

Mortality and tree-size distributions in natural mixed-age forests

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Summary

1 Tree-size distributions are changing in many natural forests around the world, and it is important to understand the underlying processes that are causing these changes. Here we use a classic conceptual framework – the shifting mosaic of patches model – to explore the ways in which competitive thinning and disturbance influence tree-size distributions, and to consider the effects of temporal variability in disturbance frequency on the size structure of forests.

2 We monitored 250 stands of *Nothofagus solandri* var. *cliffortioides* (mountain beech), randomly distributed over 9000 hectares, for 19 years. Mountain beech is a light-demanding species that forms monospecific forests in New Zealand mountains. For the purposes of our model, we assumed that each stand functions as an even-aged population: it is initiated by a pulse of recruitment, undergoes competitive thinning as it matures, and is eventually destroyed by a disturbance event. The tree-size distribution of the whole forest is driven partly by the frequency and temporal patchiness of disturbance events and partly by competitive processes within the constituent stands.

3 Temporal changes in stem density and mean tree size were observed to be remarkably similar in all young stands, indicating that a consistent packing rule operates during this phase of stand development. A popular idea in the self-thinning literature is that the maintenance of constant leaf area index (LAI) provides the mechanism for this packing rule, but our analyses suggest that LAI increased by about 30% during the thinning phase. We use leaf economic theory to develop a new packing rule based on light interception, and argue that LAI increases with stand age because of changes in canopy organisation.

4 Smaller trees were significantly more likely to die than larger trees within the young stands. Tree-diameter distributions within young stands were left skewed but those of older populations were normally distributed. These observations are consistent with asymmetric competition winnowing out small, suppressed trees from young stands but having less effect in older stands.

5 Large-scale disturbances created gaps of sufficient size to allow mass recruitment of seedlings in about 0.8% of stands each year. Older stands were most susceptible to such large-scale disturbance, but the trend was weak.

6 The diameter-distribution of the whole *Nothofagus* forest was found to be approximately exponential in form. Simulation models only produced realistic diameter distributions when competitive packing rules and disturbance were included. Therefore, the shifting mosaic model provides a general framework for understanding the ways in which these mortality processes determine forest size structure.

7 The diameter distribution of the forest was not in equilibrium over the 19-year study. Using simulation models, we show that temporal variability in disturbance frequency can generate enormous deviations in tree-diameter distributions away from the long-term mean, leading us to conclude that modern-day disequilibrium in natural forests may be the legacy of past disturbance events.

Key-words: asymmetric competition, density dependence, forest dynamics, leaf economic spectrum, scaling relationships, size frequency distribution, WBE metabolic scaling theory, Weibull function

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Introduction

The tree-size distribution for a natural forest is a property that emerges from the demographics of individuals and therefore should be predictable from tree growth, mortality and recruitment processes. However, many factors influence these demographic processes, and it is difficult to decide on the level of complexity to include in predictive models. Enquist & Niklas (2001) predicted that the relationship between tree size and stem density in natural forests is given by an invariant scaling relationship, basing their calculation on an assumption that competition for space is the only determinant of mortality within stands. In fact, the tree-size distributions seldom follow this pattern, because large trees die at a much greater rate than predicted by competition alone, probably because of disturbance and senescence (Coomes *et al.* 2003; Muller-Landau *et al.* 2006). Indeed, many studies have shown that disturbance has a profound influence on forest structure, particularly in the later stages of stand development (e.g. Parker *et al.* 1985; Lorimer 1989; Oliver & Larson 1996; Runkle 2000; Miura *et al.* 2001). Therefore, general models for tree-size distributions need to take disturbance and competition into account (see Goff & West 1975; Shugart 1984; Harcombe 1987; Kohyama 1987; Clark 1991; Coomes *et al.* 2003).

This paper seeks to derive a general theory of tree-size structure for natural forests by taking into account the effects of both disturbance and competitive thinning on demographic processes. Our premise is that a forest develops as a shifting mosaic of patches (Fig. 1a,e; Watt 1947; Franklin *et al.* 2002). This conceptual model views a forest as being comprised of populations (= patches) that establish as a result of asynchronous disturbance events. Each population is regarded as functioning as an even-aged stand. The populations go through a series of developmental phases; there is a seedling recruitment phase, followed by a phase in which the canopy is closed and competitive thinning takes place. Later, the stands become mature and disturbance plays an increasingly important role in killing trees, gaps are opened that do not refill by lateral branch spread, and the openings provide opportunities for seedlings to establish, whence the cycle starts again (Fig. 1a; Franklin *et al.* 2002). This model allows three aspects of demography to be identified and quantified that together shape the tree-size structure of the forest (i.e. the diameter distribution of the metapopulation DDM).

The first aspect is the diameter size distribution of trees within each population (DDP; Fig. 1b). Research

in plantations indicates that tree cohorts initially have diameter distributions that are highly skewed at the time of canopy closure, a pattern that can be reproduced mathematically by allowing seedlings to differ in relative growth rates or starting sizes (Westoby 1984). After canopy closure, relatively small trees are hugely disadvantaged in the battle to intercept light, which slows their growth rate and increases their likelihood of death (Weiner 1990; Adler 1996; Reynolds & Ford 2005). This 'hierarchy of dominance and suppression' has two effects: variation in growth broadens the distribution, while the loss of smaller trees reduces its skewness (Fig. 1c; Mohler *et al.* 1978; Hara 1984; Weiner & Thomas 1986; Knox *et al.* 1989). We hypothesize that many natural forests may function similarly, particularly where most seedlings recruit within a narrow time frame after canopy disturbance. We also expect this in any forest where light limitation leads to a dominance hierarchy, even in mixed-age populations.

The second aspect shaping size structure concerns competition for light as the mechanism behind loss of stems during competitive thinning. Long & Smith (1984) argued that mortality within densely packed stands occurs because individuals increase their leaf area as they grow but the total leaf area of the population is capped (i.e. the leaf area index or 'LAI' is capped). A tree's leaf area is directly proportional to its basal area, so it follows that LAI scales approximately with $N \times BA_m$, where BA_m is the mean basal area of the trees within a stand and N is the number of stems, and this in turn leads to $\log(N) \propto -\log(BA_m)$. A cap on LAI provides an explanation for self-thinning relationships, which are observed to control development in even-aged plantations (Midgley 2001). We test the hypothesis that constant LAI limits stem densities in young natural-forest stands (Long & Smith 1984; Franco & Kelly 1998), because at this stage the trees are densely packed and so competition is particularly important (White & Harper 1970; Westoby 1984; Enquist *et al.* 2000).

