DRA* when R_{30} was < 100 mm would have been one possibility, the preferred solution took *DRA*-values when rainfall was below *MDR* (the average R_{30} of *MDR* being 232.2 mm), i.e. when the forest received less water than 'expected' (Fig. 1). Both 'conditional accumulations' ($CARA_{100}$, $CARA_{232}$) highlighted the main droughts at Danum during the period of climate records.

If a low precipitation event is taken to have occurred when ARA_{365} was < 0 (events were allowed to be interrupted by up to 8 days without breaking continuity), 19 such events occurred at Danum between July 1985 and December 2003 (Appendix 1). Six events were less than 10 days in duration. The longest-lasting event was that in 1990–1993, followed by 1997–1998, 1986–1988 and 1993–1994.

Drought intensity can thus be expressed as the sum of all daily rainfall anomalies (total *DRA*) within an event, the deficit in rainfall derived from the antecedent rainfall history (*DEFARH*).

Neglecting $R_{30} > 232$ mm ($CARA_{232}$), the 1997–1999 event was severest with $DEFARH = -1,846$ mm, followed by the 1990–1993 one with $DEFARH = -1,567$ mm (Appendix 1). In conclusion, between July 1985 and December 2003 three drought events were shown to be strong. Most severe was the one centred on 1998, followed by those centred on 1992 and 1987. The longest drought-free period by far was between April 1999 and March 2002.

Spectral analysis

The power spectral density function (or 'spectrum') was derived for several of the variables (Chatfield 2004; S-Plus 6 2001 version 7.0). Plots of $\log_{10}$ of spectral value versus $\log_{10}$ of frequency have characterizing slopes ranging from ~ 0 through -1 to ~ -2, these being commonly referred to as white, pink and brown noise, respectively (Steele 1985; Vasseur and Yodzis 2004). Results: *ADR*, -0.161; *DRA*, -0.153; R_{30}, -1.91; ARA_{365}, -1.96; $CARA_{100}$, -2.19; $CARA_{232}$, -1.98.

Forest dynamics

Overall response

Between periods P1 and P2, for all trees in plots, annualized mortality (m_a) and recruitment (r_a), and stem relative growth rate (*rgr*), increased by 45% (interval-corrected 25%), 12% and 12%, respectively (Table 1). Changes in the weighted means of the 34 most abundant species were very similar. Between period P1 and sub-period P2a, for small trees in subplots, m_a increased by 41% (interval-corrected 6%) but *rgr* decreased by 38%; and between period P1 and sub-period P2b the corresponding changes were increases of 51% (16%) and 11%. Thus, whilst m_a increased during the drought (P2a) and continued to rise slightly afterwards (P2b), *rgr* had a substantial decrease followed by a larger overcompensating increase. The weighted means of the 22 most abundant species at this level showed a similar response for m_a, but a stronger one for *rgr* (Table 1).

Table 1 Mortality (m_a), recruitment (r_a) and stem relative growth (rgr) rates for all (≥ 10 cm gbh) and small (10 to <50 cm gbh) in plots and subplots, respectively, over all individuals of all species

	m_a (% year^{-1})	r_a (% year^{-1})	rgr (mm m^{-1} year^{-1})
All trees/plots			
P1	1.59 (1.87)	1.24	11.14
P2	2.30 (2.34)	1.39	12.48
Small trees/subplots			
P1	1.54 (1.70)	1.31	10.85
P2a	2.17 (1.81)	–	6.79
P2b	2.32 (1.97)	–	13.36

Mortality values in parenthesis are 5.0-year interval corrected rates

Size class analysis

For all trees in the main plots the difference in m_a between periods P1 and P2 increased with tree size, and the R_{D1-2} became increasingly negative (Fig. 2a). Across the smaller size classes, for small trees in the subplots, trends were not apparent except in the

30–40 cm gbh class where m_a increased across periods and sub-periods (Fig. 2b). By contrast, for all trees in plots, rgr decreased roughly in parallel across size classes in periods P1 and P2 (Fig. 2c), but within the smaller size classes of small trees in subplots there was a strong change in relative differences between periods and sub-periods. In the lowest 10–20 cm gbh size class the decrease in rgr from period P1 to sub-period 2a, and the increase from sub-periods 2a to 2b, was much greater than in the highest 40–50 cm gbh class. The R_{D1_2a} and R_{D2a_2b}, respectively, increased and decreased in a linear manner with gbh (Fig. 2d).

Species dynamics

Plot and period scales

Between periods P1 and P2, the forest, as shown by the most abundant 34 species, became more dynamic (Table 2). Sample sizes are given in Appendix 2. Thirty-one species increased, and three decreased in m_a between P1 and P2 (Table 2). Species differed

Fig. 2 Annualized mortality (m_a) (**a**, **b**) and relative stem growth (rgr) (**c**, **d**) rates for all trees within three size classes (see text for definitions) in the main plots (**a**, **c**) for periods P1 (open bars) and P2 (grey bars), and for small trees within four smaller size classes in the subplots (**b**, **d**) for period 1 (open bars), and sub-periods P2a (light grey bars) and P2b (dark grey bars) at Danum. Error bars indicate 95% confidence limits. Weighted percent changes (% wresp) are shown by inverted triangles: P1–P2 and P1–P2a (open) and P2a–P2b (closed)
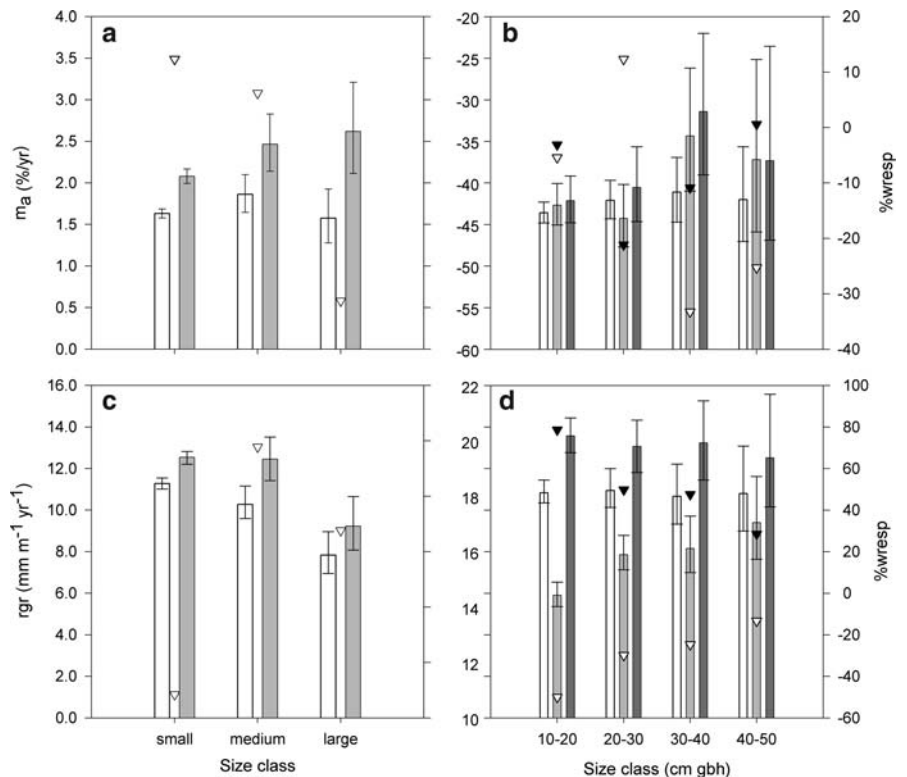
Table 2 Mortality (m_a; % year^{-1}), recruitment (r_a; % year^{-1}) and relative (rgr; mm m^{-1} year^{-1}) growth rates in periods P1 and P2 for the 34 most abundant species within plots at Danum

