Understanding forest dynamics and plantation transformation using a simple size-structured model

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Abstract

1. Concerns about biodiversity and the long-term sustainability of forest ecosystems have led to changing attitudes with respect to plantations. These artificial communities are ubiquitous, yet provide reduced habitat value in comparison with their naturally established counterparts, key factors being high density, homogeneous spatial structure, and their even-sized/aged nature. However, transformation management (manipulation of plantations to produce stands with a structure more reminiscent of natural ones) produces a much more complicated (and less well understood) inhomogeneous structure, and as such represents a major challenge for forest managers.

2. We use a stochastic model which simulates birth, growth and death processes for spatially distributed trees. Each tree’s growth and mortality is determined by a competition measure which captures the effects of neighbours. The model is designed to be generic, but for experimental comparison here we parameterise it using data from Caledonian Scots Pine stands, before moving on to simulate silvicultural (forest management) strategies aimed at speeding transformation.

3. The dynamics of simulated populations, starting from a plantation lattice configuration, mirror those of the well-established qualitative description of natural stand behaviour conceived by Oliver and Larson (1996), an analogy which assists understanding the transition from artificial to old-growth structure.

4. Data analysis and model comparison demonstrates the existence of local scale heterogeneity of growth characteristics between the trees composing the considered forest stands.

5. The model is applied in order to understand how management strategies can be adjusted to speed the process of transformation. These results are robust to observed growth heterogeneity.

6. We take a novel approach in applying a simple and generic simulation of a spatial birth-death-growth process to understanding the long run dynamics of a forest community as it moves from a plantation to a naturally regenerating steady...
state. We then consider specific silviculture targeting acceleration of this transition to “old-growth”. However, the model also provides a simple and robust framework for the comparison of more general silvicultural procedures and goals.

1 Introduction

Forest stand development has been studied for many decades, and a practical understanding of the general patterns and forms observed in the population dynamics is well established (Oliver and Larson, 1996). However, despite the development of a great body of simulation models for multi-species communities (e.g. Botkin et al., 1972; Pacala et al., 1996; Busing and Mailly, 2002), the elucidation of general rules for the structural development of monocultures is not clear. This is due in part to the huge variation in physiological and morphological traits of tree species, but also because of the importance of space and size dependent interactions.

Great progress has been made in the analysis of both size-structured (see e.g. Sinko and Streifer, 1967) and, more recently, spatially-structured population models (see e.g. Bolker and Pacala, 1997; Law et al., 2003). However, an understanding of the dynamics of real communities, structured in both size and space, has been limited by a lack of application of simple models, amenable to analysis and approximation, to the communities in question (Gratzer et al., 2004).

An important concept in forest conservation and uneven-aged stand management is that of “old-growth”. This is an autogenic state which is obtained through an extended period of growth, mortality and regeneration, in the absence of external disturbances. It is often seen as an “equilibrium” state, and is characterised by a fully represented (high variance) age and size structure, and non-regular spatial pattern. Depending on the species involved, it may take several centuries to attain (Oliver and Larson, 1996). The habitat created in this state is generally considered a paradigm of what conservation oriented forest management might hope to achieve.

Whilst marked point process simulations have recently been used to analyse the effects of plantation stand management (Comas, 2005; Renshaw et al., 2009), we seek to develop and directly apply a generic process-based model, which is closely related to those of Bolker and Pacala, 1997 and Law et al., 2003, to understanding the key elements of observed stand behaviour, from planting through to old-growth, which can also be applied to guide silviculture. Our approach is illustrated via application to data on Scots Pine (L. Pinus Syisvestris).

Transformation management aims to speed the transition to the old-growth state, from the starting point of a plantation stand. Schutz (2001, 2002) suggested methods for the attainment of this “sustainable irregular condition”; some transformation experiments have taken place or are in progress (Edwards and Mason, 2004; Loewenstein, 2005), whilst other work has made more in-depth analysis of the structural characteristics of natural forest stands (Stoll et al., 1994; Mason et al., 2007). An example of a “semi-natural” stand, of the type studied by Mason et al., (2007) is shown in Figure 1. However, the management
history of such stands is generally not known sufficiently (if at all) before around 100 years ago, complicating parameter estimation and model validation.

A generic spatial, size-structured, individual based model of interacting sessile individuals is presented in Section 2. Parameters are estimated and the model assessed using data obtained from Scots Pine ($L.\ Pinus\ Sylvestris$) communities. Section 3.1 studies model dynamics: an initial growth dominated period gives way to a reduction in density and a meta-stable state governed by reproduction and mortality, all of which correspond with field observations of the growth of stands of a range of species. Keeping in mind this long-term behaviour, Section 3.2 considers examples of the application of management practices which may accelerate transformation.

2 Materials and Methods

2.1 Model

The model is a Markovian stochastic birth-death-growth process in continuous (two-dimensional) space. Individuals have fixed location, and a size which increases monotonically; these jointly define the state space of the process. The model operates in continuous time by means of the Gillespie algorithm (Cox and Miller, 1965; Gillespie, 1977; this generates a series of events (i.e. growths, births, deaths) and inter-event times. After any given event, the rate ($r_{\text{event}}$) of every possible event that could occur next is computed. The time to the next event is drawn from an exponential distribution with rate $R = \sum r_{\text{event}}$; the probability of a particular event occurring is $r_{\text{event}}/R$.

Interaction

Interaction between individuals plays a key role, operating on all population dynamic processes in the model.