The final aspect defining size structure is disturbance. Whilst it is generally recognized that stands become increasingly susceptible to senescence and disturbance as they age (Runkle 1982, 1985, 2000; King 1986; Dahir & Lorimer 1996; Canham *et al.* 2001; Lorimer *et al.* 2001), it is equally recognized that disturbance is highly unpredictable and spatially patchy (Runkle 1982, 1990; Pickett & White 1985; Clark 1991; Oliver & Larson 1996; Allen *et al.* 1999). Here we use simulation modelling to explore the effects of disturbance on the size distribution of trees in forests. Disturbances often produce a shifting mosaic of patches of varying age at the landscape level,



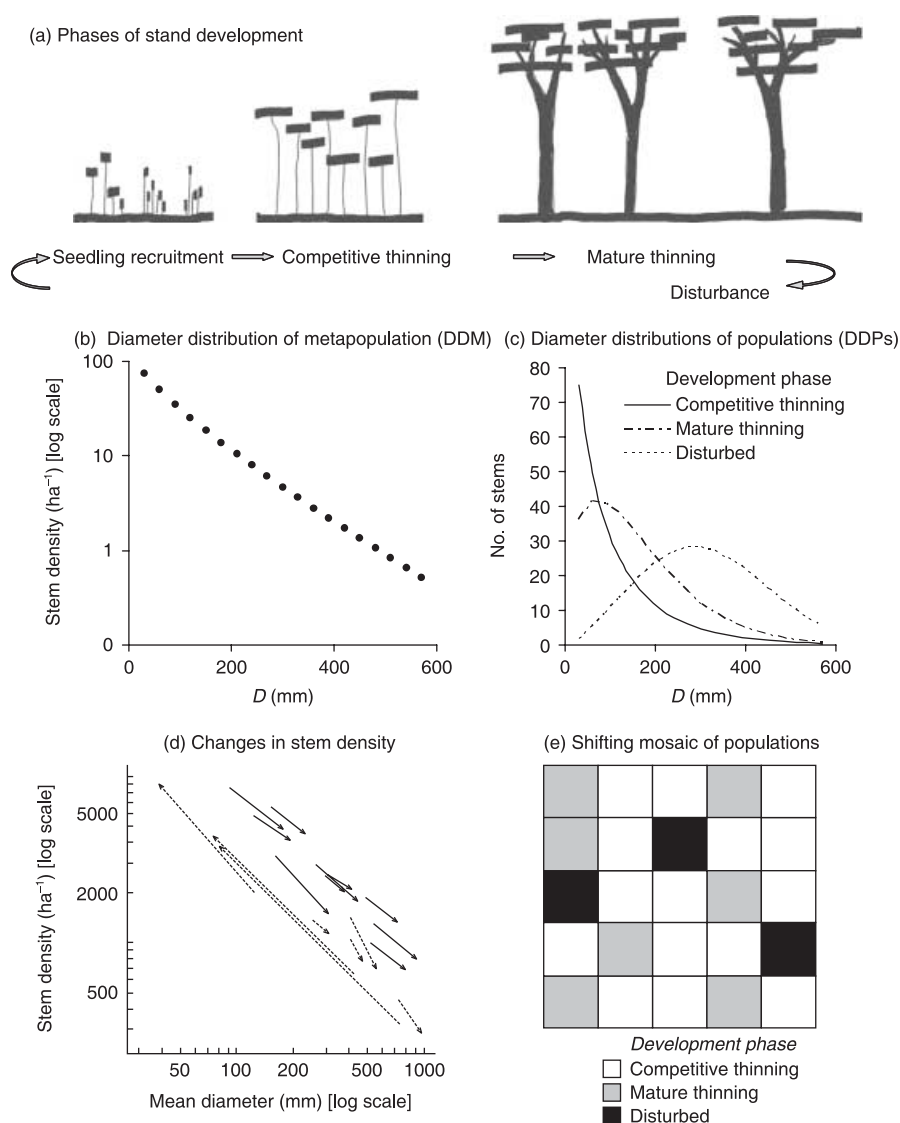


Fig. 1 (a) Factors influencing the diameter distribution of trees in natural mixed-aged forests can be discerned by recognizing forests as consisting of a shifting mosaic of patches at different developmental stages (seedling recruitment, competitive thinning, mature thinning and disturbed). Using this approach, the diameter distribution of the metapopulation (DDM), as shown in (b), is seen to be influenced by three aspects of population size structure: (c) the way in which the diameter distribution of populations (DDPs) varies as they age; (d) the way in which stem density decreases over time in thinning stands as a result of competition for space (solid arrows), and increases over time in disturbed stands as a result of seedlings recruit (dashed arrows); and (e) the age distribution of populations, which is controlled by disturbance.

and these have an approximately stationary age structure (Fig. 1c; Watt 1947; Leibundgut 1959; Bormann & Likens 1979; Shugart 1984; Clark 1990, 1991). The diameter size distribution of the metapopulation (DDM) can be calculated from the age (or size) distribution of stands, and the stem density and diameter distribution of each of the constituent populations (Fig. 1b). The simulations thereby allow us to test the extent to which changes in disturbance regime modify forest stand structure.

This study makes use of long-term data from 250 plots sampling stands of *Nothofagus solandri* var. *cliffortioides* (Hook. f) Poole (mountain beech) growing naturally in New Zealand. *Nothofagus solandri* is strongly light demanding and regenerates in cohort-like pulses following canopy damage (Wardle 1984), so natural stands are assumed to function similarly to even-aged plantations

(the limitations of this assumption are discussed later). We classify the stands into development phases, examine whether the DDPs change in the way expected from competition, and then examine whether thinning-stands follow the constant-LAI rule and whether disturbance occurs mostly in mature stands. The general rules derived from these analyses are then used to simulate DDMs and explore the consequences of different types of disturbance regime (Fig. 1).

Methods

DESCRIPTION OF FIELD SITE

Nothofagus solandri forms monospecific forests on the eastern slopes of the Southern Alps (Wardle 1984).

Seedlings of *Nothofagus solandri* can persist for many years in the semi-shade, but the species is widely recognized as a light-demander that requires large gaps to regenerate successfully, and produces cohort-like populations (Wardle 1984). The data set from these forests consists of 20 330 trees situated in 250 permanently marked plots that randomly sample 9000 ha of forests. The plots were established systematically along 98 compass lines over the austral summers of 1970/71 and 1972/73 with line origins located randomly along stream channels (30–1000 m apart), and aligned along a random compass direction. Plots were then located at 200-m intervals along each line until the tree line was reached, giving rise to lines containing between one and eight plots (mean = 2.6). Each plot was 0.04 ha (20 × 20 m), and in the austral summer of 1974/75 all stems within the plots > 30 mm diameter at breast height were tagged, and diameters at breast height recorded. New recruits were tagged in subsequent measurements and deaths were recorded. The plots were re-measured during the austral summers of 1983/84 and 1993/94.

Windstorms and snowstorms in 1968 caused extensive damage to the forests, which had previously consisted largely of mature stands (Wardle & Allen 1983). In the winter of 1973, a further moist heavy snowfall damaged trees in 30% of stands; there was branch breakage in large trees, and stem snapping of smaller trees (Wardle & Allen 1983; Harcombe *et al.* 1998). Populations of pinhole beetles (*Platypus* spp., Platypodidae, Coleoptera), and associated pathogens, built up on the woody debris that accumulated after these storms and the beetles then attacked live trees, resulting in ongoing mortality and a decline in stem biomass through to 1987. This resulted in a pattern of dispersed, low-intensity disturbance (Harcombe *et al.* 1998).

DEFINING DEVELOPMENTAL PHASES

Stands were classified into developmental phases (Fig. 1a) based on whether they were gaining or losing stems over time, and whether mortality was focused particularly on small stems. A gain in stem number over 19 years, associated with a decrease in mean tree size, was the result of multiple tree deaths within a stand followed by a pulse of seedling recruitment, and stands showing this pattern were classified as ‘disturbed’. Stands in which a net loss of individuals had occurred over 19 years, accompanied by an increase in the mean tree size, were defined as ‘thinning’ stands, and these were further divided into those in which mortality was greatest among smaller trees (‘competitive thinning stands’), vs. the remainder in which no such size discrimination was observed (‘mature thinning stands’). This was done by noting which of the 10–650 trees present on plots in 1974 were dead in 1993, and then using generalized linear models to test whether the probability of dying varied with initial stem diameter. The function $\text{logit}(p_D) = a + bD$ was fitted, where p_D is the probability of death and D is initial stem size, using the *GLM* routine in R

v 2.1.0 (R Foundation 2005), with a binomial error structure. Stands for which b was significantly less than zero ($P = 0.05$) were classified as competitive thinning (Fig. 1a).