Code	Species	m_a		r_a		rgr	
		P1	P2	P1	P2	P1	P2
aj	*Alangium javanicum* Koord.	1.27	3.45	0.86	2.45	7.99	6.99
an	*Antidesma neurocarpum* Miq.	3.20	3.64	1.12	1.17	3.01	5.56
af	*Aporosa falcifera* Hook. f.	1.74	2.00	0.74	0.00	12.12	10.61
as	*Ardisia sanguinolenta* Blume	1.14	1.87	1.79	2.68	11.24	11.33
bt	*Baccaurea tetrandra* Müll. Arg.	1.06	1.46	0.40	1.06	8.10	7.59
bl	*Barringtonia lanceolata* (Ridl.) Payens	0.29	1.41	0.68	1.07	5.47	7.11
cs	*Chisocheton sarawakanus* Harms	1.16	1.48	0.87	0.52	12.06	11.88
cc	*Cleistanthus contractus* Airy Shaw	1.17	1.26	0.67	1.64	6.89	9.60
dr	*Dacryodes rostrata* (Blume) H. J. Lam	0.75	1.26	0.26	0.00	7.97	6.64
dm	*Dimorphocalyx muricatus* (Hook. f.) Airy Shaw	1.05	1.07	0.59	0.85	5.43	8.00
dc	*Dysoxylum cyrtobotryum* Miq.	1.65	1.43	0.69	0.62	17.63	15.91
fs	*Fordia splendidissima* (Blume ex Miq.) J. R. M. Buijsen	1.13	1.88	1.76	1.95	10.21	12.22
gk	*Gonystylus keithii* Airy Shaw	0.77	1.11	1.17	1.51	11.34	14.22
kl	*Knema latericia* Elmer	0.22	0.49	1.96	0.36	12.24	13.02
ln	*Lithocarpus nieuwenhuisii* (Seem.) A. Camus	1.01	1.24	0.47	0.68	15.30	17.87
lc	*Litsea caulocarpa* Merr.	2.45	3.88	2.56	1.88	16.26	20.36
lo	*Litsea ochracea* Boerl.	1.73	4.33	0.95	1.47	13.54	11.05
lb	*Lophopetalum beccarianum* Pierre & Ridl.	0.79	0.88	2.01	1.23	15.24	18.95
mk	*Madhuca korthalsii* H. J. Lam	0.58	1.22	1.11	1.06	10.65	12.21
mp	*Mallotus penangensis* Müll. Arg.	1.23	1.57	2.35	2.34	11.74	14.94
mw	*Mallotus wrayi* King ex Hook. f.	1.55	1.99	1.21	1.59	9.10	11.58
mc	*Maschalocorymbus corymbosus* (Blume) Bremek.	3.67	3.53	1.39	2.17	8.24	9.90
pm	*Parashorea malaanonan* Merr.	1.91	2.82	0.65	0.59	14.03	14.84
pl	*Pentace laxiflora* Merr.	1.28	3.45	1.08	0.45	21.03	20.54
pc	*Polyalthia cauliflora* Hook. f. & Thomson	1.29	1.42	0.56	1.22	5.01	6.58
pr	*Polyalthia rumphii* Merr.	0.96	1.02	0.82	0.98	11.95	14.03
ps	*Polyalthia sumatrana* King	1.14	1.19	1.04	0.88	15.50	17.15
px	*Polyalthia xanthopetala* Merr.	2.82	4.79	1.76	0.00	9.50	10.20
rh	*Reinwardtiodendron humile* (Hassk.) D. J. Mabberly	2.59	4.13	0.71	1.20	6.19	6.43
sf	*Shorea fallax* Meijer	2.35	3.25	2.52	1.84	17.97	15.75
sj	*Shorea johorensis* Foxworthy	4.01	5.12	1.32	1.98	38.35	29.71
sp	*Shorea parvifolia* Dyer	3.71	4.67	1.32	3.11	43.78	37.41
se	*Syzygium elopurae* (Ridl.) Merr. & L. M. Perry	1.42	1.77	0.51	0.00	5.66	6.17
st	*Syzygium tawaense* (Merr.) Masam.	1.37	2.44	1.00	0.00	13.41	15.39
	Means						
	Unweighted	1.60	2.31	1.15	1.19	12.77	13.28
	Weighted*	1.55	2.11	1.22	1.38	11.08	12.34

Families are found in Appendix 2(a)

* By the number of trees per species at the start of each period

considerably in annualized mortality rate (m_a) with ranges of 0.22–4.01 widening to 0.49–5.12% year^{-1} between P1 and P2 (Table 2). Weighted average m_a

in P2 was 36% higher than P1. During both periods, 21 species had lower, and 13 species had higher, than average m_a. Across the 34 species, m_a was

significantly correlated between periods ($r = 0.850$, df $= 32$, $P < 0.001$).

For annualized recruitment rate (r_a) species also ranged widely from 0.26–2.56 in P1 to 0.00–3.11% year^{-1} in P2. Fourteen species decreased and 20 increased in r_a between P1 and P2. Weighted mean r_a was only slightly (0.17% year^{-1}) higher in P2 than P1. The r_a was also significantly correlated between periods ($r = 0.445$, df $= 32$, $P = 0.008$). Mean turnover increased from 1.37 to 1.75% year^{-1} between periods, and mean difference between m_a and r_a widened from 0.46 to 1.12% year^{-1}.

Twenty-three species had higher relative growth rate (rgr) in P2 than P1, and eleven lower rgr. Weighted mean rgr increased by 11%, although ranges in rgr contracted slightly from 3.0–43.8 to

5.6–37.4 mm m^{-1} year^{-1} (Table 2). Across species, ln(rgr) was strongly positively correlated between periods ($r = 0.943$, df $= 32$, $P < 0.001$). The m_a, r_a and rgr were only weakly to marginally significantly positively inter-correlated, however ($r = 0.214$ to 0.348, df $= 32$, $P = 0.043$ to 0.225). The mean m_a of the 34 species was lower than that for all trees in the plots, whilst for r_a and rgr the means were closer (Table 1).

