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# Mortality and recruitment rate evaluations in heterogeneous tropical forests

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## Summary

**1** The methods commonly used to estimate stem turnover rates (i.e. mortality and recruitment) in species rich tropical forests suffer from a previously unrecognized artefact. The estimated rate is not independent of the census period.

**2** An average rate estimate will decrease with time if the sample population cannot be characterized as homogeneous. This artefact may have considerable significance for comparisons between permanent plot studies that have used different census periods.

**3** We present a theoretical consideration of this census effect. The artefact will be severe when a fraction of the population has a very much higher mortality rate than the average.

**4** Using a simple formulation we provide a mathematical proof that rate estimates will decline with increasing census periods for all but perfectly uniform populations.

**5** The phenomenon of apparent rate decrease may be used to provide ecologically significant information about the diversity and dynamics of the population as it is related to the variance of life expectancies within the sample.

**6** Such an artefact complicates evaluation of change over nonstandard time intervals and requires careful and detailed attention. Similar problems will effect any estimation procedure which cannot account for all the rate variation within a study population. Recognition of the problem is a necessary first step.

*Keywords*: environmental change, monitoring, mortality, permanent plot, recruitment, tropical forest, turnover

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## Introduction

Many ecological studies examine population changes using census information gained by counting and later re-counting a defined sample population and assessing survivors, losses and gains (recruits). In tropical forest studies such information is commonly summarized as rates of mortality, recruitment, or turnover (e.g. Phillips *et al.* 1994; Sheil *et al.* 1995). A previously unrecognized artefact arises from evaluating mortality and recruitment rates when census intervals are unequal. It can be shown that estimated rates will decline with increasing census interval as a consequence of population heterogeneity.

Much of what is known about tropical forest dynamics has been derived from census-based permanent plot data. The collection of such data sets is difficult and expensive and there is little standardization of census periods. Comparative studies have and are being made (e.g. Swaine *et al.* 1987a; Hartshorn 1990; Phillips *et al.* 1994), and conclusions of considerable significance are being reached (e.g. Phillips & Gentry 1994). The interpretation of such comparative evaluations must remain unclear if rate estimates are not independent of census period (Sheil 1995a). Artefacts associated with estimating rates in heterogeneous populations may confound, or perhaps cause much of the variation currently inferred from tropical forest turnover studies. In this paper the reasons for reaching this conclusion are presented.

Mortality and recruitment of trees can be very irregular at small spatial and temporal scales (e.g. Brokaw 1982), but it is nonetheless widely assumed that when samples from large areas are recorded over long periods the data allow the estimation of 'vital' rates (mortality and recruitment) which are characteristic for that vegetation. Given the current interest in studying permanent plots in order to examine many aspects of tropical forest ecology and management (e.g. Hubbell & Foster 1992; Condit 1995) the identification and characterization of errors and artefacts is essential (Sheil in press). Some issues relating to the calculation and comparison of mortality rates have been considered previously (Mervart 1972; Swaine & Hall 1983; Lieberman *et al.* 1985; Swaine & Lieberman 1987; Rankin-de-Merona *et al.* 1990; Phillips *et al.* 1994; Sheil *et al.* 1995; Sheil 1995a,b).

Simple stand level parameters such as annual mortality and recruitment rates are likely to remain fundamental to the ecological description of forests generally. Even in temperate forests a satisfactory understanding of tree mortality remains elusive as the necessary quality of data is scarce (e.g. McCune & Menges 1986). Hamilton (1986) introduces his study of mixed conifer stands in northern Idaho with the following observations: 'Mortality remains one of the least understood components of growth and yield estimation. Unfortunately, few studies have been designed specifically to increase our understanding of the mortality process. Little of the data collected for other purposes can be readily used in the development of mortality (or survival) models. In the absence of adequate data, mortality appears to have been handled by assumption or subjective judgment.'

The standard methods of mortality rate estimation used in tropical forests are based on models which assume a simple population in which each member has an equal and constant probability of dying over any unit of time thus giving an exponential decline (c.f. radioactive decay). The issues raised by treating heterogeneous populations in this way have not been widely recognized. Such errors have been termed *type three* artefacts by Sheil (1995b) being errors due not to the method of data collection, nor to its impact upon the sample population, but to occasions when 'data are inappropriately manipulated, analysed and/or assessed.... These artefacts usually arise from a limited understanding of the data and systems under examination, and often from the need to make unrealistic and unexamined simplifications'.

## Apparent declines in vital rates

The estimation methods commonly used in tropical forest studies will generally indicate a decline in mortality rate with increasing census period in any population that maintains a consistent variation in the probabilities of loss of its individual members. This is intuitively obvious, because the fraction of the surviving sample members with high mortality rates will decrease faster as 'low-mortality' survivors increase in relative terms. We would argue that this situation occurs in mixed species evaluations, and will also be relevant within more superficially 'homogeneous' populations (e.g. mixed size or age classes, phenotypically differentiated populations, population members in heterogeneous or competitive environments—as is certainly the case in virtually all closed canopy forests).