Individuals interact with their neighbours by means of a predefined “kernel” which takes a value dependent upon their separation and size difference. Assuming that interactions act additively, and that the effects of size difference and separation are independent, we define a measure of the competition felt by tree $i$

$$\Phi_i(t) = \sum_{j \in \omega_i} f(s_i(t), s_j(t))g(\vec{x}_i, \vec{x}_j)$$

(1)

where $\omega_i$ is the set of all individuals excluding $i$. $s_i$ is the size of tree $i$ and $\vec{x}_i$ its position.

We here consider a generic form for the interaction kernel; a flexible framework implemented by Raghib-Moreno (2006); Schneider et al. (2006). Competitive inhibition is a Gaussian function of distance to neighbours. This is then multiplied by the size of the competitor, and a tanh function, which represents size asymmetry in the effects of competition.
That is

\[ f(s_i(t), s_j(t)) = s_j(t) \left( \tanh \left( k_s \ln \left( \frac{s_i(t)}{s_j(t)} \right) \right) + 1 \right) \]  

\[ g(\vec{x}_i, \vec{x}_j) = \exp(-k_d|\vec{x}_i - \vec{x}_j|^2) \]

where \( k_d, k_s \in [0, \infty) \). The tanh function allows anything from symmetric \((k_s = 0)\) to completely asymmetric competition \((k_s \rightarrow \infty)\) \cite{Schneider2006}. Multiplying interaction by the size of the neighbour considered reflects the increased competition from larger individuals, independent of the size difference (consider two tiny individuals with given separation/size-difference, compared to two large ones with the same separation/difference).

**Growth**

We consider trees with a single size measure, “dbh” (diameter at breast height (1.3m)), a widely used metric in forestry, due to its ease of measurement in the field. Dbh has been shown to map linearly to exposed crown foliage diameter (which governs light acquisition and seed production) with minimal parameter variation across many species (Purves, unpublished data, and see Larocque, 2002).

We use the Gompertz model for individual growth \cite{Schneider2006}, reduced by neighbourhood interactions \cite{Wensel1987}. This leads to an asymptotic maximum size, and was found to be the best fitting, biologically accurate, descriptor of growth in statistical analysis of tree growth increment data (results not shown).

Trees grow by fixed increments \( ds = 0.001m \) at a rate

\[ G_i(t) = \frac{1}{ds} s_i(t) \left( \alpha - \beta \ln(s_i(t)) - \gamma \Phi_i(t) \right) \]  

In the absence of competition \((\Phi_i = 0)\), the asymptotic size of an individual is thus \( s^* = \exp(\alpha/\beta) \). Under intense competition, the right hand side of Equation 3 may be negative. In this case, we fix \( G_i(t) = 0 \) (similarly to e.g. \cite{Weiner2001}). Variation in \( ds \) has minimal effect on dynamics provided it is sufficiently small that growth events happen frequently compared to mortality and birth.

**Mortality**

Mortality of an established individual occurs at a rate

\[ M_i(t) = \mu_1 + \mu_2 \Phi_i(t) \]  

\( \mu_1 \) is a fixed baseline \cite{Wunder2006}, and \( \mu_2 \) causes individuals under intense competition to have an elevated mortality rate \cite{Taylor2007}. 
Reproduction

Existing individuals produce offspring of size $s = 0.01m$ at a rate determined by their seed production. This is proportional to crown foliage area, and hence also to basal area. The individual rate of reproduction is thus $f_i(t) = f\pi s_i(t)^2/4$.

Offspring are placed at a randomly selected location within 10m of the parent tree with probability of establishment/survival $P_e = (1 - (\mu_1 + \mu_2\Phi_{\text{offspring}}(t)))^y$. This approximation assumes $y$ years taken to reach initial size (0.01m dbh) and avoids introduction of time-lagged calculations, which would impair computational and mathematical tractability.

The fecundity of trees and accurate quantification of seed establishment success is a long standing problem in forest ecology, due the combination of seed production, dispersal, neighbourhood and environmental effects involved (Clark et al., 2004; Gratzer et al., 2004). Submodels for regeneration are often used, but due to data collection issues, precise definition of their structure and parameterisation is more difficult (e.g. Pacala et al., 1996). The approximation described above effectively removes this stage of the life cycle from the model, allowing a focus on structure in mature individuals only.

Our presented simulations use an establishment time ($y$) of 20 years, which is supported by field studies of Scots Pine regeneration (Sarah Turner, unpublished data).

2.2 Statistics

Community structure is tracked via various metrics: density (number of individuals per m$^2$), total basal area ($\sum \pi s_i^2/4$), size and age density distributions, and pair correlation and mark correlation functions (relative density and size multiple of pairs at given separation, Penttinen et al., 1992; Law et al., 2009). All presented model results; means and standard deviations (in Figures, lines within grey envelopes) are computed from 10 repeat simulation runs.

The simulation arena represents a 1ha plot (100 $\times$ 100m). Periodic boundary conditions are used. Results are not significantly altered by increasing arena size, but a smaller arena reduces the number of individuals to a level at which some statistics cannot be computed accurately.

2.3 Parameterisation

We use data from two broad stand types (collected in Scotland by Forest Research, UK Forestry Commission): plantation and “semi-natural” (see Edwards and Mason, 2006; Mason et al., 2007).

Plantation datasets ($6 \times 1.0ha$ stands) from Glenmore (Highland, Scotland) incorporate location and size, allowing comparison of basic statistics at a single point in time (stand age $\approx$ 80 years).

Semi-natural data is available from several sources. Spatial point pattern and increment core data (measurements of annual diameter growth over the lifespan of each tree, at
1.0m height) for four 0.8ha stands in the Black Wood of Rannoch (Perth and Kinross, Scotland) allows estimation of growth (and growth interaction) parameters. Location and size measurements (at one point in time) from a 1.0ha semi-natural stand in Glen Affric (Highland, Scotland) provide another basis for later comparison.