Subplot and sub-period scales

Within the subplots, of the 22 most common species (Table 3; sample sizes in Appendix 2), individual species' mortality rates (m_a), which had a range of 0.55 to 3.86% year^{-1} in P1, became more variable in

Table 3 Annualized mortality (m_a; % year^{-1}) and relative growth rates (rgr, mm m^{-1} year^{-1}) in period P1 and sub-periods P2a and P2b for the 22 most abundant species within subplots at Danum

Code	Species	m_a			rgr		
		P1	P2a	P2b	P1	P2a	P2b
af	*Aporosa falcifera*	0.85	1.17	1.35	12.80	5.42	9.52
as	*Ardisia sanguinolenta*	1.28	1.45	2.59	12.35	4.88	13.59
bt	*Baccaurea tetrandra*	1.27	1.12	2.07	8.37	3.92	12.49
cc	*Cleistanthus contractus*	1.24	1.23	1.30	7.81	4.03	14.93
dr	*Dacryodes rostrata*	0.72	3.54	1.74	7.49	6.99	9.06
dm	*Dimorphocalyx muricatus*	0.95	1.78	0.37	5.26	3.72	16.54
dc	*Dysoxylum cyrtobotryum*	2.10	2.90	1.16	20.28	12.56	18.76
fs	*Fordia splendidissima*	0.99	2.31	3.09	9.52	5.99	12.22
lc	*Litsea caulocarpa*	2.32	7.39	3.04	18.20	11.58	18.23
lo	*Litsea ochracea*	1.43	1.58	5.83	16.98	8.08	10.19
lb	*Lophopetalum beccarianum*	0.57	0.00	0.00	15.11	14.32	24.39
mk	*Madhuca korthalsii*	0.55	0.72	1.70	10.35	7.71	12.44
mp	*Mallotus penangensis*	1.47	1.41	0.00	12.10	8.35	13.87
mw	*Mallotus wrayi*	1.49	2.00	1.99	9.08	5.73	14.83
mc	*Maschalocorymbus corymbosus*	3.86	3.44	8.28	8.44	4.45	11.80
pl	*Pentace laxiflora*	2.31	4.14	2.72	16.03	9.03	16.41
pc	*Polyalthia cauliflora*	1.28	1.41	2.03	4.77	2.63	7.37
pr	*Polyalthia rumphii*	1.00	0.00	3.59	8.60	6.81	17.91
ps	*Polyalthia sumatrana*	1.06	2.70	2.31	17.54	15.18	23.57
px	*Polyalthia xanthopetala*	3.06	9.96	4.01	11.17	9.01	12.50
rh	*Reinwardtiodendron humile*	3.18	4.06	4.45	4.97	−2.46	7.84
sf	*Shorea fallax*	2.10	4.57	4.76	17.51	6.80	8.67
	Means						
	Unweighted	1.59	2.68	2.65	11.60	7.03	13.96
	Weighted*	1.52	2.26	2.26	10.11	6.08	14.11

* As Table 2

subperiods P2a and P2b where two species each had zero mortality, and maximum values were 10.0 and 8.3% year^{-1}, respectively (Table 3). Sixteen of the 22 species showed increases in m_a in P2a compared to P1. Six species decreased in m_a. Between P2a and P2b, 12 species increased and nine species decreased in m_a; and one species remained at zero mortality. Weighted mean m_a increased between P1 and P2a by 50% but then did not change in P2b. For rgr all species decreased between P1 and P2a, and all increased between P2a and P2b (Table 3).

Hypothesis testing of species' responses

Each set of 34 species' P-values from the randomization tests of $R_{D\_1,2}$, for m_a, r_a, rgr and cmp, were ranked from smallest to largest separately. The condition of a one-step procedure for multiple (simultaneous) testing that P-values be uniformly distributed was tested with the χ^2-statistic (df = 4) on frequencies in five bins of 0.2 between 0 and 1 (expected frequency in each = 6.8). The observed distributions were significantly non-uniform for r_a ($\chi^2 = 37.47$, $P \ll 0.0001$) and cmp ($\chi^2 = 21.59$, $P < 0.001$), but not for m_a ($\chi^2 = 4.53$, $P > 0.3$) and rgr ($\chi^2 = 5.41$, $P > 0.2$). Holm's sequential step-down procedure (Holm 1979) was used accordingly.

There existed a very low degree of logical interdependence between values when randomizing (without replacement) across species, i.e. one dead tree or recruit allocated to any one of the 34 species cannot be allocated to any of the others, or a high or low rgr value allocated to one species cannot be given to another species. The means ($\pm$SE) of the 528 pair-wise Pearson correlation coefficients ($N = 5,000$ simulated values) for each of the four variables, and the percentage variance accounted for by principal components analysis (based on r) on the first three axes, showed that the correlations involved were in fact negligible (Appendix 3).

For the 22 species of small trees in the subplots testing of responses for m_a was restricted. In an appreciable percentage of the randomization runs double-zero cases for the numbers of dead trees meant that R_D could not be found, and substitution of so many results with $R_D = 0$ would have been unsatisfactory. Furthermore, many species (15/22 with zero r_a-values c. 50–800 times out of 5,000) had 95%, and often 99%, upper and lower confidence

limits at the maximum or minimum of R_D possible, and so rejection of the individual-species' null hypotheses was largely impossible.

Species' response indices

Plot and period scales

Most species had increased R_D-values for m_a in P2 compared to P1, about equal numbers had increases and decreases in r_a, two-thirds increases in stem rgr, and two-thirds decreases in cmp (Fig. 3). The randomization tests followed by family-wise error rate adjustment highlighted one significant ($P < 0.01$) negative case for m_a (*Barringtonia lanceolata*) and one positive case for rgr (*Dimorphocalyx muricatus*) (Fig. 3a, c). For r_a, five species (*Aporosa falcifera*, *Dacryodes rostrata*, *Polyalthia xanthopetala*, *Syzygium elopurae* and *S. tawaense*) showed significantly ($P < 0.01$) negative responses, one other (*Knema latericia*) less so ($P < 0.05$); two species (*Cleistanthus contractus* and *Baccaurea tetrandra*) responded significantly and positively ($P < 0.05$) (Fig. 3b). Of 34 species, only one (*D. muricatus*) showed a significant cmp response (positive, $P < 0.01$; Fig. 3d).