So far, we are aware of only two published examples of tropical tree mortality which appear to demonstrate census-period dependence. Mervart (1972, his figure 10) found that mortality in a predefined population (i.e. only stems recorded at the first census were followed) of Nigerian forest trees tended to decrease with time. A similar result for trees in Budongo Forest, Uganda, was presented by Sheil (1995a). We can suggest two reasons why so few observations of period dependence can be found in the literature: the lack of recognition of the phenomenon; and the paucity of suitable multicensus long-term data.

A closely related phenomenon has previously been recognized in failure rate analysis based on life-time data (i.e. not census records) by Proschan (1963) who examined the time between breakdowns in aircraft air-conditioning systems: he suggested that 'an observed decreasing failure rate may well be the result of mixing exponential distributions having different parameters' and provided a proof that the artefact will occur in such circumstances. This 'mixing exponential distributions' corresponds to cryptic subpopulations having a different breakdown ('mortality') rate and is thus closely analogous to the arguments presented here.

## Mortality

For the derivations and arguments which follow it is useful to review briefly the mathematical form and assumptions implicit in the methods commonly used to estimate mortality rates in tropical forest studies. For a population experiencing mortality of a constant fraction $m$ $(1 \geqslant m \geqslant 0)$ each year, the cumulative loss after $t$ years compounds as

$$N_t = N_0(1-m)^t \tag{1}$$

$N_0$ and $N_t$ are population counts at the beginning and end of the measurement interval, $t$.

Thus $m$ may be estimated as

$$m = 1-(N_t/N_0)^{1/t} \tag{2}$$

Some studies of mortality in tropical forest have indeed used this form (e.g. Primack *et al.* 1985).

The assumption of a common and constant probability of mortality throughout the entire population is the basis of this model and allows confidence limits to be generated by use of the inverse $F$ distribution (Johnson & Kotz 1970; Nelson 1982) as:

$$m_u = 1-[1-1/\{1+F_{\text{inv}}[\alpha, 2(N_0-N_t)+2, 2N_t]N_t/(N_0-N_t+1)\}]^{1/t} \tag{3}$$

$$m_l = 1-[1-1/\{1+F_{\text{inv}}[\alpha, 2(1+N_t), 2(N_0-N_t)](N_t+1)/(N_0-N_t)\}]^{1/t} \tag{4}$$

Here $m_u$ is the upper confidence limit and $m_l$ is the lower confidence limit on $m$. $F_{inv}\alpha$, numerator degrees of freedom, denominator degrees of freedom) gives the inverse of the $F$ cumulative probability distribution at a confidence level defined by $\alpha$. Although based entirely on the assumption of constant and equal probabilities of mortality this formulation provides some guidance to the comparisons of rate information.

A commonly used alternative to the calculation of $m$ is to estimate the instantaneous or 'exponential' rate measure, $\lambda$ (e.g. Swaine & Hall 1983; Manokaran & Kochummen 1987; Lieberman *et al.* 1990; Clark & Clark 1992; Condit *et al.* 1993; Milton *et al.* 1994), which considers continuous, rather than discrete, time. This estimate derives from the differential equation:

$$dN/dt = -\lambda N. \tag{5}$$

This integrates to give the standard exponential relation

$$N_t = N_0 e^{-\lambda t} \tag{6}$$

In what follows we consider the two forms of rate estimation, $m$ and $\lambda$, separately but it should be recognized that the estimates are related independently of time as $m = 1 - e^{-\lambda}$ (see Sheil *et al.* 1995).

The simplest method of rate calculation is linear, i.e. percentage lost divided by time $\{'m' = 1/t\,[(N_0 - N_t)/N_0]\}$ and this is sometimes encountered in the literature (e.g. Busing & Pauley 1994). This rough approach ignores the compounding required for any period not identical to one year and will be biased for any comparisons over unequal census periods. The expected rate estimate will thus decrease with increasing census interval even for simple homogeneous populations. This method is not considered further.

### A GENERALIZATION FOR COMPOSITE POPULATIONS

In a mixed population composed of subpopulations, each with a different mortality rate, a generalization of eqn 1 is required. Each subpopulation, $i$, is characterized by its own annual mortality, $m_i$, and its own population of stems:

$$N_t = \sum_{i=1}^{S} n_{it} = \sum_{i=1}^{S} n_{i0}(1 - m_i)^t \tag{7}$$

Here $n_{i0}$ and $n_{it}$ are the counts of subpopulation members at time 0 and survivors at time $t$, respectively.