In none of the stands is there adequate information to reliably estimate mortality ($\mu_1$, $\mu_2$) or fecundity ($f$). These are thus tuned to satisfactorily meet plantation and steady state (semi-natural stand) density. The baseline mortality rate used gives an expected lifespan of 250 years (Featherstone 1998; Forestry Commission 2009).

A nonlinear mixed effects (NLME) approach (Lindstrom and Bates 1990) was used to estimate growth parameters $\alpha$, $\beta$ and $\gamma$. Best-fitting growth curves were computed for each of a subset of individuals from two of the Rannoch plots, and the mean, standard deviation and correlation between each parameter within the population was estimated. Details are given in Appendix 1, Electronic Supplementary Materials (ESM). Mean values for $\alpha$ and $\beta$ are used for simulation, though large variation between individuals was observed. $\gamma$ was difficult to estimate from the semi-natural data, its standard deviation being larger than its mean. However, it has a large effect on the simulated “plantation” size distribution, whilst semi-natural stand characteristics are relatively insensitive to its precise value (Appendix 2, ESM). Therefore a value slightly lower than the estimated mean was used in order to better match the size distribution in both plantation and semi-natural stages.

$k_d$ was selected to provide an interaction neighbourhood similar to previous authors (e.g. Canham et al. 2004). $k_s$ determines early (plantation) size distribution, and was selected accordingly (it has minimal effect on long-run behaviour).

All parameter values used for simulation are shown in Table 1. Sensitivity to parameter variation over broad intervals was also tested, a brief summary of which is provided in Appendix 2, ESM.

A standard planting regime implemented in Scots Pine plantations is a 2m square lattice, typically on previously planted ground. Old stumps and furrows prevent a perfectly regular structure being created, so our initial condition has 0.01m dbh trees with small random deviations from exact lattice sites.

3 Results

3.1 Model Behaviour and comparison with data

Starting from the plantation configuration, the model community displays three distinct stages:

- initial growth dominated period, during which the plantation structure largely remains

- a period of high mortality and basal area reduction as the impact of interactions begin to be felt, together with an increase in regeneration as the canopy opens
Table 1: Model parameters, description and values.

| Parameter            | Description                          | Value    |
|----------------------|--------------------------------------|----------|
| **population rates** |                                      |          |
| \( f \)             | reproductive rate per m² basal area  | 0.2      |
| \( \mu_1 \)         | baseline mortality                   | 0.004    |
| \( \mu_2 \)         | mortality interaction                | 0.00002  |
| \( \alpha \)        | gompertz a                           | 0.1308   |
| \( \beta \)         | gompertz b                           | 0.03158  |
| \( \gamma \)        | growth interaction                   | 0.00005  |
| **interaction kernels** |                                    |          |
| \( k_d \)           | distance decay                       | 0.1      |
| \( k_s \)           | size asymmetry                       | 1.2      |

- the long-run meta-stable state, during which stand structure is more irregular and determined by the levels of mortality and birth

Oliver and Larson’s (1996) qualitative description of the development of natural forest stands from bare ground is now well established (Peterken, 1996; Wulder and Franklin, 2006). It provides the following characterisation of the overall behaviour of the community: stand initiation → stem exclusion → understory reinitiation → old growth. This is similar to our plantation initiated model, except we find that stem-exclusion and regeneration occur simultaneously.

The characteristics of each stage will now be discussed in more detail. A summary of the effects of parametric variation upon key properties is given in Appendix 2, ESM.

**Plantation stage (“stand initiation”)**

The plantation structure initiated by forest management has a higher density than a natural self-regenerating forest. We define this transient stage of development as the period from time zero to the point at which basal area initially peaks. Reproduction is low, due to individuals’ small size. Density is thus dominated by mortality, and falls rapidly. Competition is also relatively low, meaning that individuals can express the majority of their potential growth. Basal area increases rapidly as a consequence (see Figure 2).

Our simulated density and size distribution of the model are fairly close to those of plantation stands at Glenmore (simulated at 80 years vs. dataset: 0.09063 vs 0.08523 individuals per m²). However, basal area is notably underestimated (29.22 vs 36.67 m²·ha⁻¹). The reason for this is apparent in Figure 2b; the growth parameters estimated from seminatural data alone give too slow growth in the simulated population (the modal size at 80 years is lower). There are also more very small individuals in the simulation at this stage. This may indicate problems with the recruitment process in the model, or be related to poor deer control at the Glenmore plantations.
Figure 1: Pictorial representation of 1ha Scots Pine forest. Field data (Highland, Scotland, data from Forest Research, left column): 78 year old plantation in Glenmore, semi-natural stand in Glen Affric. Simulated data (centre and right columns) at 50, 150, 300 and 1000 years from planting. The diameter of each circle is proportional to the size (dbh) of the tree.
Figure 2: The transition from plantation to steady state: development of key metrics through time, based on parameters in Table 1. Mean simulation results are represented by lines within a grey envelope (standard deviation). (a) Evolution of density (dashed) and stand basal area (solid line), averaged over 10 simulations of a 1ha plot. (b) Size distribution at 80 (dash-dot) and 800 (solid) years. Points with error bars show the mean and standard deviation of 6 Glenmore plantation stands (78 years old). Steady-state comparison with natural stands is shown in Figure 3. (c) Pair correlation function – time/colour as (b). (d) Mark correlation function – time/line style as (b).
Stochastic variation in growth, and asymmetric competition, lead to an increase in the spread of sizes of individuals (the initial size distribution is a delta peak at $s = 0.01m$). Size asymmetry is often cited as a key driving force in plant community dynamics (Adams et al., 2007; Perry et al., 2003; Weiner et al., 2001). In our model, competitive size asymmetry is the primary factor affecting the variance (spread) of the size distribution during the plantation stage: it is almost independent of any other parameter, or even starting spatial configuration (see Table 3, Appendix 2, ESM).