Allowing for a $\leq 5\%$ false discovery rate (FDR), the analysis revealed just three further significant ($P < 0.05$) cases for r_a (negative—*Pentace laxiflora*, positive—*Polyalthia cauliflora* and *Shorea parvifolia*), and for rgr ($P < 0.01$) one more (positive—*Mallotus wrayi*) (Fig. 3b, c). The rate of increase in R_D per ranked-species (linear regression line) was highest for r_a (7.57%), less for m_a (3.59%) and lowest for rgr (1.90%), with cmp between m_a and rgr (2.47%). The R_{D1_2} of m_a, r_a and rgr were not significantly correlated with one another ($r = 0.047$ to 0.132, df = 32, $P > 0.25$). Mean m_a of the 34 species was lower than that of all trees in the plots, whilst for r_a and rgr it was close (Fig. 3). Note that among the positively responding species one, aj, in Fig. 3b was not significant because its sample size was the smallest of all species ($n = 101$), compared with the four significant species ($n = 206 - 324$): see Appendix 2 for full range of sample sizes. Applying the Bernoulli formula, a minimum of $k = 2, 5, 3$ and 2 (out of 34) individually significant results would have been needed to meet a family-wise level of $\alpha = 0.05$. On this basis r_a qualified with
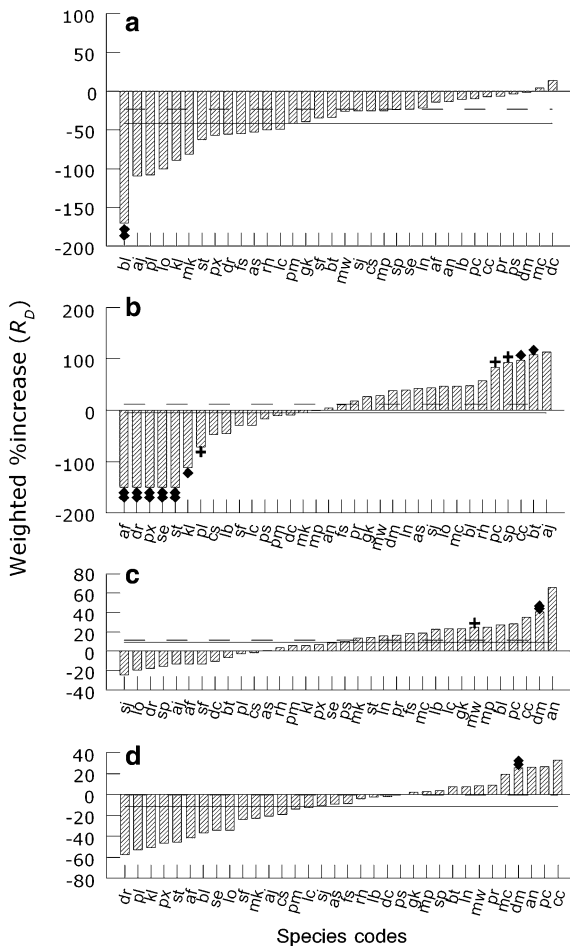
Fig. 3 Weighted percent changes between periods P1 (1986–1996) and P2 (1996–1999) in **a** mortality (m_a, inverted scale), **b** recruitment (r_a), **c** relative growth rate (*rgr*) and **d** a composite index (*cmp*) of the three variables, ranked for the 34 most common species in the main plots at Danum: solid line, weighted mean of the 34 species; dashed line, the overall values for all trees in plots. Codes for species are explained in Table 2. Species significance, determined by randomization tests and family-wise adjusted probability levels, is signified by number of diamonds over/under bars: two, $P \leq 0.01$; one, $P \leq 0.05$; and none, ns or $P > 0.05$. Crosses above bars indicate species additionally significant ($P \leq 0.05$) after controlling for false discovery rate

eight strong and three protected cases, but not m_a, *rgr* and *cmp*.

Subplot and sub-period scales

Within subplots three-quarters of the 22 species showed an increase in R_D-values for m_a in P2a and in P2b compared to P1: between P2a and P2b increases

balanced decreases (Fig. 4a–c). Despite the wide range in responses none could be shown to be significant ($P \leq 0.05$). All species had lower *rgr* in P2a than P1, all higher *rgr* in P2b than P2a which led to three-quarters with higher *rgr* in P2b than P1 (Fig. 4d–f). Randomization tests showed just one species with a significantly ($P \leq 0.01$) reduced *rgr* between P1 and P2a (*R. humile*), two with similarly significant increases between P2a and P2b (*R. humile*, *D. muricatus*) and P1 and P2b (*D. muricatus*, *Mallotus wrayi*), and one decrease ($P \leq 0.05$) in the last (*Shorea fallax*). Allowing for the FDR level led to no further significant cases.

Rates of increase in R_D with ranked species (outlier *R. humile* excluded) were similar for R_{D1-2a}, R_{D2a-2b} and R_{D1-2b} using m_a (11.8, 12.9 and 12.7 respectively), but increased for *rgr* (3.10, 4.97 and 6.61). Again, R_D for m_a and *rgr* were not significantly correlated within each of the (sub-) periods ($r = -0.103$ to 0.284, df = 20, $P \geq 0.20$). R_{D1-2a} and R_{D2a-2b} were significantly negatively correlated for m_a ($r = -0.497$, $P = 0.019$) and *rgr* ($r = -0.854$, $P < 0.001$); and conversely R_{D1-2b} and R_{D2a-2b} significantly positively so for m_a ($r = 0.735$, $P < 0.001$) and *rgr* ($r = 0.428$, $P = 0.047$): R_{D1-2a} and R_{D1-2b} being insignificantly correlated for m_a and *rgr* ($P > 0.45$). Mean m_a of the 22 species was very close to that for all trees in the plots, although for *rgr* it differed slightly (Fig. 4). Applying the Bernoulli formula again, a minimum of $k = 2$, 2 and 3 out of 22 individually significant results were needed to qualify for family-level significance. This requirement was met for *rgr* in sub-periods 2a–2b and period 1—sub-period 2b (Appendix 3).

Since m_a remained insignificant at the family level when the less conservative FDR procedure was applied to the 34 species, and the relationship between m_a and size (*gbh*) within the small trees was weak, it may be reasonably inferred that differences at the 22 species level would be insignificant too. Mortality was also likely to have shown much less response that *rgr* when moving from a 5.0-year to a 2.5-year period.