Using the conventional mortality estimate (eqn 2) to characterize an overall average mortality, $m_{all}(t)$, for the mixed population (as estimated at time $t$) leads to the expression:

$$m_{all}(t) = 1 - \left\{ \sum_{i=1}^{S} [n_{i0}(1 - m_i)^t] \middle/ \sum_{i=1}^{S} n_{i0} \right\}^{1/t} \tag{8}$$

Thus defined, the behaviour of $m_{all}(t)$ as a function of census interval, $t$, depends upon the distribution of values of $n_{i0}$ and $m_i$. **In all cases, however, $m_{all}(t)$ decreases as $t$ increases** unless $m_i$ is identical for all subpopulations (i.e. is truly a 'simple' population). This general result is proved in Appendix 1.

If time, $t$, is a continuous rather than a discrete variable, then the definition of an overall average mortality rate, $\lambda_{all}(t)$, analogous to eqn 8 for $m_{all}(t)$ is:

$$\lambda_{all}(t) = -(1/t)\log_e \left\{ \sum_{i=1}^{S} n_{i0} \exp(-\lambda_i t) \middle/ \sum_{i=1}^{S} n_i \right\} \tag{9}$$

Again, as shown in Appendix 1, $\lambda_{all}(t)$ always decreases as the census interval $t$ lengthens except in the limiting case of a genuinely homogeneous population (i.e. when all $\lambda_i$ are identical) whereupon $\lambda_{all}(t)$ remains constant.

## Theoretical determinants of changing rates

The general theorem that we have established is useful but does not provide an intuitive feeling for the behaviour of $m_{all}(t)$ in mixed populations other than proving the expectation of monotonic decline. A clearer insight into the behaviour of $m_{all}(t)$ is provided by consideration of specific cases and examples. Examination of numerical solutions to eqn 8 (e.g. Fig. 1) indicates that the severest artefact, in terms of operational significance, will occur when a fraction of the population has a very much higher $m_i$ than the rest. The phenomenon of apparent decline in $m_{all}(t)$, if adequately characterized, may provide useful information about the sample population, serving essen-

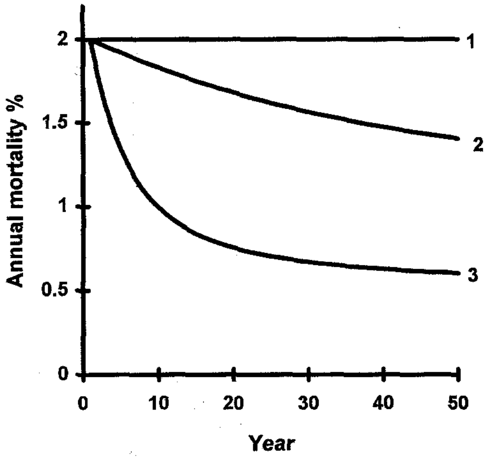

**Fig. 1** Three solutions to eqn 8 are plotted against census interval in order to indicate the behaviour of $m_{all}$; $\langle m \rangle = 2\%$ per year (at $t = 1$) for all three solutions. The line labelled 1 is the solution for a perfectly homogeneous population. Curve 2 is a composite of two populations: $n_{1,0} = 0.8$, $m_1 = 1\%$ per year and $n_{2,0} = 0.2$, $m_2 = 6\%$ per year. Curve 3 is also composed of two populations : $n_{1,0} = 0.95$, $m_1 = 0.5\%$ per year and $n_{2,0} = 0.05$, $m_2 = 30\%$ per year.

tially as a measure of variation in life expectancies that can be termed 'dynamic diversity'.

If the variance in the statistical distribution of $m_i$ values is not too large, an approximation to eqn 8 for $m_{\text{all}}(t)$, or eqn 9 for $\lambda_{\text{all}}(t)$ can be provided. For the case of discrete intervals this approximation is

$$m_{\text{all}}(t) \approx \langle m \rangle + (t-1)\sigma^2/2(1-\langle m \rangle) + \cdots \tag{10}$$

Here $\langle m \rangle$ is the mean of the $\{m_i\}$ distribution, defined by eqn A7 of Appendix 1, and $\sigma^2$ is the variance, defined in the usual way:

$$\sigma^2 \equiv \sum_{i=1}^{S} p_i(m_i - \langle m \rangle)^2 = \langle m^2 \rangle - \langle m \rangle^2 \tag{11}$$

For continuous census intervals, the corresponding approximation is:

$$\lambda_{\text{all}}(t) \approx \langle \lambda \rangle - \tfrac{1}{2}\sigma^2 t + \cdots \tag{12}$$

Here again, $\langle \lambda \rangle$ is the mean and $\sigma^2$ is the variance of the $\{\lambda_i\}$ distribution (as defined in Appendix 1 and as the direct analogue of eqn 11 respectively). These approximate results are established in Appendix 2.