CHANGES IN WITHIN-POPULATION DIAMETER DISTRIBUTIONS OVER TIME

We used various statistics to describe the tree-diameter distribution of each stand (DDP). The mean stem basal area (BA_m) and mean stem diameter (D_m) were calculated for each measurement for each plot. Size inequality within stands was characterized by coefficient of variation in stem diameter ($CV = \text{standard deviation}/\text{mean}$) and deviation from normality was quantified using skewness. Note that Gini coefficients provide an alternative measure of inequality (Knox *et al.* 1989), but are not presented here because they were very closely correlated with CV ($r = 0.96$). Foresters commonly use a two-parameter Weibull function to describe the size structure of a forest stand; it has the probability density function $f(D) = c/d(D/d)^{c-1} \exp(-(D/d)^c)$, where c and d are the shape and scale parameters, respectively, and D is the stem diameter. Two-parameter Weibull functions were fitted to the diameter distributions from each of the 250 stands in 1974 and in 1993, using the *fit.distr* function in the *MASS* library of R. The ways in which c and d varied with D_m were assessed by least-squares linear regression, using the *lm* function of R.

Finally, we explored the way in which mortality varied with tree size within each of the development phases. For each category, the total number of deaths within each of 30 diameter-size classes was calculated, and compared with the total number of stems initially present, using a cumulative-interest-rate formula to calculate annual mortality rates. The size-class boundaries were selected so that each class contained the same number of stems (obtained using the *quantile* function in R), and the mean stem diameter D_i within each bin was used in plots of mortality against size.

THINNING RELATIONSHIPS

Thinning relationships were quantified by examining the temporal trajectories in population density (N) and mean basal area (BA_m) of trees within each stand. Temporal trajectories were visualized by plotting vectors of changes in $\log N$ and $\log BA_m$ over 19 years for stands in each development phase. The thinning slopes were calculated for each stand as $(\log N_{1999} - \log N_{1974})/(\log BA_{1993} - \log BA_{1974})$ and the average slope calculated among stands from these (Roderick & Barnes 2004). If the slope is -1 this suggests that LAI remains constant during stand development, provided that a tree's leaf area scales isometrically with its basal area, which appears to be the case for *Nothofagus solandri* trees ($M_L \propto BA^{0.99}$, where M_L is mass of leaves, calculated from data in Osawa & Allen (1993) using SMA regression).

A less powerful approach than following temporal changes is to compare stands at different developmental stages using only a single enumeration (see Weller 1990), and we also explored the data in this way. The self-thinning rule does not apply in even-aged stands in which there is incomplete canopy cover (Westoby 1984; Begon *et al.* 1996), so it is usually deemed necessary to quantify the thinning process by fitting an upper boundary to the relationship between $\log(N)$ and $\log(BA_M)$ (Osawa & Allen 1993). Quantile regression was used to fit these 'upper boundary' lines (the *rq* function in the *quantreg* library of R, setting tau at 0.95) to the data from 1974 and 1993, and standard errors were estimated by the 'xy' bootstrapping method (Cade & Guo 2000). For the 1993 data, we had information on which of the stands belonged to which developmental phase based on their dynamics during the previous 19 years, and fitted regression lines through the centre of the data set. Scaling relationships were fitted using RMA regression, using the *slopes.s* function in R.

EFFECTS OF DISTURBANCE ON FOREST SIZE STRUCTURE

The diameter distribution of the metapopulation (DDM) was obtained by assigning each of the 20 330 stems to a diameter class (bin widths = 30 mm), and totalling the number of stems within each size-class bin. **Scaling and exponential functions were fitted to the DDM using linear regression and we tested which function was most strongly supported, using the Akaike Information Criterion.** Simulation modelling allowed us to identify which processes have the greatest influence on the DDM. The models are based on an assumption that the DDPs and density of stems change in predictable ways over the course of stand development (according to functions defined from field data), and asynchronous destruction of individual stands gives rise to a shifting mosaic of patches across the landscape. All our functions were derived at the whole-stand level, rather than attempting to keep track of individual trees.

One thousand stands were simulated, each of which was given an initial age of 20 years. At the end of each time step (1 year) a percentage of the stands were destroyed, and were replaced by stands of zero age. The choice of which stands were destroyed was made by random draws from a probability density function that depended upon stand age. This process was repeated for 5000 years, by which stage the age structure was independent of starting conditions. The mean stem diameter of each stand was then estimated from its age. We used non-linear regression modelling to fit the following relationship between mean stem diameter in 1974 and 1993, $D_{m,1974} = (D_{m,1993}^{\theta} + 19\lambda)^{-\theta}$; and then used the parameter estimates (λ and θ) in the following relationship between size and time since recruitment into the 30-mm size class (t), $D_{m,t} = (30^{\theta} + \lambda t)^{-\theta}$; this model assumes that growth is a power function of size, and is obtained by integrating the power function (see Muller-

Landau *et al.* 2006). Next, the number of stems per stand, N , was estimated using the thinning scaling function obtained by RMA regression; then the diameter distribution within each stand was obtained, by drawing N stems from a Weibull distribution (using the *rweibull* function in R) with shape and scale parameters appropriate for the mean stem diameter of trees in the stand. Finally, the DDM of the 1000 populations was constructed by assigning the individual stems into diameter-size classes (bin width = 30 mm), and totalling the number of stems within each size class bin.

The simulated distribution was compared with the actual DDM. We explored the way in which intensity of disturbance affects the size structure by varying the number of plots destroyed each year. The effects of temporal variability in disturbance were explored by allowing the frequency to vary among years, while maintaining a constant long-term average; the number of plots destroyed each year was sampled from a negative binomial distribution (using the *rnbinom* function in R). This may result in considerable variation among years, depending on the size parameter c (e.g. when $c = 0.05$, mortality occurs in only 30% of years).

Results

POPULATION DIAMETER DISTRIBUTION CHANGES IN DEVELOPMENT PHASES

Of the 250 stands, 212 were categorized as 'thinning' because they increased in mean stem diameter, D_m , over the 19 years and decreased in population size, N . These thinning stands were separated into competitive and mature stages according to whether relatively small trees were observed to suffer greater mortality than expected by chance. Small trees were significantly discriminated against in 76 of the 212 stands ($P < 0.05$, 'competitive thinning stands'), while larger trees were discriminated against in only seven thinning stands, which is less than the 11 expected by chance at $P < 0.05$ (Fig. 2a). **The strength of size-discrimination was greatest in small-stemmed stands** (Fig. 2a; Spearman's rank $\rho = 0.34$, $n = 211$, $P < 0.0001$). Thinning stands in which b (the size dependence of mortality risk) did not differ significantly from zero, or was positive, were classified as belonging to the mature thinning phase (136 in total). Finally, 38 stands were categorized as 'disturbed', because their D_m decreased and their N increased over time; this resulted from the death of mature trees followed by seedling recruitment. **Although our categorization was not based on tree sizes, the development phases followed a logical progression with respect to mean stem diameter (146 ± 4.8 mm for competitive thinning stands, 183 ± 4.5 mm for mature thinning stands, and 214 ± 9.3 mm for disturbed stands).** These differences were statistically significant ($F_{2,247} = 25$, $P < 0.0001$) but there was a great deal of overlap among the groups (Fig. 3), and mean stem diameter of disturbed plots was particularly variable.