Low reproduction means that spatial structure is governed by the starting configuration. The pair correlation function (PCF), giving the relative density of pairs of individuals with given separation (Penttinen et al., 1992), clearly shows the signature of the lattice during this stage (Figure 2c, 80 years – peaks are at multiples of the lattice spacing). In field data, however, the lattice pattern is less clearly defined: this is a data collection issue, individuals’ locations were measured to an accuracy of one metre. However, the PCF displays the same short range inhibition as the data.

The mark correlation function (MCF) measures the relative size of individuals forming pairs at a given separation, compared to the global average (Penttinen et al., 1992). Figure 2d suggests that the average size of pairs at short ranges (less than 2m separation) in the simulation is inhibited. However, this feature is an artefact of regeneration seen in the simulation (that is, the peak of small individuals discussed above) that is not present in the data. Recomputing the mark correlation function ignoring these individuals recovers the structure seen in the data (not shown) – interaction has less differential effect on growth of older individuals.

**Thinning stage (“stem exclusion/understory reinitiation”)**

The high basal area (and high competition) state generated during the plantation stage means that individual growth becomes stunted, and mortality rates are elevated. Basal area thus reaches a peak. Removal (“stem exclusion”) of suppressed (competitively inhibited) individuals occurs, opening gaps in the canopy. This allows more substantial regeneration to occur (gaps heighten $P_e$ for many of the potential offspring, high basal area ensures a large seed source – “understory reinitiation”). The initial regular structure is erased during this period, through mortality, regeneration and differential growth. This change is apparent in both spatial correlation functions (not shown), and in maps of the stand at 300 years (Figure 1).

This transitional period (from peak basal area to meta-stable state) is around 4-5 times the length of the plantation stage. This is notable; if “old-growth” refers to the long-run meta-stable state, the model suggests that this is slower to attain than is commonly assumed. Indeed, Oliver and Larson (1996) point out that due to external catastrophic disturbances, true old growth is rarely reached, taking up to 1000 years to attain.
Long-run metastable state ("old-growth")

In the long run, the model reaches a steady state where fecundity, mortality and growth are in balance. Figure 2b (solid line) shows the typical size structure present in the long run. Only a small proportion of juveniles attain canopy size, but the asymptotic nature of growth means that individuals accumulate in the higher size classes.

The size distribution is stable. For a dense forest, this is evident intuitively – when a gap in the canopy opens, the smaller younger trees are waiting to grow into it. Here, reductions in canopy density reduce local interactions, and temporarily allow trees that have stopped growing to increase in size, quickly refilling gaps.

Spatial structure displays a more irregular pattern than earlier stages. The effect of individual interactions upon growth are evident in the reduced size of adjacent pairs (Figure 2d), whilst local dispersal of seedlings leads to a heightened PCF at short ranges (Figure 2c). Some authors (e.g. Barbeito et al., 2008) have noted that regeneration sometimes occurs in explicitly clustered patterns. This may be due to external environmental factors, but lead to a similar observed PCF.

Comparison with "semi-natural" data

We would like to identify whether the long run steady state behaviour of the model mimics that of a real forest. The basic numbers appear roughly correct (simulated vs data: density - 0.0327 vs 0.0165-0.025 individuals per m$^2$; basal area - 23.9 vs 18.6-25.2m$^2$ha$^{-1}$). However, all available data is from "semi-natural", as opposed to "equilibrium" stands. Whilst relatively untouched over the last 90 years, these stands have been managed in the past, their current state reflecting these historic interventions.

The most recent management of these stands was the removal of the strongest trees to assist with the war effort (ending in 1918). For the Rannoch stands, their state at this time may (in part) be deduced using the individual growth/age data from the annual increment cores discussed in Section 2.3. Working back from the current (actual) diameter, the size of each tree at 1918 can be estimated, and consequently the total basal area (in 1918) of the trees still present today (plot 4: 9.2m$^2$, plot 6: 2.5m$^2$). There is known to have been low mortality in these stands over this period (the study plots were established in 1948).

To simulate this, the model equilibrium state is thinned to 10m$^2$ basal area, by removing trees from the largest 60%. The model is then run for a further 80 years before comparison (Figure 3).

The data stands display high variability, reflecting the effect of site-specific processes and previous management on each site. Similar signatures are seen, however: the PCF (Figure 3a) shows clustering of individuals in all stands, whilst the MCF (Figure 3b) displays inhibition of growth/size at short ranges. The PCF of the simulation displays the same form as the data. However, the MCF generated by the model appears too homogeneous. Glen Affric displays the strongest size inhibition at short range (lowest MCF), but also has the largest relative density of small trees (and larger than that of the model).

Interestingly, the MCF for Glen Affric omitting juveniles (< 0.1m dbh) does not display
any significant inhibition at short ranges (not shown). The implication is that interaction affects diameter growth of juveniles more than that of mature trees (not incorporated into the model).