Equations 10 and 12 demonstrate explicitly that the overall average mortality rates estimated by the methods considered are indeed time-independent constants when derived for perfectly homogeneous populations when the variance, $\sigma^2$, is zero, along with all higher moments of the distribution. For relatively small values of the variance-to-mean ratio, $\sigma^2/\langle m \rangle$, the variance in the mortality rate distribution can be estimated from the slope of the initial decrease in $m_{\text{all}}$ and $\lambda_{\text{all}}$ with increasing census interval, $t$. Such variation in mortality rates might be expected to be related to diversity among life expectancies in the sample population, and could prove a useful community characteristic in itself.

Explicitly, such estimates of the community-wide variance in mortality rates can be obtained from eqns 10 and 12. For discrete census intervals,

$$\sigma^2 \approx 2[m_{\text{all}}(1) - m_{\text{all}}(t)][1 - m_{\text{all}}(1)]/(t-1), \tag{13}$$

For continuous census intervals,

$$\sigma^2 \approx 2[\lambda_{\text{all}}(0) - \lambda_{\text{all}}(t)]/t. \tag{12}$$

We emphasize that these approximate expressions are based on neglect of all higher moments of the statistical distribution in $\{m_i\}$ or $\{\lambda_i\}$. Note also that for this derivation $\langle m \rangle = m_{\text{all}}(1)$.

An illustrative example can be given by accepting the regression for mortality decline in timber trees in Budongo, Uganda presented by Sheil (1995a). We are unhappy about using $\mathrm{d}m_{\text{all}}/\mathrm{d}t$ at $t = 1$ as there is considerable uncertainty about the initial data points (however $m_{\text{all}} = 0.011\Delta t^{-0.33}$, thus $\mathrm{d}m_{\text{all}}/\mathrm{d}t = -0.0037\Delta t^{-1.33}$; so initial decrease at time 1 is therefore 0.0037 and since this is equivalent to $\sigma^2/2(1-\langle m \rangle)$; $\sigma^2 \approx 0.0037 \times 2(1-0.011)$ per year$^2$ $\approx 0.0073$ per year$^2$ or a standard deviation (SD) of mortality rate of around 8% per year). We recognize that the variance in mortality rate of the survivor population will decrease with time, so that linear approximations over long periods are likely to underestimate the variance of the original sample. However, as we need sufficient census counts to make evaluation meaningful, a compromise is required; thus we have taken the more cautious though arbitrary approach, which avoids using the $t = 1$ data, by using the rates at time $t = 3$ and $t = 20$ years (rates 2.2 and 1.2% per year respectively): this provides, from eqn 13:

$\sigma^2 \approx 2[0.022-0.012]\;[1-0.022]/(17-1) \approx 0.0012$ per year$^2$ which is equivalent to a mortality rate SD of $\approx$3.5% per year. A skewed distribution is implied as the estimated magnitude of the SD for $m_{\text{all}}$'s is greater than the value of $m_{\text{all}}$ itself.

## A consideration of recruitment

This analysis has focused on mortality, but a similar theoretical time dependence can be shown for recruitment. Intuitively this is clear, because by any consistent method of assessment a steady-state population would be expected to tend towards equal rates for recruitment and mortality when a long enough time period is considered (i.e. recruits = losses). However, the mathematical framework for unbiased assessment is not well developed, and few published figures account for the mortality of recruits that occur between observations. Phillips *et al.* (1994) use mortality in the lowest stem size class as a proxy for the mortality rate of recruited stems: an approach not considered here due to the circularity of explicitly including biased estimates of mortality within the procedure for calculating recruitment and then demonstrating that this too is biased. We will consider an alternative approach.

To compute total new counts, $N_r(t)$, among intervals of unequal length, requires a simple differential equation. Assuming the rate of recruitment is constant, with each stem then having a constant probability of mortality per unit time, provides a simple differential relationship:

$$\mathrm{d}N_r/\mathrm{d}t = kA - \lambda N_r. \tag{15}$$

Here $k$ is the recruitment rate per unit of plot area $A$, and the instantaneous mortality rate is $\lambda$ per unit of recruitment present (a rate independent of sample size is defined by $kA/N^*$ where $N^*$ is the steady state population). Initially, $N_r(0) = 0$; the count of new recruits begins at $t = 0$.

In eqn 15, the $-\lambda N_r$ term corresponds to stems that are newly recruited and subsequently lost within the census interval, without ever being recorded. Such 'lights which wink on and off while we are out of the room' are not counted directly in measures of recruitment or mortality. Such uncounted losses are allowed for in the earlier mortality calculations by limiting consideration to the compounded loss of precounted stems. Uncounted recruits cannot be similarly disregarded in assessments of recruitment rates without introducing a serious bias over longer measurement periods. So, unlike mortality, recruitment rates even in homogeneous populations cannot be estimated in a simple way, independently of time. Unbiased estimates require assessment of both rate constants $k$ and $\lambda$. An analogous problem, relating to the way estimates of species turnover depend on census interval, for island bird communities, has been provided previously (Diamond & May 1977).