Between-scales correlation

The 16 subplots were nested stratified random sub-samples of the plots. Selecting the dynamics variables for the same 22 species studied at the subplot level

Fig. 4 Weighted percent changes in **a–c** mortality rate (m_a, inverted scale) and **d–f** relative growth rate (rgr) between period P1 (1986–1996) and sub-periods P2a (1996–1999) and P2b (1999–2001), as (**a** and **d**) P1–P2a, (**b** and **e**) P2a–P2b and (**c** and **f**) P1–P2b; ranked for the 22 most common species in the subplots at Danum. Lines, significance levels and species codes as in Fig. 3
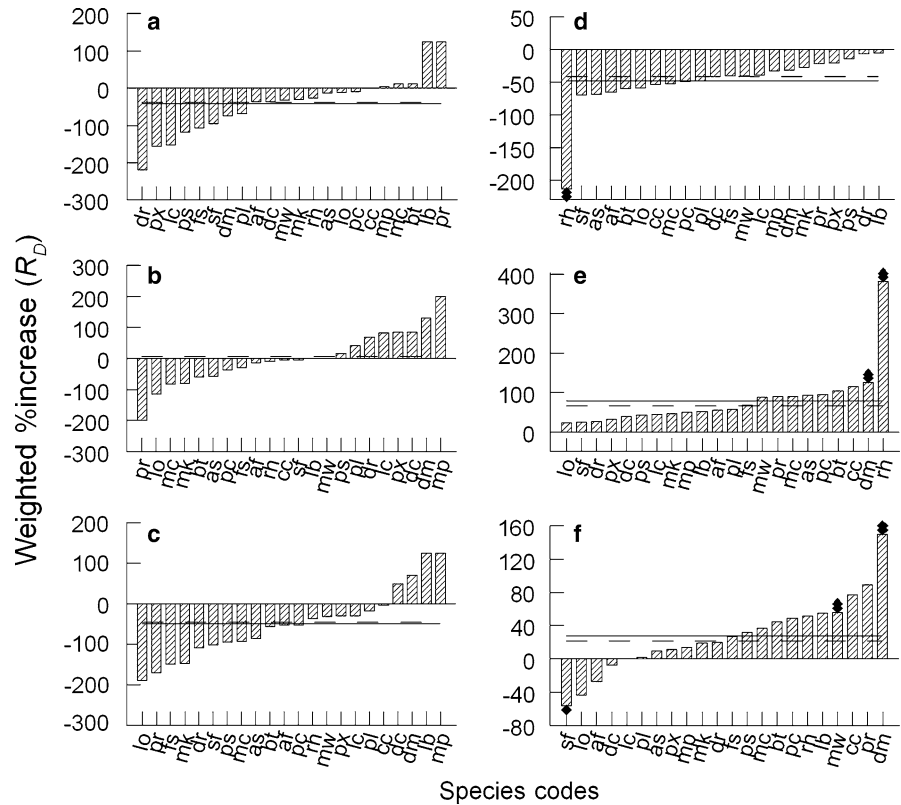
from the 34 used at the plot level, the trends across species were in good agreement. Mortality rate and rgr for P1 were each strongly correlated between the subplot and plot levels ($r = 0.912$ and 0.919 respectively), and correspondingly so were mean rates of P2a and P2b at the subplot level and those for P2 at the plot level ($r = 0.877$ and 0.782). The correlation between $R_{D1–2}$ and the average of $R_{D1–2a}$ and $R_{D1–2b}$ for the 22 of 34 species at the subplot level were significant for m_a ($r = 0.468$, df = 20, $P = 0.028$) and for rgr ($r = 0.646$, $P < 0.001$) indicating that the subplot sampling was a good representation of the plot for the species' responses also. Correlations between rgr in period P1, and $R_{D1–2}$ for rgr, for 21 species in the subplots (rh omitted again) with subsequent m_a in sub-periods P2a and P2b, and $R_{D1–2a}$, $R_{D1–2b}$ and $R_{D2a–2b}$, were all insignificant ($r = -0.332$ to 0.224, df = 19, $P = 0.13$ to 0.94).

Stability analysis

Analysis for m_a, showed that octants $2'$ and $3'$ were unoccupied, most species fell in $4'–6'$, and a few in $1'$,

$7'$ and $8'$ (Fig. 5a)—a wide range of trajectory dynamics. For rgr, $1'–5'$ were empty, most species were in $7'$ and $8'$ and a few in $6'$ (Fig. 5b)—a largely stabilizing response. Octants $1'$ up to $4'$ may be described, respectively, as over-enhanced, enhanced, not enhanced and under-enhanced, whilst $8'$ down to $5'$ as over-recovered, recovered, not recovered and under-recovered. Thus, in terms of m_a most species either did not recover or they under-recovered, whilst in terms of rgr most species recovered or over-recovered. The species that 'benefited' from, or were promoted by, the drought were in $1'$ and $8'$, while those that suffered or were disadvantaged were in $4'$ and $5'$. Four species (if *Dimorphocalyx muricatus* very close to the line is allowed) were thus promoted in terms of m_a and eight (including *Polyalthia cauliflora* on the line) in terms of rgr (Fig. 5). One species, *Cleistanthus contractus*, had zero change in m_a and therefore appeared resistant.

Post-drought response in growth was strongest for understorey species. Across the 16 species which were > 0.75 composed of very small (10 to <30 cm gbh) stems, R_{D2a_2b} and R_{D1_2b} for rgr increased
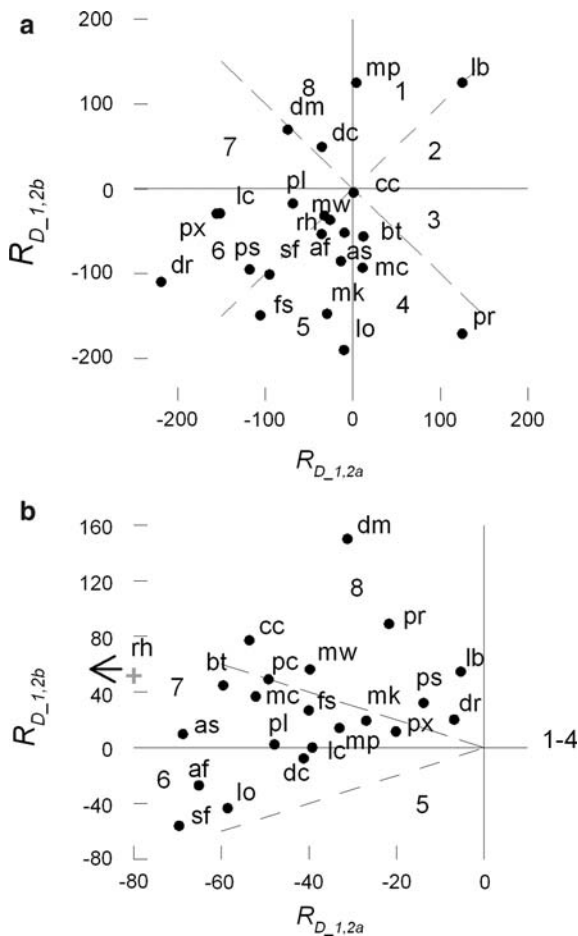
Fig. 5 Weighted percent changes of **a** mortality rate (m_a, inverted scale) and **b** relative growth rate (*rgr*), between period P1 (1986–1996) and sub-period P2a (1996–1999) plotted against the same between period P1 and sub-period P2b (1999–2001) for the 22 most common species in the subplots at Danum. Codes for species are explained in Table 2; rh has an *x*-axis value of −213. Octant numbers 1′–8′ are shown without primes