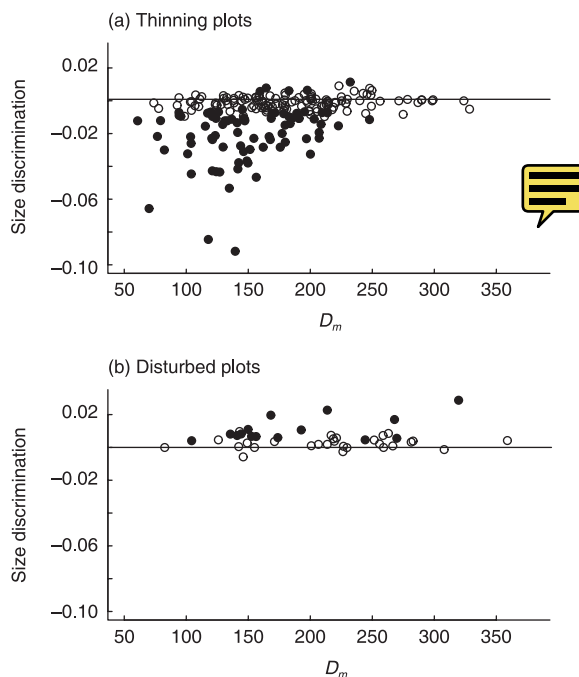


Fig. 2 Size-discrimination of mortality processes within (a) thinning, and (b) disturbed *Nothofagus* stands, in relation to the mean stem diameter of the stands (D_m). The extent of size-discrimination was estimated by modelling death as a function of stem diameter by fitting the function $\text{logit}(P) = a + bD$ using logistic regression, where P is the probability of death, D is stem diameter, and b is the parameter which indicates the degree of size discrimination (● = significant and ○ = not significant at $P = 0.05$). When $b < 0$, smaller trees within stands are most likely to die, and when $b > 0$ the larger trees are more likely to die.

SIZE STRUCTURE OF POPULATIONS (DDPS)

The DDPS were positively skewed in 200 of the 212 thinning stands, the skew being greatest in the young stands of small stems, and decreasing as stands aged (Figs 3 and 4b). Skewness also decreased with increasing D_m (Fig. 4a, $F_{1,207} = 82.1$, $P < 0.00001$). Similarly, coefficients of variation (CV) decreased over time ($CV_{1993} = 0.049 (\pm 0.011) + 0.76 (\pm 0.017) CV_{1974}$, $F_{1,211} = 2070$,

$P < 0.00001$) and with increasing mean stem diameter ($CV_{1974} = 0.97 (\pm 0.043) - 0.0022 (\pm 0.00024) D_m$, $F_{1,210} = 84.1$, $P < 0.00001$). Weibull functions provided the sort of flexibility required to model such size distributions. The scale parameter was found to be closely related to the mean stem diameter of the individuals in the stand (scale = $1.118 (\pm 0.00138) D_m$, $r^2 = 0.99$), while the shape parameter, which is inversely correlated with CV, increased significantly with mean stem diameter (shape = $0.825 (\pm 0.152) + 0.00715 (\pm 0.00085) D_m$, $r^2 = 0.25$).

The 38 disturbed populations functioned differently to thinning populations. Within each stand it was the relatively large trees that tended to die, perhaps because they were especially exposed to wind or snow damage; the logistic regression of mortality against size gave rise to b -values that were significantly greater than zero in 13 of the 38 plots (Fig. 2b), and the mean b -value was greater than zero (0.0087 ± 0.0042 ; $t = 2.0$, d.f. = 37, $P = 0.048$). Seedling recruitment resulted in huge changes in CV and skewness over time, to the extent that the values in 1974 were completely uncorrelated with those in 1993 (Pearson correlation, $r = 0.25$, $P > 0.10$; skewness $r = 0.11$, $P > 0.50$).

When data from stands within each development phase were pooled, very different size-specific mortality curves were observed. Mortality declined with tree size in the competitive thinning stands (Fig. 5a), consistent with asymmetric competition being the predominant mortality process. A U-shaped mortality function was apparent in the mature thinning stands (Fig. 5b), consistent with competition and senescence/disturbance simultaneously affecting the stands. An increasing probability of death with size was apparent in the disturbed stands (Fig. 5c), perhaps indicating that large trees are particularly susceptible to damage.

MORTALITY IN THE COMPETITIVE THINNING PHASE: A CONSTANT LAI RULE?

The thinning trajectories for competitively thinning stands were found to be highly consistent among stands

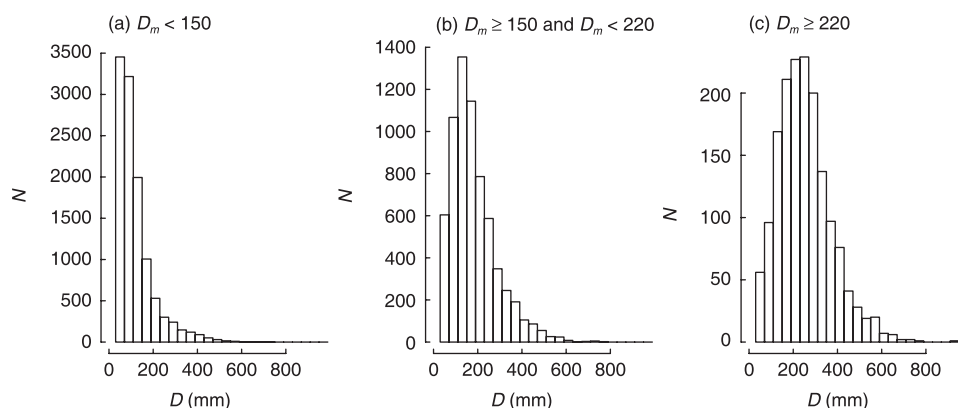


Fig. 3 Diameter distributions within stands in which the mean stem diameters D_m are (a) small, (b) medium, and (c) large. The diameter distributions were obtained by pooling data from 90, 50 and 110 stands, respectively. N is the total number of trees within a size bin. A decrease in skewness is observed with increasing D_m .

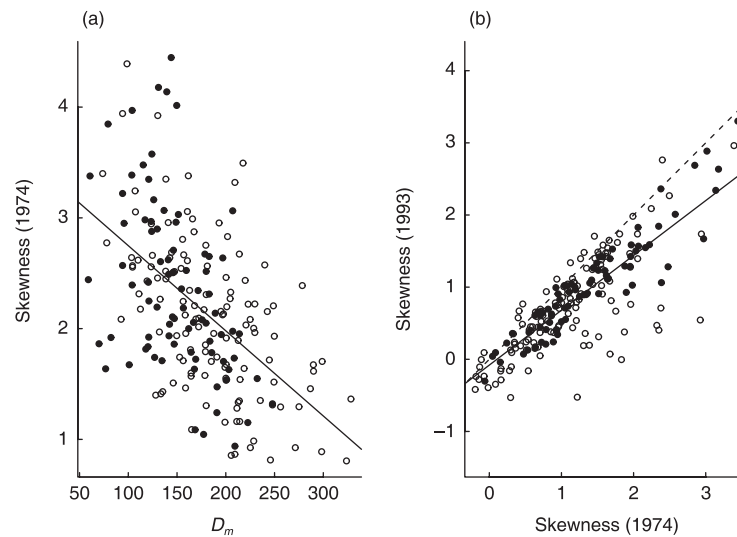


Fig. 4 Skewness of diameter distributions within 212 thinning stands of *Nothofagus* in which evidence of light competition was (●) and was not (○) evident; skewness in the year 1974 (a) related to mean stem diameters ($S_{1974} = 2.55 - 0.0078D_m$; $r^2 = 0.64$), and (b) compared with 1993 (dashed line is the 1 : 1 relationship, for which the regression line is $S_{1993} = -0.1 + 0.76S_{1974}$ ($r^2 = 0.68$)).