Equation 15 can be integrated, to provide an expression for $N_r(t)$, the total number of new stems at time $t$ after the initial census:

$$N_r(t) = (kA/\lambda)(1-e^{-\lambda t}) \tag{16}$$

This equation can be rearranged to express $k$ as a function of $N_r(t)$ and $\lambda$. It will also provide $\lambda$ if $N_r(t)$ and $k$ are known.

In practice the only available information will be $N_r(t)$. We can however make progress if it is reasonable to make assumptions about $N^*$, the asymptotic, steady state value to which $N_r(t)$ tends after sufficiently long times have elapsed. By assuming a steady state situation $N^*$ can be equated with $N_0$ or the complete population count during any census. From eqn 16 in the limit $t \to \infty$, so that $N^*$, $k$ and $\lambda$ are related by

$$N^* = kA/\lambda. \tag{17}$$

Clearly, this steady state relation can only be used if there are no long-term secular changes in recruitment and/or mortality processes over the time period in question i.e. if $k$ and $\lambda$ are truly constant.

From eqns 16 and 17, we can obtain explicit expressions for the mortality rate, $\lambda$, and for the recruitment rate, $k$, in terms of the directly observable quantities $N_r(t)$ and $N^*$ ($N_r \to N^*$ as $t \to \infty$):

$$\lambda = -(1/t)\ln[1-\mathrm{N}_r(t)/N^*], \tag{18}$$

$$k = -(N^*/At)\ln[1-\mathrm{N}_r(t)/N^*] \tag{19}$$

Taking, as before, a heterogeneous system made up of $S$ distinct subpopulations, with recruitment and mortality rates $k_i$ and $\lambda_i$ ($i = 1, 2, \ldots S$). We can apply the above analysis to each subpopulation, and, when combined, these distinct versions of eqns 16 and 17 provide

$$N_{ri}(t) = N_i^*[1-\exp(-\lambda_i t)] \tag{20}$$

$N_i^*$ being the steady-state population of subpopulation $i$. Equations 18 and 20 lead directly to the recruitment-process analogue (of eqn 9) for the overall average mortality rate at time $t$, $\lambda_{\text{all}}(t)$:

$$\lambda_{\text{all}}(t) = -(1/t)\ln\left[\sum_{i=1}^{S} N_i^*\exp(-\lambda_i t)/N^*\right] \tag{21}$$

By exactly the same arguments used in Appendix 1, we can show that $\lambda_{\text{all}}(t) \leqslant \langle\lambda\rangle$, for all time intervals, $t$ (with equality only when all $\lambda_i$ are equal). From the linearity of the basic relation of eqn 17, we likewise have $k_{\text{all}}(t) \leqslant \langle k\rangle$ for such 'simple' estimates of recruitment rates.

Although the analysis of this section has been presented in the formulations of continuous census intervals, the results also hold – as before – in formulations with discrete census intervals.

## Discussion

The common methods for calculating tropical forest turnover rates – both mortality and recruitment – do not provide unbiased estimates when applied to census data from heterogeneous populations. These conclusions will apply to other fields where census data are used to estimate rates. Our consideration of mixed populations composed of simple subpopulations attempts to address variation present in real communities, but cannot claim to be fully realistic. Three aspects of the model require further consideration: (1) how different aspects of population heterogeneity might influence rate estimates; (2) how violation of our assumptions might occur and how this would be recognized; and (3) what are the appropriate statistical techniques needed to evaluate and critically assess real census data.

That different forest tree species have different mortalities at a common site is well recognized (e.g. Primack *et al.* 1987; Manokaran & Kochummen 1987; Hubbell & Foster 1990; Clark & Clark 1992; Burslem & Whitmore, unpublished; Sheil, unpublished). Evidence also supports the assertion that mixed tropical forest tree populations, with individual stems exceeding a defined minimum size (generally considered 10 cm diameter at reference height), demonstrate a mortality that does not significantly differ with size (e.g. Lieberman *et al.* 1985; Swaine *et al.* 1987; Manokaran & Kochummen 1987; Swaine 1989; Condit *et al.* 1993; Gentry & Terborgh 1990; Kohyama 1991; Milton *et al.* 1994). Exceptions to this generalization are Hubbell & Foster's (1990) evidence for differentially increased death of larger trees following drought, and Mervart's (1972) observation that mortality in very large trees (trees over 6 feet girth) is greater than for smaller stems, with his 'medium large' stem class (1–6 feet girth, i.e. 0.3–1.8 m circumference) proving the most long lived on average. In neither of these cases, however, is a statistical test of the differences provided. Other reports of drought creating differential mortality between size classes includes Hartshorn's (1990) observation that drought appears to impact smaller stem sizes selectively at La Selva, Costa Rica and at Palcazú Valley, Peru. In Asia however, drought appears often to have the greatest impact on emergent stems as has been reported by Tang & Chang (1979) for ridge top sites in peninsular Malaysia, by Seth *et al.* (1960) for seasonal dipterocarp forests in India, and by Leighton & Wirawan

(1986) in eastern Borneo during the 1982–83 droughts. Canopy and emergent stems are often considered more vulnerable to drought conditions in temperate forests (e.g. Liu & Muller 1993).