Fig. 6 Weighted percent changes (R_D) in relative stem growth rate (*rgr*) between period P1 and sub-period P2a (open circles), sub-periods P2a and P2b (closed circles) and period P1 and sub-period P2b (open triangles) regressed against the proportion of very small trees, *pvs* (10–30 cm *gbh*) for those 16 species in the subplots at Danum which had ≥ 0.75 of their small-tree stems in this size class. $R_{D1-2a} = -1.5 - 42.5\,pvs$; $R_{D2a-2b} = -216 + 325\,pvs$; and $R_{D1-2b} = -265 + 342\,pvs$ (see text for statistics). Extrapolated R_{D1-2a} and R_{D1-2b} lines cross at *pvs* = 0.685. Codes for species (upper line) are explained in Table 2; codes for other lines may be found by down projection

significantly with this proportion ($F = 15.9$ and 5.22, df = 1, 14; $P = 0.001$ and 0.038; resp.; Fig. 6) although for R_{D1_2a} the relationship was not significant ($F = 0.38$, $P = 0.55$).

Discussion

Resilience of the tree community

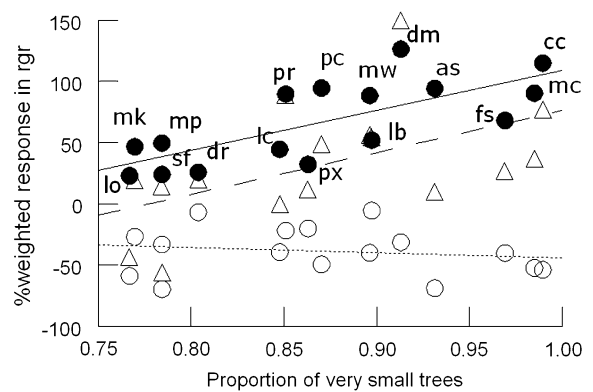During the 1997/1998 ENSO the rainfall in April reached an exceptionally low value. Based on the concept of antecedent rainfall history, the conditional accumulated rainfall deficit also then fell to its lowest level during the period of recording, highlighting the importance of the 1997/1998 event (Fig. 1). The 1982/1983 event (Walsh 1996a, b; Walsh and Newbery 1999; Newbery and Lingenfelder 2004) may have affected Danum to a similar extent and less extreme lows (relevant to the period of forest measurements here) were found in 1987 and 1992.

Drought evidently perturbed, but did not disturb, the forest at Danum: its effect on tree mortality was quite small overall. The forest community, nevertheless, showed a high resilience to the 1997/1998 event, with immediate negative *rgr* responses followed by recovery. This suggests that interspecific variation in drought responses may be driving community dynamics. Recruitment of about a third of the common species decreased or increased significantly within 5 years: mortality, however, appeared to be much less species-specific. Using family-wise statistical procedures, the forest community overall was shown to have been significantly affected. The 'family' is the community in the present context.

The interpretation is that stochastic environmental variation in accumulated rainfall deficit primarily controls tree growth rate (through a limitation in water supply); and recruitment is growth-dependent

because saplings advance into the smallest size class enumerated. Species differ in susceptibility to increasing deficit because of their differences in morphology and physiology (Gibbons and Newbery 2002). In this way the dynamics of the forest and its tree community interactions are largely reducible to, and understandable in terms of, the plant-environment physical processes in operation.

Drought is a complex factor and the physical variables behind it can have a distinctive signal. Spectral analysis showed that raw rainfall values from Danum displayed white noise (low and high frequencies evenly distributed) yet the various accumulated drought indices all indicated brown noise with a higher proportion of contributions from low frequencies. On this basis realizations of rainfall depletion are stochastic in nature. Only long-term measurements that capture forest dynamics before and after an event for several years are therefore likely to provide sufficient relevant information.

Because the driving water deficit variable is stochastic, none of the species can 'tune in' to regular cycles and each is continually experiencing immediate and lagged effects of the perturbations. Neighbourhood competitive interactions would also be expected to be undergoing continual change. This leads to complex yet predictable dynamics in the short-to-medium term (10–50 years), which—if stationarity holds—might be expected to average out towards quasi-constant structural and species composition in the longer term (50–200 years).

The conditional accumulated rainfall anomaly variable represents what the tree is likely to experience over time. Arguably, relatively high as opposed to low antecedent rainfall will, respectively, buffer, or make more susceptible, the forest over those months preceding a period of strong rainfall deficit. Such a formulation has not hitherto been made for trees, let alone tropical ones. This is illustrated by the inferred weak effect in 1991/1992 versus strong effect of drought in 1997/1998. Better growing conditions presumably lead to more stored water which allows trees to ameliorate the drought effect.

Perturbation response niche

Species-specific responses were very different which leads here to the idea of a perturbation response niche. Different species having greater-than-average

restrictions in growth and reduced recruitment in drought periods would be expected to compensate in the wetter inter-event periods; those enhanced by, or over-compensating to, the drought are likely at competitive disadvantage in the wetter periods (currently under test). Further, differentiation of the niche would be emphasized by the effect of topography acting through soil water relations, i.e. ridges being drier than lower slopes. The concept is somewhat akin to the regeneration niche of Grubb (1977) where in the former case time is more important, whilst in the latter it is space.

The new results accord well with the spatial distributions of the common understorey species across the two plots with respect to topography. *Dimorphocalyx muricatus*, *Cleistanthus contractus* and *Lophopetalum beccarrianum*, in decreasing order of importance, cluster and are associated on drier ridge locations at Danum (Newbery et al. 1996). The first showed strong positive *rgr* and *cmp* responses to drought perturbation (Figs. 3, 4), the second positive r_a, *rgr* and *cmp*, and the third reduced mortality responses—as did *Polyalthia rumphii* and *Mallotus penangensis* (Fig. 3). Additionally, *Polyalthia cauliflora* showed a positive increase in r_a (Fig. 2). Those mentioned are the six species in the outer sector or octant 8′ in Fig. 5b, and it underlines the likely central driving role of *rgr* in species' dynamics in response to drought. Three addenda are: (1) for the seven species with negative r_a we have no explanation at present; (2) *Mallotus wrayi*, the ubiquitous numerically dominant species, responded positively to drought in terms of *rgr*; (3) *Reinwardtiodendron humile* is a potential drought phytometer. Importantly, all those species just discussed are understorey taxa (Newbery et al. 1992, 1996, 1999a, b).