Size distribution of the data is generally characterised by a wide spread and a “canopy” peak at a moderate size (Figure 3c). This is similar to the simulation output, but there are two important issues. Firstly, the estimated growth parameters (Appendix 1, ESM) limit the asymptotic size at \( \exp(\alpha/\beta) = 62.9\text{cm} \), meaning that the few very large trees observed in data cannot be created by the model. Secondly, the variation in size in the data is not directly related to variation in age, as it is in the model (Figure 3d). Both issues are tackled below.

Size vs age - random asymptotic size

There are two possible causes of the discrepancy between the model and size and size/age distributions. Firstly, the difference may be induced by the model, in its characterisation of competition and growth. Secondly, it may be due to intrinsic or environmental variation between the growth of the trees in real stands.

To address these issues we first explored increasing the strength of competition, by increasing \( \gamma \). This increases variability in modelled growth histories, but at early times leads to unrealistic size distributions compared with plantation data (results not shown, but see Appendix 2, ESM, for generalisations of behaviour). An alternative hypothesis was that observed growth variation could be accounted for by competition “accumulating” throughout an individual’s life, causing a permanent adjustment to its asymptotic size. Unfortunately, this does not provide a greatly improved explanation of the data either (in NLME analysis, despite an improvement in fit, parameter standard deviations are not reduced – see Appendix 1, ESM). Furthermore, model behaviour is not altered significantly without increasing \( \gamma \) from the estimated value, as above (which is again inconsistent with plantation data).

NLME analyses of simulated data (where simulated individuals have identical parameter values) recovers the growth parameters used accurately and with low standard deviation, across a range of scenarios (not shown). This contrasts with analysis of observed data (Appendix 1, ESM), suggesting the existence of genuine variation between individuals in the data stands, or small scale environmental variation.

Therefore, rather than use the mean values of growth parameters obtained from the NLME analysis as Section 2.3, we also performed simulations selecting \( \alpha, \beta \) from the bivariate Normal distribution estimated by that analysis (with estimated correlation \( \rho = 0.988 \)). This obtains accurate steady state behaviour, but there is excessive size variance at age 80 years. The variability inferred from the semi-natural data is inconsistent with the plantation data, where initial growth rate is relatively uniform across individuals.

In Equation 3, \( \alpha \) controls the initial growth rate, while \( \alpha/\beta \) determines asymptotic size. Thus, a second approach was devised: fixing \( \alpha \) at the mean from the NLME analysis, whilst drawing \( \exp(\alpha/\beta) \) (asymptotic size) from the observed sizes of individuals greater than 100 years old in the data stands. This obtains a much better overall match with
Figure 3: Comparing statistics from “semi-natural” datasets with simulation output. The data stands were heavily managed prior to 1918; we approximate this by running a model stand to equilibrium, thinning to $10\text{m}^2$ basal area (removing trees randomly from the largest 60%), and running for a further 80 years (see Section 3.1). Solid line and grey envelopes in (a),(b) and (c) are simulated results. Data: Rannoch plot 4 (dashed), Rannoch 7 (fine dash), Glen Affric (dotted). Spatial correlation functions display a similar signature for all stands - clustering of individuals (a), and inhibition of growth/size at short ranges (though this is not seen to a great extent in simulation, see main text) (b). Size distribution (c) varies between the stands, reflecting the management history. (d) shows the variability in size attained at a given age present in the data (individual trees represented by □ – data only available for Rannoch stands), compared with the simulation 80 years after the intervention (×).
available data than other methods (including the joint age-size distribution, see Figure 4) and avoids unrealistic maximum tree size as seen previously. It can also be sampled directly from a target stand.

3.1.1 Summary

We have constructed a simple model that, when parameterised from observed data, matches fairly well the qualitative and quantitative behaviour of real forests on a stand level, despite large uncertainties in management and environmental history for the available data stands. This model will now be used to demonstrate the effectiveness of simple thinning strategies in accelerating the transition to old growth. Simulations in Section 3.2 use the homogeneous growth model for clarity; analogous results using the model incorporating individual variation are presented in Appendix 3, ESM.

3.2 Acceleration of transition to old-growth state

Stands possessing appealing characteristics are not necessarily naturally formed (see e.g. Edwards and Mason, 2004). Is the “sustainable irregular condition” (Schütz, 2001) the same as the old-growth state described here? The expected qualities are (Malcolm et al., 2001; Mason et al., 2007):

- Full representation across the size classes with high variance in canopy size
- Non-regular spatial distribution
- High recruitment

These conditions are met by the long term state of the model. What are the main factors in achieving such a state? Natural regeneration is key, and can be encouraged by thinning the existing canopy. Basal area can be reduced (Hale, 2001; Edwards and Rhodes, 2006), though creation of open space (i.e. gaps) is also likely to be useful for light demanding species such as Scots Pine.

We investigate thinning treatments applied to a mature plantation intended to bypass or escape the period of unnaturally high basal area, remove the lattice spatial pattern, and create suitable conditions for the generation of a high-variance size structure.

Thinnings are often made on individuals’ size relative to neighbours and other members of the stand (e.g. Edwards and Mason, 2004). For simplicity these “size-selection” thinnings alone are presented here; future work will compare these with spatially correlated (e.g. patch) and interaction-selection (removing neighbours of selected trees) thinnings. The presented results are however robust to variation in size range and the use of spatial criteria instead of size.