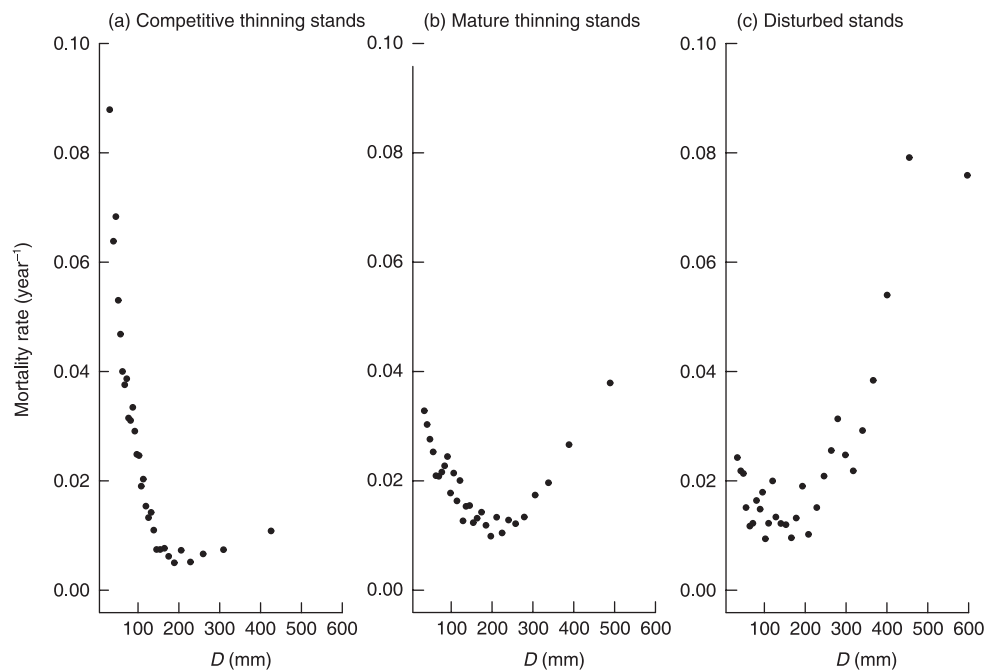


Fig. 5 Size-specific mortality relationships obtained by pooling data from (a) competitive thinning stands, (b) mature thinning stands, and (c) disturbed stands. Mortality rates were determined for 30 size-class bins, with the size of the bins set to contain equal numbers of individuals.

(Fig. 6a), but the slopes of these trajectories do not support the theory of constant LAI. For competitively thinning stands, the mean slope was -0.92 and was significantly different from -1 (95% CI = -0.87 to -0.97 , $t = 2.86$, d.f. = 74, $P < 0.005$). The mean thinning relationship is $N \propto BA_m^{-0.92}$, and the total basal area of a stand BA is given by $N \times BA_m$, so it follows that $BA \propto BA_m^{0.08}$. Further, the leaf biomass of mountain beech trees M_L scales with $BA^{0.99}$ (recalculated from Osawa & Allen 1993) so the total leaf mass also scales with $BA_m^{0.08}$. The findings suggest that stands gradually increase in leaf mass (and presumably LAI) as they develop,

Adherence to the thinning trajectory was less evident in mature thinning stands because large stems were lost without sufficient compensatory growth of the remaining trees (Fig. 6b). The mean slope was -1.81 in these stands (95% CI = -2.47 to -1.13 , $t = 2.39$, d.f. = 129, $P < 0.018$), and 77% of slopes were more negative than -1 , a far greater proportion than expected by chance (binomial test, $P < 0.0001$).

In the disturbed stands, many large trees died in 1974–83 (almost double the number dying in the following 9 years), giving rise to size-density trajectories with more negative slopes than expected under the constant



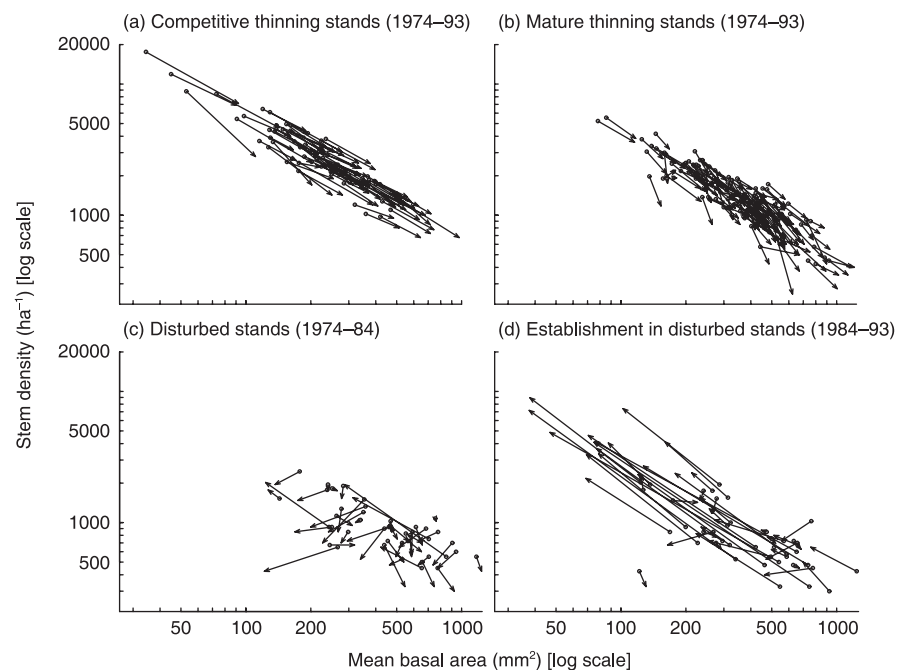


Fig. 6 Temporal changes in mean tree basal area (mm^2) and stem densities (ha^{-1}), plotted on log-log axes, in (a) competitive thinning stands (1974–93), (b) mature thinning stands (1974–93), (c) disturbed stands (1974–84), and (d) disturbed stands in which seedling recruitment is occurring (1984–93).

LAI rule (Fig. 6c; mean = -3.85 (95% CI = -6.4 to -1.2 , $t = 2.2$, d.f. = 37, $P < 0.03$)). These deaths created gaps that allowed light to penetrate to the forest floor, and during the following 9 years, thickets of saplings grew within these stands, and became sufficiently large for inclusion in the 1993 census, causing a large decline in mean tree size and increase in stem density (Fig. 6d). Despite large-scale disturbance of the forests in the 1970s and 1980s, there was only a slight reduction in mean basal area over the 19 years (from $51.4 \text{ m}^2 \text{ ha}^{-1}$ in 1974 to $47.6 \text{ m}^2 \text{ ha}^{-1}$ in 1993). This was because the disturbed stands recovered much of their lost basal area in the second period.

A traditional way of quantifying competitive thinning is to analyse stem densities within stands of different ages, using data collected from a single survey (see Weller 1990). Such space-for-time substitutions are much less precise than directly measuring thinning over time, because the density of stems is controlled by factors such as altitude, as well as by competitive packing rules, so the estimated thinning trajectories have much wider confidence intervals as a results. For this reason, the results of spatial comparisons are provided in Appendix S1 in the Supplementary Material.

DISTURBANCE

The frequency of disturbances was about 0.8% of stands per year, based on 38 of 250 stands being disturbed in 19 years, but the study period coincided with a period of high disturbance (Wardle 1984; Allen *et al.* 1999), and the long-term average disturbance rate is probably lower than 0.8%. The 38 disturbed stands were not a random

subsample of the 250 stands in the forest; the probability of a stand being disturbed increased with D_m according to the function $\logit(p) = -4.41 (\pm 0.75) + 0.014 (\pm 0.0033) D_m$, determined by logistic regression (significance of size dependence, Wald $z = 4.2$, $P < 0.00001$).