No correlation at the species level between *rgr* in period P1 and m_a in subperiods P2a and P2b was detectable, suggesting that faster or slower growing species were neither more nor less affected by the drought. Species appeared to respond over time in a highly idiosyncratic manner, each species with its own trajectory.

That larger trees died more often than smaller ones under drought meant that a moderate degree of random canopy opening followed the defoliation observed and evidenced by a large increase in small end branch abscission (Walsh and Newbery 1999). The drought-adapted small-stemmed understorey

species (many in the Euphorbiaceae) were able to benefit from the temporarily increased light levels. This in part corroborates the understorey facilitation hypothesis (Newbery et al. 1999; Newbery and Lingenfelder 2004), which proposes that drought-tolerant or drought-avoiding understorey species in some Bornean rain forests nurse saplings and small trees of the drought-sensitive canopy species (particularly of the canopy-forming Dipterocarpaceae), through the crucial dry periods. The saplings of the canopy species are thought to be protected from the direct light and drier conditions caused by canopy opening.

Complex forest dynamics driven by perturbations

The most remarkable general result from this study is that the common species at least show highly specific and different dynamics from one another. Furthermore, different species responded differently to drought, to varying degrees, sooner or later after the event, and with more or less extent of recovery. The oscillating dynamics of several species is what might be expected of a system that is moderately perturbed and returning to an equilibrium (Botkin and Sobel 1975; DeAngelis and Waterhouse 1987; Ives 1995). The impression of all these changing patterns of dynamics and their interactions can be likened to a kaleidoscope. The challenge is to find the attractor which bounds the system: this may be the topographic gradient.

The results do not sit well though with the suppositions of the recently debated neutral theory of biodiversity for tropical forests (Hubbell 2001, 2005, 2006). In that thesis equivalence of species and individuals, and random mortality, lead to weakly diffuse competitive interactions and a slow non-adaptive drift in species composition over time. That species could be so ecologically and evolutionary similar has been often challenged (Chave 2004; Bell 2005; Purves and Pacala 2005; Bell et al. 2006): the theory says any differences that do occur are of little consequence. Under the neutral theory the patterns of species' responses and dynamics recorded at Danum would presumably be labelled as 'random'; which seems highly implausible to us given the supporting ecological information on forest structure and tree physiology (Gibbons 1998; Gibbons and Newbery 2002), and the topographic gradient effect on species patterning (Newbery et al. 1996).

There is then an underlying structure to the forest community at Danum, which is determined to a large degree by the species-specific dynamic responses to perturbation. This tends to refute neutrality and species equivalence, rather the forest at Danum functions on the basis of *plurality* of species' responses. A further serious and over-looked problem with the neutral theory is that it assumes a constant environment. This too seems not to be the case at Danum, and is arguably unlikely to be realistically so anywhere, including the tropics.

A possible alternative to the descriptive neutral theory (which in any case is very difficult to test directly, if at all) is to take a dynamic ecosystems approach (Shugart 1998) in which testable mechanisms and processes may allow understanding of structural equilibria (or dis-equilibria) in multi-species population dynamics with reference to a measured stochastically varying environment (May 1974; Ives and Carpenter 2007). It has been shown theoretically that a stochastic environment can result in community stability (Chesson 1982; Chesson and Huntly 1997), and possibly a plurality of responses might play an important role. One caveat to the present work, however, is that only one ENSO event was followed. Predicting and testing for similar patterns of response after future events will be valuable.

This new postulate does not attempt to explain species diversity per se but aims primarily at quantifying, and finding the limits to, complex forest community dynamics. Rare species, for which data will be always insufficient to make reliable estimates of dynamics parameters, could be treated as being neutral (i.e. as indeterminate), whilst the common species, for which estimates can be made reliably a non-neutral way (determinate), could be followed over time using physical, physiological and statistical models.

Apart from large historical disturbances, stochastic droughts perturb the forest at Danum on a short time scale and the forest appears to accommodate them by being resilient. This may work up to a certain threshold of frequency and intensity, one to which the main constituent species are avoidance- or tolerance-adapted. But if, as a result of prognosticated climatic change, droughts were to increase, then higher tree mortality rates and longer periods of restricted growth would be expected to

ensue, the latter inevitably lowering critically the recruitment of many species to the extent that they may not recover in the shortened inter-drought periods; and hence an end-effect change in forest structure and species composition. With the continuing long-term observations at Danum, it might soon be possible to model different scenarios with statistical confidence, and on that basis take the necessary measures to conserve the lowland tropical rain forests of Borneo in its original and natural form of a mosaic of perturbed and, it seems, resilient ecosystems.

Appendix 1

Climate

The low precipitation events at Danum 1985–2003

Event[a]	Start	End	Duration (d)	$DEFARH$ (mm)[b]
1	8/30/86	5/1/88	610	−905.1
2	11/7/88	12/7/88	31	−38.1
3	2/13/89	2/20/89	8	−7.5
4	3/29/89	5/13/89	44	48.9
5	6/1/89	6/6/89	6	n.a.[c]
6	10/23/90	3/23/93	883	−1,566.9
7	6/18/93	6/3/94	351	−357.3
8	6/15/94	6/23/94	9	−65.8
9	9/15/94	9/23/94	5	−17.8
10	10/25/94	11/1/94	6	−28.5
11	4/2/95	5/27/95	56	−8.6
12	6/29/95	8/13/95	44	−91.8
13	1/18/97	4/15/99	818	−1,846.0
14	3/18/02	6/26/02	101	−25.4
15	7/10/02	9/2/02	54	21.7
16	11/1/02	11/25/02	23	−73.9
17	12/4/02	3/26/03	112	−126.4
18	6/27/03	6/29/03	3	9.8
19	9/3/03	9/26/03	24	17.0

[a] When $ARA_{365} < 0$

[b] (Total DRA) when $ARA_{365} < 0$ and $R_{30} < 232$ mm

[c] $ARA_{365} < 0$ but $R_{30} > 232$ mm across all 6 days

Appendix 2

Trees

Appendix 2(a) Sample sizes at the start of the periods P1 and P2 (n_{86}, n_{96}) and corresponding numbers of valid trees (nv_{P1}, nv_{P2}) for the calculation of annualized mortality (m_a; % year^{-1}) and recruitment (r_a; % year^{-1}) rates, and relative (rgr; mm m^{-1} year^{-1}) growth rates, in periods P1 and P2 for the 34 most abundant species (and their families) at Danum