A single thinning has minimal effect on the subsequent stand dynamics. However, multiple thinnings can alter the dynamics significantly. A target basal area for the stand
Figure 4: Results obtained from populations with fixed $\alpha$, sampling $\exp(\alpha/\beta)$ from observed sizes of individuals greater than 100 years old at 1990 in Rannoch plots. Corresponding Figures for the non-random model are given in italics. Again, simulation means are represented by lines within a standard deviation envelope. (a) density (dashed) and basal area (solid) (Figure 2a). Comparison with real stand data: (b) size versus age 80 years after the intervention described in Section 3.1, compared with the Rannoch plot (Figure 3d). (c) size distribution at 80 years (line) versus Glenmore plantation average and standard deviation (error bars) (Figure 2b). (d) size distribution at 880 years (solid line) versus Rannoch 4 (dashed line), Rannoch 7 (fine dash), and Glen Affric data (dotted) (Figure 3c).
determines the extent of thinning, although this may not be attained with a single treatment. Thinnings to a target basal area of 18m$^2$, repeated 5 times with an interval of 2, 5 or 10 years are presented in Figure 5.

The basal area reduction due to thinning is temporary. Thinning releases some of the remaining large individuals from interaction stress, which suddenly grow quickly. Widely separated interventions have a more significant effect on the evolution of basal area than those made in rapid succession (Figure 5a). However, the initial boom in basal area above that of the steady state seems unavoidable.

Basal area does not tell a complete story, however. Stand density after the treatments shown approaches and stays close to the steady state density (Figure 5b).

Figure 5c compares the average size distribution at 200 for each stand in 5a with the long run average steady state size distribution. Management causes a clear reduction in canopy density, and increases the average size of the canopy trees. As the time between treatments increases, the overall canopy density falls, and the number of trees at the very largest sizes slightly increases, bringing the stand closer to an old growth state.

Spatial structure is also improved; Figure 5d compares the PCF at 200 years obtained by the thinning regimes described with that of an unmanaged forest at 200 years (dotted), and its steady state (thick solid). Despite the non-spatial thinning, the PCF is closer to the steady state after this short time. Spatially structured thinning may further assist in generating specific patterns.

These results hold when fixing management interval and varying instead the number of interventions, and also in thinning regimes approaching the target basal area gradually – it is the overall length of management that is important.

4 Discussion

We have presented a model for the assembly of a single species forest community incorporating both size and spatial structure. Although simple, our model can be parameterised to give a good qualitative agreement with data for both plantation and semi-natural Scots Pine forests that are geographically widely separated.

The model depends on parameters describing maximum size, growth, competition and death. While the growth and death parameters could be taken as constant for all trees, it proved necessary for the maximum size parameter to be drawn from a distribution. This may represent either genetic diversity or a variation in the ability of a given location to support a tree.

The structure of simulated forests is strongly dependent on the initial conditions, even after hundreds of years. The long-time equilibrium state of the model has rather low density, with a highly varied size (diameter) distribution. It appears to be stable, with no evidence of cyclical variation in structural characteristics.

We applied the model to determine whether thinning treatment can be effective in bringing a forest from a plantation to this steady state more effectively than natural (unmanaged) regeneration.
Figure 5: Thinning randomly from 60-100% of the size distribution, but altering the interval between treatments (again, 5 treatments starting at 80 years, with a target basal area of $= 18\text{m}^2\text{ha}^{-1}$). Intervals: 2 years (solid), 5 years (dash), 10 years (fine dash). Again, the effect on dynamics is demonstrated by (a) basal area (b) density (c) size distribution at 200 years (d) pcf at 200 years. Dotted lines show the dynamics of an unmanaged forest, whilst the thick solid lines in (c) and (d) show the long-run steady state.
Our work suggests that management can have a clear effect on the dynamics of a forest starting from a plantation state. Figure 5 shows that the effects of management are not insignificant; first-order properties, and size/spatial structure can be manipulated somewhat favourably. More complex planting and thinning regimes than those considered here can also be implemented, though initial tests suggest high levels of specificity are required to have the desired effect on community structure. Overall, there would appear to be no direct “short-cut” to the old-growth state.

There are fundamental reasons for this. Firstly, the stand must be old enough to have very large and mature trees, which are a central component of the desired habitat. This rules out attainment of the steady state size distribution after only one or two centuries.

Secondly, a young plantation is in a very low recruitment state. This means that the community consists of individuals from a single age cohort, which are either in the canopy or are very suppressed. Even mediated by a planting scheme, this initial size and age structure will persist in the community for some time.

Spatial structure on the other hand can be manipulated over short timescales. A particular pattern of trees may be obtained quickly and easily by selective thinnings. This also alters development of size structure, by releasing selected individuals from competition, and providing large gaps in which regeneration may readily occur. Creating an old growth type state is also difficult with selective planting: the trouble here is that one cannot predict which trees will flourish into maturity.

While our emphasis has been on obtaining the steady state, the model can also be used to investigate the management strategies needed to achieve other aims such as maximum production of wood, of mature trees, or even removal of CO$_2$ from the atmosphere.

To summarise, we find a relatively simple model can capture the main features observed in the dynamics of a single-species Scots Pine woodland at various developmental stages. We applied the model to investigate the attainment of an equilibrium “old-growth” state. Whilst there appears to be no management strategy which will bring a plantation rapidly to the natural state, structure can be manipulated favourably over shorter timescales.

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A Growth parameter estimates

Growth parameters were estimated from increment core data (radial sections providing measurements of annual diameter growth over the lifespan of each tree, taken at 1.0m height) from several semi-natural Scots Pine stands in the Black Wood of Rannoch. Parameters were estimated from individual data taken from plots “4” and “6” (5 and 7 have less well known management history). To ensure estimation based upon known competitive neighbourhoods, those individuals less than than 10m from the plot boundary were excluded. Furthermore, only increments applying to growth after 1918 were used, this being the date after which management (and consequently the state of the community) is known with sufficient accuracy.

