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Published in:
Ecological Modelling
Publication date:
2011

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Download date: 17. Jan. 2019
Effects of local interaction and dispersal on the dynamics of size-structured populations

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\textbf{A R T I C L E I N F O}

\textbf{Article history:}
Received 19 October 2010
Received in revised form 2 February 2011
Accepted 5 February 2011
Available online 1 March 2011

\textbf{Keywords:}
Spatial ecology
Forest dynamics
Plant population
Size structured
Spatial structure
Individual based model

\textbf{A B S T R A C T}

Traditional approaches to ecosystem modelling have relied on spatially homogeneous approximations to interaction, growth and death. More recently, spatial interaction and dispersal have also been considered. While these leads to certain changes in fine-scale community dynamics, their effect is sometimes fairly minimal, and demographic scenarios in which this difference is important have not been systematically investigated.

We take a simple mean-field model which simulates birth, growth and death processes, and rewrite it with spatially distributed discrete individuals. Each individual's growth and mortality is determined by a competition measure which captures the effects of neighbours in a way which retains the conceptual simplicity of a generic, analytically-solvable model. Although the model is generic, we here parameterise it using data from Caledonian Scots Pine stands. The dynamics of simulated populations, starting from a plantation lattice configuration, mirror those of well-established qualitative descriptions of natural forest stand behaviour; an analogy which assists in understanding the transition from artificial to old-growth structure.

When parameterised for Scots Pine populations, the signature of spatial processes is evident, but their effect on first-order statistics, such as density and biomass, is fairly limited. The sensitivity of this result to variation in each individual rate parameter is investigated; distinct differences between spatial and mean-field models are seen only upon alteration of the interaction strength parameters, and in low density populations. Under the Scots pine parameterisation, dispersal also has an effect on spatial structure, but not density and biomass. Only in more intense competitive scenarios does altering the relative scales of dispersal and interaction lead to a clear signal in first order behaviour. The study acts as an important reminder that, even in scenarios where individual processes are localised in space, simple models are often sufficient to capture many population scale aspects of observed ecological dynamics.

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1. Introduction

Ecological communities exhibit structure and variation on a range of spatial scales. This variation may be broadly classified into “landscape” and “local” level effects. The processes leading to these effects are diverse, but landscape level variation is often the result of geographical variation in environmental conditions or human influence (Mladenoff and Baker, 1999) while local variation is more frequently ascribed to interactions between the individual members of the population themselves (Busing and Mailly, 2004). At local scales, much work has focused on the outcome of competitive interactions between species (Tilman and Wedin, 1991; Pacala and Deutschman, 1995; Chesson, 2000; Perry et al., 2003) and in the analysis of both size-structured (e.g. Sinko and Streifer, 1967) and, more recently, spatially-structured population models (e.g. Bolker and Pacala, 1997; Law et al., 2003). However, a mechanistic understanding of the fine-scale 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); the work of Murrell (2009) being a notable exception.

In the case of forest populations, a practical understanding of the general patterns and forms observed in population dynamics is well established (Franklin et al., 2002). A great body of simulation models for multi-species communities (e.g. Botkin et al., 1972; Pacala et al., 1996; Busing and Mailly, 2004) has also been developed over the years. However, the potential for useful results derived from the study of monocultures is far from exhausted. While pure forest monocultures may be rare in nature, many communities are dominated by a single species, and their theoretical study presents a clear

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and accessible way to understand and identify driving processes and mechanistic changes over time, and the effect of demographic rates on fundamental properties such as size and spatial structure (Bolker and Pacala, 1997; Law et al., 2003).

An important concept in forest conservation is that of an “old-growth” state. This is an autogenic state which is obtained through an extended period of growth, mortality and regeneration, in the absence of external disturbances, which may take several centuries to attain (Oliver and Larson, 1996). 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, even in small neighbourhoods. The habitat created in this state is often considered a paradigm of what conservation oriented forest management might hope to achieve (Schultz, 2002); as such, we would like to understand more clearly the processes that affect its general properties. Here, we develop and directly apply a generic process-based model, closely related to those of Bolker and Pacala (1997) and Law et al. (2003), to understanding the key elements of fine-scale community behaviour, from a plantation through to old-growth. Data for Scots pine (Pinus sylvestris L.) populations at various stages of development provide a baseline for comparison. However, our investigation also focuses more generically on the importance of small–scale spatial effects in populations.