Species	Family*	m_a and r_a		rgr	
		n_{86}	n_{96}	nv_{P1}	nv_{P2}
Alangium javanicum	Alan	101	91	69	60
Antidesma neurocarpum	Euph	119	100	77	70
Aporosa falcifera	Euph	261	238	157	143
Ardisia sanguinolenta	Myrs	568	591	430	444
Baccaurea tetrandra	Euph	250	233	189	168
Barringtonia lanceolata	Lecy	141	147	129	120
Chisocheton sarawakanus	Meli	155	150	116	105
Cleistanthus contractus	Euph	289	273	223	212
Dacryodes rostrata	Burs	153	145	130	118
Dimorphocalyx muricatus	Euph	840	801	667	645
Dysoxylum cyrtobotryum	Meli	170	155	129	122
Fordia splendidissima	Legu	520	543	394	414
Gonystylus keithii	Thym	121	126	104	101
Knema latericia	Myri	141	166	128	140
Lithocarpus nieuwenhuisii	Faga	125	115	94	70
Litsea caulocarpa	Laur	322	319	197	215
Litsea ochracea	Laur	163	147	115	95
Lophopetalum beccarianum	Cela	234	267	200	221
Madhuca korthalsii	Sapo	508	532	433	429
Mallotus penangensis	Euph	204	233	172	196
Mallotus wrayi	Euph	2,268	2,207	1,781	1,723
Maschalocorymbus corymbosus	Rubi	403	335	245	243
Parashorea malaanonan	Dipt	149	133	111	93
Pentace laxiflora	Tili	240	214	163	145
Polyalthia cauliflora	Anno	324	302	271	258
Polyalthia rumphii	Anno	141	138	119	119
Polyalthia sumatrana	Anno	222	221	192	186
Polyalthia xanthopetala	Anno	241	223	172	156
Reinwardtiodendron humile	Meli	262	221	166	140
Shorea fallax	Dipt	371	395	264	298
Shorea johorensis	Dipt	197	157	82	72
Shorea parvifolia	Dipt	206	170	124	104
Syzygium elopurae	Myrt	134	120	100	97
Syzygium tawaense	Myrt	124	120	85	74
Totals		10,667	10,328	8,028	7,796

* Family abbreviations; Alan, Alangaceae; Anno, Annonaceae; Burs, Burseraceae; Cela, Celastraceae; Dipt, Dipterocarpaceae; Euph, Euphorbaceae; Faga, Fagaceae; Laur, Lauraceae; Lecy, Lecythidaceae; Legu, Leguminosae; Meli, Meliaceae; Myrs, Myrsinaceae; Myrt, Myrtaceae; Rubi, Rubiaceae; Sapo, Sapotaceae; Thym, Thymelaceae; Tili, Tiliaceae

Appendix 2(b) Sample sizes at the starts of period P1 (n_{86}) and sub-periods P2a and P2b (n_{96}, n_{99}) and corresponding numbers of valid trees (nv_{P1}, nv_{P2a}, nv_{P2b}) for the calculation of annualized mortality rates (m_a; % year^{-1}), and relative growth rates (rgr, mm m^{-1} year^{-1}), for the 22 most abundant species within subplots at Danum

Species	m_a			rgr		
	n_{86}	n_{96}	n_{99}	nv_{P1}	nv_{P2a}	nv_{P2b}
Aporosa falcifera	74	65	62	57	54	57
Ardisia sanguinolenta	166	138	130	125	114	109
Baccaurea tetrandra	76	66	62	57	52	55
Cleistanthus contractus	118	103	97	85	75	86
Dacryodes rostrata	58	54	48	51	45	40
Dimorphocalyx muricatus	276	250	236	227	209	213
Dysoxylum cyrtobotryum	53	41	36	39	32	32
Fordia splendidissima	157	134	122	119	105	101
Litsea caulocarpa	105	72	56	66	52	46
Litsea ochracea	60	49	45	47	42	35
Lophopetalum beccarianum	71	66	63	64	60	56
Madhuca korthalsii	112	103	98	97	89	86
Mallotus penangensis	57	48	45	48	44	44
Mallotus wrayi	713	612	573	569	517	493
Maschalocorymbus corymbosus	120	80	71	65	58	52
Pentace laxiflora	58	36	31	34	27	26
Polyalthia cauliflora	123	108	104	104	97	94
Polyalthia rumphii	53	48	47	46	45	41
Polyalthia sumatrana	50	43	36	45	35	31
Polyalthia xanthopetala	59	42	32	41	30	26
Reinwardtiodendron humile	76	55	48	49	42	40
Shorea fallax	85	64	55	62	51	43
Totals	2,720	2,277	2,097	2,097	1,875	1,806

Appendix 3

Tests

Appendix 3(a) Means ($\pm$SE) of 34-spp pair-wise correlations ($n = 528$) for each of four dynamics variables and % variance accounted for by first three axes of corresponding principal components analyses

	Coefficient r	1*	2	3
m_a	-0.014358 ± 0.000732	3.48	3.41	3.35
r_a	-0.014434 ± 0.000738	3.49	3.43	3.41
rgr	-0.014838 ± 0.000778	3.49	3.39	3.35
cmp	-0.014510 ± 0.000777	3.55	3.42	3.37

* % Var. = 100/34 = 2.94 had all axes been equal

Appendix 3(b) Species which had significant differences in their dynamics variables from random expectation adjusted for multiple hypothesis testing: 34 species in plots

Variable	Species codes#	Holm (Sidak) adjusted P	Family-wise P
m_a	bl	0.001508	0.0068
r_a	af, dr, px, se, st	0.001605	0.0068
	kl	0.001767	0.0116
	bt, cc	0.001804	0.0220
rgr	dm	0.001508	0.0068
cmp	dm	0.001508	0.0068

species codes are those of Table 2 in the main text

The Benjamini-Hochberg step-up FDR procedure gave the same results as the Holm step-down one for m_a and cmp; but for r_a three further species were significant: pc, pl and sp (adjusted P = 0.0132, 0.0147 and 0.0162 resp.), and for rgr there was one further case: mw (adjusted P = 0.0029). Note that mw was ranked 4th highest yet was significant (unlike pr and cs) due to its very much larger population size (maximum in Appendix 2)

Appendix 3(c) Species which had significant differences in their *rgr* from random expectation adjusted for multiple hypothesis testing: 22 species in subplots

Period	Species codes#	Holm (Sidak) *P*	Family-wise *P*
P1-P2a	rh	0.002329	0.0044
P2a-P2b	rh	0.002329	0.0044
	dm	0.002440	0.0042
P1-P2b	dm	0.002329	0.0044
	mw	0.002440	0.0084
	sf	0.002500	0.0400

Species codes are those of Table 2 in main text

The FDR procedure resulted in the same results, i.e. no additionally significant species

Appendix 3(d) Bonferroni minimum *P*-critical values from the step-down FDR procedure which are used in the Bernoulli formula

1. P1 − P2: m_a, 0.0002; r_a, 0.0152; *rgr*, 0.0024; *cmp*, 0.0024
2. *Rgr*: P1 − P2a, 0.0002; P2a − P2b, 0.0002; P1 − P2b, 0.0020

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