NLS is a non-linear least squares fitting tool in R ([R Development Core Team](https://www.r-project.org) 2005), here applied to the complete set of increment measurements. The fit computed is equivalent to assuming a single growth curve generated all data points, which are regarded as independent. NLME is another tool in R, computing a non-linear mixed effects model ([Pinheiro et al.](https://www.r-project.org) 2009). This approach goes a step further, in computing a nls fit for each individual in the population separately (that is, hypothesised individual growth curves). This explicitly estimates the variability present in the population by computing the mean (the “fixed effect”) and standard deviation (the “random effect”) of each parameter, and the correlation between them.

The precise definitions of the three models being fitted are:

\[
growth = \text{size} \times (\alpha - \beta \log(\text{size})) \\
\text{“no competition”} \quad (5)
\]

\[
growth = \text{size} \times (\alpha - \beta \log(\text{size}) - \gamma \Phi) \\
\text{“competition”} \quad (6)
\]

\[
growth = \text{size} \times \left( \alpha - \beta \log(\text{size}) - \gamma \sum_{t_0 < t' < t} \Phi(t') \right) \\
\text{“cumulative competition”} \quad (7)
\]

Residual Standard Error (RSE) summarises the difference between observed and estimated values in the model \((RSE = \sqrt{V/n} \text{ where } V \text{ is the variance of the residuals and } n \text{ is the number of observations})\). Aikake’s An Information Criterion (AIC, [Aikake](https://www.r-project.org) 1974) is a likelihood-based measure with a penalisation related to the number of model parameters \(k\): \(AIC = -2\log(L) - 2k\). A lower value indicates a more parsimonious model.

Given the structure of the data (subsets of the complete data describe the growth curves of individual trees), the NLME approach is conceptually more appropriate, a point confirmed by the uniformly lower RSE and AIC for the NLME models. That different numbers of measurements are available for different trees (depending on their age) makes this all the more important. It transpires that there is rather large variation in growth rates, that cannot be described by a fixed set of parameters across the population. In the NLME analysis, the computed standard deviation for each parameter is on the same order as the mean, and in the case of \(\gamma\), is actually larger. \(\alpha\) and \(\beta\) were found to be strongly correlated (in the “competition” model, \(\rho_{\alpha,\beta} = 0.988, \rho_{\alpha,\gamma} = 0.557, \rho_{\beta,\gamma} = 0.481\)).

Despite the improved fit offered by the cumulative competition model, the basic competition model was selected for analysis and simulation due to its lack of dependence upon
history (maintaining the Markov property of the process). It is also important to realise that spatio-temporal data of the type provided by these increment cores are much more laborious to collect, and as a consequence far less widely available, than the marked point process (single point in time) data that are usually used in spatial analyses.

Table 2: Estimated parameters for non-linear growth models fitted to data from Rannoch plots 4 and 6 combined (plot 5 and 7 omitted due to missing recent management history; growth curves computed based upon increments after 1918 for individuals further than 10m from an edge). Function fitted: Gompertz with and without competition term (interaction formulated as in model description with parameters shown).

|                   | nls          |   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
|-------------------|--------------|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|                   | LS Estimate | RSE | AIC  | Fixed (µ) | Random (σ) | RSE | AIC  |
| **no competition**|              |     |      |            |           |     |      |
| α                 | 0.0426       | 0.311 | 3256.9 | 0.132     | 0.0931 | 0.117 | -8141.2 |
| β                 | 0.00909      |     |       |           | 0.0359 | 0.0281 |
| **competition**   |              |     |      |            |           |     |      |
| α                 | 0.0828       | 0.269 | 1369.8 | 1.308     | 0.103  | 0.116 | -8194.0 |
| β                 | 0.0177       |     |       |           | 0.0318 | 0.0286 |
| γ                 | 4.46e-05     |     |       |           | 6.51e-05 |       | 6.97e-05 |
| **cumulative competition** |              |     |      |            |           |     |      |
| α                 | 0.0684       | 0.275 | 1646.8 | 0.146     | 0.0967 | 0.115 | -8251.4 |
| β                 | 0.0146       |     |       |           | 0.0410 | 0.0310 |
| γ                 | 4.56e-07     |     |       |           | -7.17e-07 |       | 1.07e-06 |
B  Effects of parameter variation

This appendix provides a brief summary of the effects of parameter variation upon various aspects of model behaviour. Model behaviour is robust: the effects described hold for at least an order of magnitude above and below the parameters used in the main text (Table 1 in main text), unless otherwise stated. The thinning stage is not included here; it is a transient state with properties dependent upon the relative properties of the plantation and steady-state under the chosen parameterisation.

B.1  Plantation stage

Largely speaking, changes to individual parameters have predictable effects upon the properties of the community’s early development. However, there are some counter-intuitive effects. For example, increasing the effect of interaction upon mortality ($\mu_2$) increases the mean size at 80 years, through density reduction and a corresponding decrease in suppression of growth rate.

Increasing “mortality” in Table B refers to increasing both $\mu_1$ and $\mu_2$ whilst fixing their ratio, ensuring that baseline and interaction induced mortality always have the same relative strength.