Higher mortality rates are commonly found in juvenile stems (diameter <10 cm at reference height), particularly in less shade-tolerant species (e.g. Connell *et al.* 1984; Swaine 1989; Hubbell & Foster 1990; Alvarez-Buyulla & Martinez-Ramos 1992; Clark & Clark 1992) and are even higher in smaller seedlings (e.g. Swaine & Hall 1986; Kitajima & Augspurger 1989). Such a differential, with mortality higher for smaller stems, will also decrease turnover estimates over time within a growing sample population. Indeed, in all populations of stems defined by a minimum size, longer observation periods become biased towards a population characterized by greater average stem size. Additional concerns have been voiced by Rankin-de-Merona *et al.* (1990) who suggest that their turnover measures (actually an estimation of average time for each stem to be replaced) 'will vary depending on the lower d.b.h. [diameter] limit used and may not be reliable when the assumption of a steady-state system is not met'.

There is good evidence that mortality rates within species often change with stem size both in temperate (e.g. Monserud 1976; Hamilton 1980, 1986; Harcombe 1987; Busing & Wu 1990) and in tropical forests (Hubbell & Foster 1990; Clark & Clark 1992; Vanclay 1991) and such a formulation is common in computer models (e.g. Vanclay 1989, 1991; Kohyama 1991). This is an interesting phenomenon as it implies that the reported size independence of total mortality in mixed tropical forests populations may be a composite property, i.e. a product of the mortality diversity considered in this paper. However developmental change for individuals is not accommodated in our analysis if the census interval allows time for stems to change into subpopulations characterized by a mortality rate ranked differently to their initial subpopulation, although this is unlikely to be a major concern over shorter measurement periods.

The operational definition of the probabilities used in our estimation models (i.e. as contained in the terms $m_i$ in eqn 8 and $\lambda i$ in eqn 9) within real populations needs to be addressed. The probability of an individual stem dying is not constant, nor is it independent of its neighbouring stems. Localized competition for limiting resources suggests that each individual stem has its own dynamic probability of mortality. Significant differentiation within a defined population is a recognized reality; e.g. slow-growing stems are significantly more likely to die than are other stems of equivalent size (e.g. Swaine *et al.* 1987a,b), and has been well characterized in temperate forests (e.g. Monserud 1976; Hamilton 1980, 1986). It will be interesting to discover how much of the variation in mortalities can be attributed to individual differences, as opposed to subpopulations defined by species and size. It is notable that both the study populations in which time dependent mortality has been identified appear, at least superficially, to be relatively homogeneous, being composed of large African forest tree species in both cases (Mervart 1972; Sheil 1995) and much of the variation may be occurring at the level of the individual.

An alternative interpretation of exponential population decline can be suggested, by assuming only that there is a stable tendency to lose a constant proportion of the population over equal time intervals (not that the individual probabilities of loss are constant and equal). Accepting such a re-interpretation brings with it the recognition of spatial and temporal auto-correlation(s) and diverse individual behaviours, which is more realistic; but considerably reduces the potential for statistical understanding and undermines the ability to calculate confidence intervals for single-sample turnover estimates. This reasoning implies a need for adequate sample replication amongst sites being evaluated.

The temporal fluctuations involved in mortality will also have an influence. It is evident that different species demonstrate varying vulnerabilities when exposed to different environmental phenomena or conditions (e.g. drought, wind, disease). In the case of occasional 'disturbance' events the meaning of a 'time-independent' rate measure is unclear. The presence of 'stochastic' and 'deterministic' aspects to mortality and recruitment has not been adequately addressed. It can be considered (e.g. Connell 1978) that there exists a continuum from stable forest environments (i.e. where catastrophic events are rare and have little recognizable influence on the system's observed dynamics) to formations that are highly influenced by catastrophic events (e.g. events such as cyclones, Whitmore 1974). In theory, severe disturbance events might be included in turnover assessments if data were averaged over sufficiently long time periods, but what period lengths are sufficient even in relatively stable communities requires empirical determination.

Simulation modelling of tree populations with explicit representation of individual stems, coupled to census-based turnover analysis, may prove useful. Such census-simulations, combined with detailed statistical evaluation, could assist in developing better strategies for measuring and comparing field data. This approach would however require a careful consideration of the adequacy of the given model to represent the real subtleties of mortality phenomena, and this is unfortunately far from clear.

Computer simulation models of forest dynamics vary considerably in their treatment of mortality (e.g. Hartshorn 1975, Ek & Monserud 1979; Hamilton 1980; Vanclay 1989, 1991, 1994). Even in the comparably well advanced models of mixed temperate forests it can be shown that a great deal of the variation in model behaviour is due to different approaches to mortality. Stage & Renner (1988) for example compared models for mixed conifer stands in the Rocky Mountains (USA) and found that over three-quarters of the variation in predicted stand volume between models was specifically due to the different treatments of mortality within the models. In the case of tropical forests this ambiguity is compounded by the difficulty in gaining sufficient data to justify a particular functional form and for adequately calibrating each species.