A GENERAL THEORY OF METAPOPULATION SIZE STRUCTURE USING SIMULATION MODELLING

The diameter distribution of the metapopulation (DDM), found by pooling data from the 250 stands, was not accurately described by a scaling function with an exponent of -2 (cf. Enquist & Niklas 2001). The DDM was strongly non-linear when plotted on log-log axes (Fig. 7a), and the best-fitting RMA regression line had a slope of -2.70 ± 0.31 , which was significantly less than -2 ($t = 3.1$, $P < 0.001$). There was much greater statistical support for an exponential than a scaling function ($\Delta\text{AICc} = 63$), with an exponent of 0.0110 ± 0.00042 (i.e. a straight-line relationship on log-linear axes; Fig. 7b). However, the exponential function was only approximate because the DDM varied over time, most notably in the small size-classes (Fig. 7c).

The simulations aimed to test whether a shifting-mosaic model would successfully reproduce the observed DDMs, using the following functions taken from our analyses.

Frequency of disturbances (year^{-1}): three frequencies were tested; $F = 0.6, 0.8, 1.6\%$.

Probability of a stand being disturbed: $P = 1 + e^{(-4.4 + 0.014069 D_m)}$, based on logistic modelling of mortality.

Diameter distribution within a stand: $f(D) = c/d(D/d)^c \exp -(D/d)^c$, where $c = 1.118 D_m$, and $d = 0.825 +$

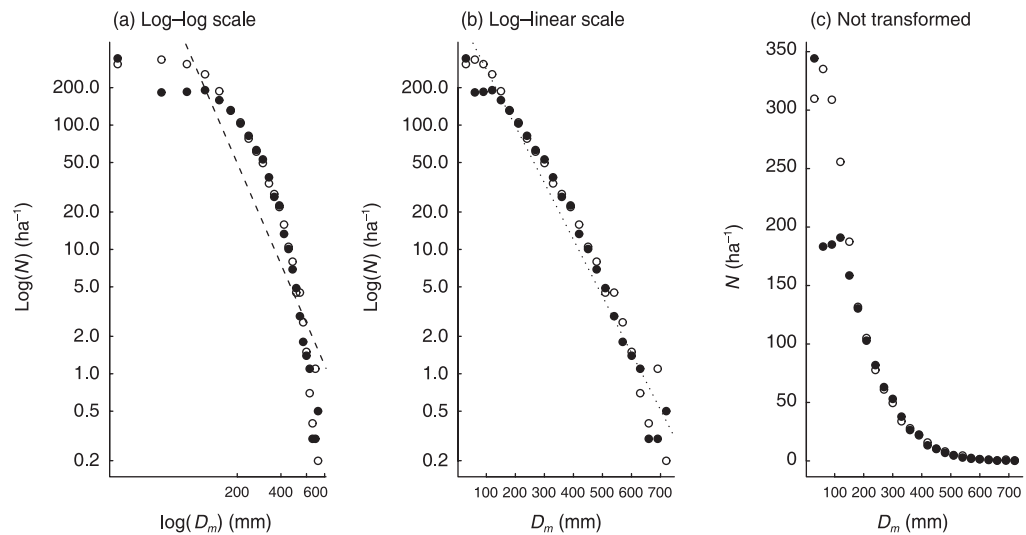


Fig. 7 Diameter distribution of the metapopulation of *Nothofagus* stands, obtained by pooling data from 250 populations in 1974 (●) and 1993 (○). The distributions are presented on (a) log-log axes, (b) log-linear axes, and (c) non-transformed axes. A scaling function is fitted to the log-log data, and an exponential function to the log-linear data (dashed lines).

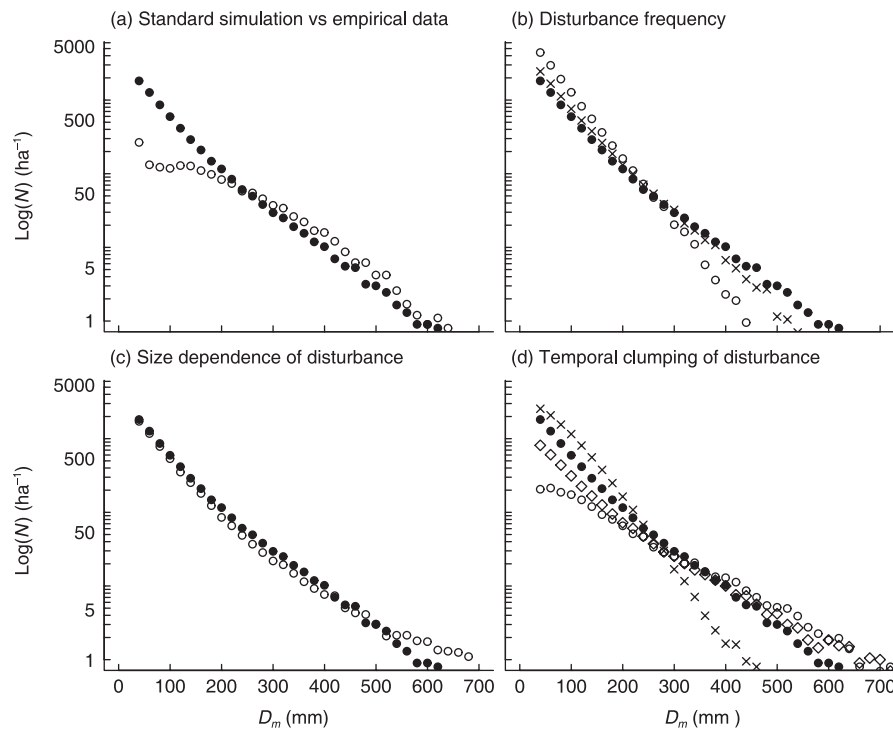


Fig. 8 Diameter distribution of the metapopulations (DDMs) obtained by simulation models. The DDM produced by our standard simulation model, with a disturbance frequency equal to 0.6% of stands per year, appears in all four panels (●) and is compared with (a) the actual DDM of the forest in 1974 (○), and with simulations in which (b) the disturbance frequency is 0.8% (○) and 1.6% (×), (c) the probability of disturbance is unrelated to stand age (○), and (d) the disturbance frequency varies among years (three different simulations indicated by ◇, ○ and ×).

$0.00715D_m$, based on fitting Weibull functions to DDPs and then fitting linear models to the relationships between a , b and D .

Density of a population (ha^{-1}): $N = 28.1 \times 10^6 / D_m^{1.89}$, based on a thinning relationship obtained by RMA regression of $\log N$ vs. $\log D_m$ for thinning stands in 1993; note that we did not distinguish between competitive thinning and mature thinning stands in these simulations.

Relationship between mean diameter of trees in a stand (mm) and the estimated age of stand: $D_m = (12.8 + 0.364T)^{1.33}$, where T is the time since recruitment (years) into the 30-mm size class.

Simulations based on these empirical demographic functions produced a DDM that was almost linear on log-linear axes (Fig. 8a), and an exponential function fitted to the simulated data had a similar exponent to

that of the field data when the frequency of disturbance was 0.6% (-0.0045 vs. -0.0058). The disturbance frequency had a huge influence on the DDM decay constant (e.g. increasing F from 0.6 to 1.6% resulted in a change from -0.0045 to -0.0093), without greatly affecting its functional form (Fig. 8b). The probability function that determines which stands are most likely to be destroyed by disturbance (p) had an influence on the shape of the DDM; when p was made independent of D_m (i.e. drawn from a uniform distribution) rather than increasing with D_m , the simulated DDM became intermediate in form between a scaling and exponential function, with a concave upwards form when plotted on log-linear axes (Fig. 8c) and a long upper tail. Thus the DDM observed in the field is reliant on large old stems becoming increasingly susceptible to mortality.