The variance of the size distribution at 80 years appears almost unaffected by any parameter, except the degree of size asymmetry in the interaction kernel ($k_s$). Interestingly, the only statistics considered here (including long-run behaviour) that are affected by $k_s$ relate to the shape of the plantation/early stage size distribution.
Table 3: A summary of the qualitative effect on plantation development (as summarised by various statistics) of increasing any parameter of the model in isolation. In columns, \( \rho \) is density and \( s \) is size, with subscripts refering to time, \( \mathbb{E} \) and \( \mathbb{V} \) to expected value and variance. \( BA_{\text{peak}} \) is the maximum basal area attained by the population, \( t_{BA_{\text{peak}}} \) the time at which it occurs Increasing “mortality” refers to increasing \( \mu_1 \) and \( \mu_2 \) whilst fixing their ratio, and increasing “growth” means increasing both \( \alpha \) and \( \beta \), whilst fixing their ratio.

| Parameter        | Statistic (plantation) | \( \rho_{80} \) | \( BA_{80} \) | \( \mathbb{E}(s_{80}) \) | \( \mathbb{V}(s_{80}) \) | \( BA_{\text{peak}} \) | \( t_{BA_{\text{peak}}} \) |
|------------------|------------------------|-----------------|--------------|-----------------|-----------------|-----------------|------------------|
| rates            |                        |                 |              |                 |                 |                 |                  |
| \( f \) mortality |                        | +               | +            | 0               | 0               | –               | –                |
| \( f \) growth   |                        | –               | –            | +               | 0               | +               | –                |
| interaction      |                        |                 |              |                 |                 |                 |                  |
| \( \mu_2 \)      |                        | –               | –            | +               | 0               | –               | –                |
| \( \gamma \)     |                        | –               | –            | –               | 0               | –               | –                |
| kernels          |                        |                 |              |                 |                 |                 |                  |
| \( k_d \)        |                        | +               | +            | +               | 0               | +               | 0                |
| \( k_s \)        |                        | 0               | 0            | –               | +               | 0               | 0                |

**B.2 Old-growth stage**

Turning to longer-run behaviour, within the parameter space presented, steady state density and basal area are increased by increasing fecundity or growth speed, or decreasing mortality (all other parameters remaining equal, results shown in Table 4). Interestingly, decreasing mortality further to unrealistically low levels leads to a decrease in steady state basal area. This somewhat surprising result occurs due to individual growth being highly limited by density, rather than by lifespan (results not shown).

Fixing population dynamic rates whilst altering the interaction multipliers and kernels also has an effect on behaviour. Increasing \( \mu_2 \) leads to a lower density, but greater sized, canopy. It also reduces the size of close pairs (lower MCF). Increasing the effect of interaction on growth (\( \gamma \)) reduces the density and size of the canopy, whilst also causing a reduction in the size (but not density) of close pairs (lower MCF).

The effects of \( k_d \) are similar to the plantation case. \( k_s \) has no noticeable effect on any aspect of long-run behaviour.
Table 4: The effect on steady state behaviour (as summarised by various statistics) of increasing any parameter of the model in isolation. Again, $\rho$ is density. $s_{\text{canopy}}$ is the mean size of canopy trees. $\rho_{\text{closepairs}}$ is the value of the PCF at short ranges, whilst $s_{\text{closepairs}}$ is the value of the MCF at short ranges. Increasing “mortality” refers to increasing $\mu_1$ and $\mu_2$ whilst fixing their ratio, and increasing “growth” means increasing both $\alpha$ and $\beta$, whilst fixing their ratio. Canopy density is relative to total density (proportion of individuals $>50\%$ of maximum size).

| Parameter | Statistic (steady state) | $\rho$ | BA | $\rho_{\text{canopy}}$ | $s_{\text{canopy}}$ | $\rho_{\text{closepairs}}$ | $s_{\text{closepairs}}$ |
|-----------|--------------------------|--------|----|-----------------------|---------------------|--------------------------|----------------------|
| rates     | $f$                      | +      | +  | +                     | −                   | +                       | +                    |
| mortality | −                       | −      | −  | +                     | 0                   | −                       | −                    |
| growth    | +                       | +      | +  | 0                     | 0                   | +                       | +                    |
| interaction | $\mu_2$     | −      | −  | −                     | +                   | 0                       | −                    |
|           | $\gamma$               | 0      | −  | −                     | −                   | 0                       | −                    |
| kernels   | $k_d$                  | +      | +  | +                     | 0                   | −                       | 0                    |
|           | $k_s$                  | 0      | 0  | 0                     | 0                   | 0                       | 0                    |

C Management under variable growth

This Section simply presents the same results relating to management as those in Section 4 of the main text (“Acceleration of transition to old-growth state”). The statistics computed using the model in which individual variation (“Model 2”) is allowed show a similar but slightly less clear pattern.

Temporal evolution of basal area and density show precisely the same pattern as those under the homogeneous growth model (“Model 1”) – the longer the duration of management, the closer they remain to the steady state after thinning.

Under Model 1, the size distribution demonstrated a shift in canopy peak as the total duration of management increased, with a larger size and lower density (Figure 5c in main text). Under Model 2, the size distribution shows no increase in the size of trees in the canopy, only a reduction in density towards that of the steady-state distribution (Figure 6c here). This is due to the much lower mean asymptotic size under Model 2.

With regards the pair correlation function (PCF), the shift towards the steady state appears to be present but is also slightly less clear – the shift towards a clustered pattern being slower to occur under Model 2 (Figure 6d here).
Figure 6: Thinning randomly from 60-100% of the size distribution, but altering the interval between treatments (again, 5 treatments stating at 75 years, with a target basal area of $= 18 \text{m}^2\text{ha}^{-1}$). Intervals: 2 years (solid), 5 years (dash), 10 years (fine dash). Again, the effect on dynamics is demonstrated by (a) basal area (b) density (c) size distribution at 200 years (d) pcf at 200 years. The dotted lines show the dynamics of an unmanaged forest, whilst the thick solid lines in (c) and (d) show the long-run steady state.
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