Among the best characterized individual-based forest models are the gap models (the numerous derivations of the JABOWA and FORET models) which were comprehensively reviewed by Urban & Shugart (1992). It is instructive to consider how well these ecologically conceived models manage mortality, and Urban & Shugart (1992) illustrate this with reference to their ZELIG model which uses two different relations, one age-related and one stress related: 'It is assumed that about 1% of individuals might survive to maximum age; the further assumption that this mortality is constant with age yields an annual probability of mortality on the order of 1–2% per year. A second source of mortality is due to loss of vigour, and is invoked when a tree fails to meet a minimal-growth threshold. This rate of 'stress' mortality is an order of magnitude greater than the ambient rate: it is assumed that a tree might survive 10 years under stress, which yields an annual stress mortality rate of 0.369%. Slow-growth mortality is most pronounced in very small and very large trees. This implementation is somewhat arbitrary, but reproduces the U-shaped mortality schedule observed for trees (e.g. Harcombe 1987). Importantly, because species differ in their inherent growth rates and tolerance to environmental stresses (suppression, drought), they may exhibit very different mortality schedules despite having the same basic implementation.' So even in the best current models Urban & Shugart (1992) find it necessary to consider the implementation of mortality 'somewhat arbitrary'.

The best calibrated models of mortality for species rich tropical forests are probably those provided by Vanclay (1989, 1991) for the north Queensland rain forests. In his 1991 paper he used a logit formulation with d.b.h., log( d.b.h.), and (overtopping basal area/ total basal area)$^3$ as explanatory variables and used 64 369 tree observations with 2781 mortalities to classify 400 tree species into 10 groups each of which has a significantly different mortality. He also demonstrated that for six of these groupings further explanatory power was provided by the additional inclusion of at least one of basal area, log basal area, or a site index factor into the formulation (see Vanclay 1991). He stresses however that for the majority of species data are insufficient to allow adequate characterization and calibration. Examination of models reveals a great deal of variation in the treatment of mortality. In all cases however it is recognized that populations are not simple and homogeneous, and much more study will be required to examine the magnitude and significance of this phenomenon.

In short, the meaning of published turnover rates must be reconsidered. We have shown how artefacts of estimation over varying census periods may confound, or perhaps cause, much of the variation currently inferred from demographic tropical forest studies. Techniques for calculating and comparing turnover values can be improved by better methodological standardization (e.g. consistent time intervals) or by an explicit calibration of the variation in mortality within sample populations. Only two studies so far provide support for the artefact hypothesis, but it is hoped that this account will encourage further case examples to be identified. Several very large and intensively evaluated monitoring plots have recently been established for ecological studies (Hubbell & Foster 1992; Condit 1995). These studies may provide some of the data needed to examine real turnover in heterogeneous populations in much more detail than is currently possible.

Evaluation requires more sophisticated analysis than has conventionally been undertaken. Consideration suggests that similar problems will effect any estimation procedure which cannot account for all the rate variation within a study population as this will cause census period dependence. The standardization of census intervals is strongly recommended.

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## Appendix 1

Proof of census interval dependence. We define $p_i$ as the proportion of the original population represented by species (or subpopulation) $i$:

$$p_i \equiv n_{i0} \Big/ \sum_{i=1}^{S} n_{i0}. \tag{A1}$$

Equation 8 can thus be re-written:

$$m_{\text{all}}(t) = 1 - \left[\sum_{i=1}^{S} p_i(1-m_i)^t\right]^{1/t} \tag{A2}$$

$[0 \leqslant m_i \leqslant 1$ for all $m_i]$.

Likewise for continuous time, eqn 6 can be re-written for a composite population as

$$\lambda_{all}(t) = (1/t)\ln\left[\sum_{i=1}^{S} p_i \exp(-\lambda_i t)\right] \tag{A3}$$

To prove that $m_{all}(t)$ and $\lambda_{all}(t)$ decline monotonically with increasing $t$, we use *Jensen's inequality*:

$$f\left(\sum_{i=1}^{S} \alpha_i \rho_i\right) \leqslant \sum_{i=1}^{S} \alpha_i f(\rho_i) \tag{A4}$$

(Hofbauer & Sigmund 1988 equation (3.13), and see Nowak & May 1992). The equality applies only when all $\rho_i$ are equal. This general result holds provided the following requirements are met:

(a) $\alpha_i$ are arbitrary positive numbers with $\Sigma\alpha_i = 1$
(b) $f(\cdot)$ is a strictly convex function on some interval $I$, and
(c) all $\rho_i$ lie in $\{I\}$.