Finally, creating temporal variability in disturbance frequency F , by sampling from the negative binomial distribution with size parameter $c = 0.02$, resulted in large fluctuations in the DDM (Fig. 8d), with waves of increased recruitment giving rise to cohorts that took many decades to work their way through the size classes. One of the simulations looks remarkably similar to the field data (Fig. 8d, open circles). When less extreme clustering of disturbance events was simulated ($c = 0.05$), the DDM flexed from being gently upward curving on the log-linear axes to gently downward curving.

Discussion

INCREASES IN LAI DURING STAND DEVELOPMENT: THE ROLE OF LEAF ECONOMICS

Self-thinning is among the most investigated processes in plant population biology. Many studies have concluded that a simple packing rule may govern the changes observed within even-aged stands, because thinning trajectories are so similar among studies (Begon *et al.* 1996; cf. Reynolds & Ford 2005). One particularly popular idea has been that the total leaf mass of a stand (or equivalently, its LAI) remains constant over the course of development (e.g. Long & Smith 1984; Osawa & Allen 1993; Enquist *et al.* 1998; Franco & Kelly 1998). Enquist *et al.* (1998) argue that this arises because 'resource use' of a population depends upon its LAI, so the LAI of a developing population increases until 'resource use' approximately equals 'resource supply' (which resource is unspecified by them). However, LAI did not remain constant during stand development in mountain beech forests. Our analyses indicate that LAI scaled with $BA_m^{0.08}$, which suggests that LAI increases by about 30%, in correspondence with mean tree basal area increases from 5 to 175 cm². Although we did not measure LAI directly, our conclusions are supported by field measurements of annual leaf-litter production, which show substantial increases in litterfall with stand age in these forests (Davis *et al.* 2004). Furthermore,

several empirical studies from different forest communities have reported that LAI increases by roughly 10–30% during the thinning phase of stand development (see Ryan *et al.* 1997; Franklin *et al.* 2002; Reynolds & Ford 2005). These findings suggest that whatever packing rule may be operating in our mountain-beech stands (Fig. 6a), it is not explained by the hypothesis that leaf area remains constant.

We suggest that changes in canopy architecture with stand age may provide an explanation for increases in LAI. From an economic perspective, a viable leaf must produce sufficient carbon in its lifetime to pay for its construction and maintenance costs while also contributing towards maintenance and production of stems, roots and seeds (Givnish 1988). When a stand has a low LAI then all the leaves have enough light to generate a carbon surplus over their lifetime and LAI increases as a result. This process would continue until LAI reaches a point at which leaves near the bottom of the canopy are so deeply shaded that they only just break even economically. To illustrate this idea, let us estimate the maximum LAI that a population can support, based on the supposition that leaves require a photosynthetic photon flux density (PPFD) of at least 120 $\mu\text{E m}^{-2} \text{s}^{-1}$ in order to break even economically. As a first approximation, the maximum LAI is given by the Beer-Lambert's law: $\text{LAI} = -\ln(Q/Q_o)/\lambda$, where Q is the minimum PPFD for economic viability, Q_o is the PPFD incident on the stand (which we take to be 1500 $\mu\text{E m}^{-2} \text{s}^{-1}$) and λ is the light extinction coefficient of the canopy (Jarvis & Leverenz 1983). Using this formula we see that maximum LAI is about 5 when $\lambda = 0.5$, but increases to 6.3 when $\lambda = 0.4$. It is our conjecture that λ declines with stand age, as a result of changes to leaf size, inclination, orientation, clustering and positioning on branches (see Hollinger 1989), allowing a greater area of leaves to be supported. Franklin *et al.* (2002) noted such a phenomenon in Douglas-fir stands: young stands were observed to cast deep shade because their needles are concentrated near the apex of stems, but older stands cast less deep shade despite having greater LAI, because of the greater vertical stratification of needles. Nobody has looked to see whether similar trends occur in mountain beech stands, but Hollinger (1989) has reported that the canopy organization of mature trees is highly dependent upon position within the vertical profile, with the upper layers transmitting much greater quantities of light than the lower layers. Hollinger's work shows that mature mountain beech trees are highly plastic in their architecture, but further research is now required to determine whether LAI and light transmission properties vary systematically with stand age.

Leaf economics are also affected by water supply. Stomata close when the supply of water to a leaf dwindles, in order to prevent the water potential of leaves from becoming too negative, and this limits CO₂ fixation (e.g. Meinzer *et al.* 1995; Hubbard *et al.* 1999). Leaf-economic theory predicts that LAI is lower in forests located in

regions of low rainfall, because leaves at the bottom of a canopy can endure less shade if their lifetime carbon gain is curtailed. Such declines in LAI are commonly observed along rainfall gradients (Coomes & Grubb 2000). By a similar logic, it might be anticipated that LAI should decline with tree size, because tall trees must transport water through long pipes, incurring high resistance to flow (Mencuccini 2003). However, our data contradict this idea, because LAI increases rather than declines with tree size. The metabolic theory proposed by West, Brown and Enquist (WBE) provides an ingenious explanation for why LAI does not decrease during stand development: it suggests that trees can prevent hydraulic resistance (per unit leaf area) from increasing as they grow taller, if vessels in their trunks have larger diameters than those in their peripheral branches (West *et al.* 1997; Enquist *et al.* 2000; Enquist 2002). This pattern of vascular design is indeed observed in mountain beech trees (Coomes *et al.*, in press), and might allow them to grow tall without substantially increasing resistance to hydraulic flow.

THE FATE OF INDIVIDUALS DURING COMPETITIVE THINNING

LAI is a population-level property that is driven by leaf-level economics, but it is important not to lose sight of the fact that competition among individual trees gives rise to the observed patterns. For plants that are competing for light, shorter trees produce many of their leaves in the shade of taller neighbours, resulting in slow growth and eventual death (Givnish 1988; Adler 1996; Begon *et al.* 1996). Such asymmetric competition for light provides the simplest explanation for greater mortality among small trees in *Nothofagus* stands (Adler 1996) and for the reduction in skewness of size distributions observed over time (Mohler *et al.* 1978; Hara 1984; Weiner & Thomas 1986; Knox *et al.* 1989). Our study provides support for general packing rules that are equally applicable to self-thinning plantations and natural mixed-aged forests.

A THINNING RULE FOR THE STANDS IN WHICH DISTURBANCE KILLS TREES

The U-shaped mortality curve observed in mature thinning stands indicates that large trees are dying in greater numbers than can be explained by competitive thinning (Fig. 5b). Similar patterns are observed in many other forests (Lorimer *et al.* 2001). Large trees may be particularly susceptible to windthrow (King 1986; Canham *et al.* 2001), or less able to ward off pathogens such as *Armillaria* (Lorimer *et al.* 2001), and their deaths create gaps in the canopy that are not immediately refilled through recruitment. However, many of the mature stands continued to follow a similar thinning trajectory to that observed in competitive thinning stands (Fig. 6b), although some had slopes < -1 , which indicates mortality without compensatory growth. In addition,

a -1 slope is evident in spatial analyses of data from 1993 (Fig. 7b). The apparent persistence of the -1 thinning trajectories might result from increased growth of surviving trees in response to the death of neighbours, which eventually compensates for the loss in large trees (D. A. Coomes & R. B. Allen, unpublished data). The surviving trees fill in single tree-fall gaps by lateral branch growth (Franklin *et al.* 2002), and although there might be a flush of regeneration in response to the opening up of the canopy, the seedling layer is then suppressed so the opening does not lead to an increase in stem density (R. B. Allen, unpublished data). This contrasts with our 'disturbed' stands, in which the openings created by multiple tree deaths were too large for compensatory lateral growth, resulting in successful regeneration of a profusion of seedlings.

GENERAL THEORY OF SIZE STRUCTURE FOR NATURAL METAPOPULATIONS

The diameter distribution of the *Nothofagus* forest did not resemble a scaling function (Fig. 7), and changed substantially over time (Figs 4 and 7, and Fig. S1 in Appendix S1). Thus, size structure was not adequately predicted by an invariant scaling function as metabolic theory predicts (Enquist & Niklas 2001). The inadequacy of the theory for predicting size distributions in these monospecific *Nothofagus* forests and in natural mixed-species forests throughout tropical and temperate regions (Coomes *et al.* 2003; Muller-Landau *et al.* 2006) is the consequence of its narrow focus on competition as the cause of mortality in forest stands, and its failure to consider the effects of disturbance (Parker *et al.* 1985; Harcombe 1987; Lorimer 1989; Clark 1991; Oliver & Larson 1996; Runkle 2000; Miura *et al.* 2001).

Our simulations suggest that the increasing probability of mortality with stand age is important in defining metapopulation structure (Clark 1989, 1990). Models in which disturbance probability did not vary with stand age produced a DDM that resembled scaling functions (Fig. 8c), and only when more realistic disturbance probabilities were introduced did the DDM take on its near-exponential form. Several other studies show that the probability of stand-scale disturbance increases with the time since the last such event (Kohyama 1987; Suzuki & Tsukahara 1987; Foster 1988), as does the probability of fire (Clark 1989). The influences of these processes on size structure, as well as non-random mortality within stands, are profound.

Even though the *Nothofagus* forest was sampled over an extensive area (c. 9000 ha) it was clear that the DDM was non-stationary, and changed substantially over the 19 years of study (Fig. 7c). Historical records speak of the study area being dominated by mature forests until the 1960s (Wardle 1984), after which there was a series of disturbance episodes (Wardle & Allen 1983; Allen *et al.* 1999). These disturbances are causing ongoing changes to the forest size structure, with a 30% increase

in small stems since the 1994 census (R. B. Allen, unpublished data). Simulations show that concentrating disturbance events into 10% of years results in major perturbations of diameter distribution from that predicted when disturbance rate is constant (Fig. 8d), and only when temporal variability was introduced did simulations produce realistic looking DDMs. Few natural forests are in equilibrium, because changes in the climate, fragmentation, disease outbreaks, earthquakes and introduced herbivores all influence size structure (Bormann & Likens 1979; Phillips & Gentry 1994; Wells *et al.* 2001; Coomes *et al.* 2003; Lewis *et al.* 2004) and disturbances are sporadic in most systems (e.g. Foster 1988). **Hence, the diameter-distributions of natural forests are unlikely to be invariant (Muller-Landau *et al.* 2006) and the predictive ability of general models is limited.**

LIMITATIONS OF THE SHIFTING MOSAICS MODEL AND FUTURE DIRECTIONS

Demographic equilibrium modelling is the simplest method for predicting size distributions from demographic process data (Kohyama 1991; Coomes *et al.* 2003; Muller-Landau *et al.* 2006). We previously found that the size structure of large trees in New Zealand's forests was accurately predicted by this approach, but numbers of small trees were massively overestimated (Coomes *et al.* 2003). Similarly, Muller-Landau *et al.* (2006) found that the general shape of size distributions was predicted accurately, but not the precise numbers of stems in size classes. **The limitations of the approach are that it assumes that forests are in dynamic equilibrium, that mortality rates are constant over time, and that variation in growth and mortality due to local competition are negligible: this imposes limitations on the predictive ability of this approach.**

Our model assumes that forests function as a shifting mosaic of discrete patches (Fig. 1) and provides a more effective tool for understanding the ways in which competition and disturbance interplay to structure forests. Nevertheless, some aspects of the model are simplistic. For example, the assumption that trees within a stand are all of similar age may be reasonable as a first approximation, but disturbances sometimes result in the incomplete destruction of mature stands, so it is not uncommon to find a few old trees nestled among a younger cohort. In addition, seedling establishment may initiate new stands, but suppressed saplings may also take advantages of gaps, so recruits may be of various ages rather than consisting of a tight cohort. Individual-based simulation models, which track the performance of every tree, have the potential to include all the demographic processes that influence size structure (Dubé *et al.* 2001; Reynolds & Ford 2005), and should in theory be capable of simulating the development of within-population size structure seen in Fig. 2. An important next step will be to develop such models for the *Nothofagus* forests.

PREDICTING THE SIZE STRUCTURE OF MIXED-SPECIES FORESTS ALONG ENVIRONMENTAL GRADIENTS

Nothofagus solandri is a light-demanding species that has cohort-like regeneration patterns, and this allowed us to draw analogies with even-aged, self-thinning stands. However, mixed-species forests function differently because succession from light-demanding to shade-tolerant species occurs over time (e.g. Franklin *et al.* 2002). DDPs may retain a 'reverse J' form throughout stand development (e.g. Niklas *et al.* 2003), if late-successional species continue to recruit after the wave of early successional trees has established (e.g. the 'additive basal area model' of Ogden & Stewart 1995). The form of the DDM will depend greatly upon the extent to which the early successional trees are effective at suppressing further recruitment (Clark 1991; Franklin *et al.* 2002). Secondly, shade-tolerant species tend to support a greater leaf area than light-demanding species of similar size (Coomes & Grubb 2000), so succession from light-demanding to shade-tolerant species might lead to large increases in LAI, and a breaking of the near-constant LAI rule of thinning. Further, development of a general theory for mixed-species forests will require individual-based modelling of plants' responses to their competitive environment (Adler 1996; Kobe 1996; Dubé *et al.* 2001; Reynolds & Ford 2005), rather than the mean-field approach adopted in this paper.

Greater generality will also require the effects of environment to be modelled. For instance, we used a single relationship between stand age and mean tree size in our simulations, but know that trees take much longer to reach a given size at higher altitudes: our results may be contingent on unaccounted variation of this sort. It is also known that *Nothofagus* forests increase in basal area with increasing altitude (Harcombe *et al.* 1998), **but nobody has yet investigated the demographic changes that underpin this trend.** A need to include environmental variation is suggested from comparison of Figs 6 and 7. Traditionally, upper boundary relationships are used to quantify self-thinning (Fig. 7), because populations that lie beneath the boundary are not fully packed and should increase in BA_m without any loss in density (Westoby 1984; Begon *et al.* 1996). What is actually observed is that all of the competitive thinning stands followed trajectories that ran parallel to the boundary line (Fig. 6a), irrespective of their initial distance from it. One explanation for this discrepancy is that the LAI of forests depends on environmental conditions, but that the 'constant leaf area rule' nevertheless applies to development within any one stand.

Conclusions

During the competitive thinning phase of stand development, changes in size structure and stem density were similar in natural mixed-age forest to those reported in

even-aged plantations. We argue that these similarities reflect a common set of physiological processes that regulate leaf-level carbon economics in both types of forest. Senescence and disturbance became increasingly important as stands matured, and exerted strong influences on metapopulation size structure. By showing that DDMs derived from our simulations provide a better description of observed field data than simple scaling theory relationships, we demonstrate an improved general theory for the size structure of tree populations in a natural forest.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1 Thinning relationships deduced from spatial variation in stem density and size.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2006.01179.x>

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