It will be sufficient to prove that $m_{\text{all}}(t)$ is less than or equal to the statistical mean of all $m_i$, i.e. $m_{\text{all}}(t) \leqslant \langle m \rangle$, for all $t > 0$. As this is general for any later time $t'$, we can then show that $m_{\text{all}}(t > t') \leqslant m_{\text{all}}(t')$ by redefining $t$ as the interval $t \rightarrow t'$ and noting that $m_{\text{all}}(t) \leqslant \langle m \rangle$ implies $m_{\text{all}}(t') \leqslant \langle m' \rangle$ (where $\langle m' \rangle$ is the statistical mean of $m_i$ in the survivor population at time $t'$), thus demonstrating that $m_{\text{all}}(t)$ shows monotonic decline with time (that is $\mathrm{d}[m_{\text{all}}(t)]/\mathrm{d}t \leqslant 0$).

The following statement can be shown to be a specific case of Jensen's inequality:

$$\sum_{i=1}^{S} p_i(1-m_i)^t \geqslant \left[\sum_{i=1}^{S} p_i(1-\mathrm{m}_i)\right]^t \tag{A5}$$

Here $\alpha_i$, $f$, and $\rho_i$ of A4 have been interpreted as:

(a) $\alpha_i \rightarrow p_i$; $p_i$ is real, positive and $\Sigma p_i = 1$;
(b) $f(x) = x^t$, which is a convex function of $x$ for all $t > 1$;
(c) and $\rho_i = (1-m_i)$, which implies that indeed $0 \leqslant \rho_i \leqslant 1$.Using eqn A2 for $m_{all}(t)$, we can rewrite A5 as

$$1 - m_{\text{all}}(t) \geqslant \sum_{i=1}^{S} p_i(1-m_i) \tag{A6}$$

The mean mortality rate, $\langle m \rangle$, is defined in the usual way as

$$\langle m \rangle \equiv \sum_{i=1}^{S} p_i m_i \tag{A7}$$

Hence A6 can be rewritten as

$$m_{\text{all}}(t) \leqslant \langle m \rangle, \tag{A8}$$

for all $t$. The equality pertains only if all $m_i$ are identical, $m_i = \langle m \rangle$.

As noted above, A8 is sufficient to establish that $m_{all}(t)$ is a monotonic decreasing function of $t$, which is the major result asserted in the main text.

The corresponding result for continuous time is similarly established from Jensen's inequality. Again we identify the $\alpha_i$ of A4 with $p_i$, but we differ from the discrete time case by now identifying $\rho_i = \lambda_i$ and $f(x) = \exp(-xt)$, which is convex for positive $x$ and $t$. The above analysis can be repeated, *mutatis mutandis*, to show that

$$\lambda_{\text{all}}(t) \leqslant \langle \lambda \rangle, \tag{A9}$$

for all $t > 0$, and again equality pertains only if all $\lambda_i$ are identical. Here $\langle \lambda \rangle$ is defined by analogy with $\langle m \rangle$ , as

$$\langle \lambda \rangle \equiv \sum_{i=1}^{S} p_i \lambda_i \tag{A10}$$

and $\lambda_{\text{all}}(t)$ is defined by eqn 9 in the main text.

## Appendix 2

An approximation for the determinants of changing estimates. In this Appendix we outline how the approximate expressions stated in eqns 10 and 12 are derived from the exact eqns 8 and 9.

We first write

$$m_i = \langle m \rangle + \Delta m_i, \tag{B1}$$

Here $\langle m \rangle$ is defined by A7, and we have introduced

$$\Delta m_i \equiv m_i - \langle m \rangle. \tag{B2}$$

We now take the version of eqn 8 presented as equation (A2) in Appendix 1, and use eqn B1 to rewrite it as

$$m_{\text{all}}(\mathrm{t}) = 1-(1-\langle m \rangle)\left\{\sum_{i=1}^{S} p_i[1-\Delta m_i/(1-\langle m \rangle)]^t\right\}^{1/t} \tag{B3}$$

The terms in the RHS of eqn B3 may be expanded as a Taylor series:

$$(1-x)^t = 1 - tx + t(t-1)x^2/2 + Ox^3, \tag{B4}$$

where $x = \Delta \mathrm{m}_i/(1-\langle m \rangle)$. Performing the sum in eqn B3, we arrive at

$$m_{\text{all}}(t) \approx 1-(1-\langle m \rangle)[1+\mathrm{t}(\mathrm{t}-1)\sigma^2/2(1-\langle m \rangle)^2 + \mathrm{O}(\Delta m)^3]^{1/t} \tag{B5}$$

This expression reduces simply to eqn 10 of the main text. Note that we have neglected terms of the order $(\Delta m_i)^3$ and higher; this corresponds to ignoring the skewness and higher moments of the $\{m_i\}$ distribution.

The process of deriving eqn 12 as an approximation to eqn 9, when time is taken as a continuous variable, proceeds along lines parallel to those above.