A variety of questions may be posed. What is the qualitative behaviour of such models, and is this robust to parameter variation? Can such models be configured to adequately explain the behaviour of forest stands at distinct developmental stages? What is the effect of including local spatial interactions in the size-structured model? What is the effect of local dispersal, and how does this relate to interaction? When is the inclusion of spatial effects critical to accurately representing a size-structured population? Do short range interactions lead to long range structure? Certain of these questions are closely related to issues in field-based forestry (a model description of stand yield), but more generally these are questions of theoretical ecology, investigating the roles of space and variability. To answer these questions, we introduce two models: a generic size-structured “mean-field” model, and an analogous spatial individual based model. The models are parameterised using available data from Scots pine populations in Scotland. Section 3.1 considers the generic behaviour seen in both mean-field and spatial models, and relates this to documented qualitative observations of forest stand behaviour. Sections 3.2 and 3.3 consider the specific effects of spatial interactions and dispersal on the basic properties of model populations. While they do cause variation in the size and spatial structure of many model generated populations, the impact on first-order properties using the Scots Pine parameterisation is fairly small. Section 3.4 thus identifies regions of parameter space in which spatial interactions are more important, enabling an assessment of the scenarios in which a mean-field model is likely to be acceptable for the representation of size-structured ecological populations. The approach of gradually extending a simple “null” (mean-field) simulation model, and comparing output with diverse population data, allows clearer identification and understanding of the drivers of ecosystem dynamics and the steady state.

2. Materials and methods

2.1. Mean-field model

Consider a population of individuals, each characterised by a single size measure s. This may be mass, height or any other metric, but in the case of trees is usually taken to be “diameter at breast height”, or dbh. In the mean-field case all individuals have an identical experience, and we are thus interested in the evolution of the density of individuals across the range of possible sizes, n(s,t).

We use the Gompertz model for individual growth, reduced by competitive interactions (Wensel et al., 1987). This function has been applied successfully to both trees and other plants (Zeide, 1993; Schneider et al., 2006). Of Richards (1959) type asymptotic growth models, it was found to be the best fitting descriptor of growth in statistical analysis of individual tree growth increment data, accounting for the effects of interaction (Adams, 2010). The growth rate is

\[ G(s, t) = \frac{ds(t)}{dt} = s(t)(\alpha - \beta \ln(s(t)) - \gamma \Phi(s, t)) \] (1)

where s is the size of an individual, \( \Phi \) is the competition experienced at that size (dependent upon current population state) and \( \alpha, \beta, \gamma \) are species dependent parameters. This leads to an asymptotic maximum size, \( s^* = \exp(\alpha/\beta) \) if competition is absent. Under intense competition, the right hand side of Eq. (1) may be negative. Following Weiner et al. (2001), we fix \( G(s, t) = 0 \) in this case.

Competition is assumed to be asymmetric, and takes a form which depends on the density, size and relative size of the other individuals in the population,

\[ \Phi(s, t) = \int_{s'} n(s', t)f(s, s')ds' \] (2)

\[ f(s, s') = s' \left( \text{tanh} \left( \frac{k'}{\ln(s')^{2}} \right) \right) + 1 \] (3)

The tanh function allows anything from symmetric \( (k' = 0) \) to completely asymmetric competition \( (k' \to 0) \) (Schneider et al., 2006). Multiplying interaction by the size \( s' \) of the neighbour considered reflects the increased competition between 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).

Mortality occurs at a rate

\[ M(s, t) = \mu_1 + \mu_2 \Phi(s, t) \] (4)

\( \mu_1 \) is a fixed baseline (Wunder et al., 2006), and \( \mu_2 \) causes individuals under intense competition to have an elevated mortality rate (Taylor and Maclean, 2007).

Finally, the boundary condition for the process is given by the establishment of seedlings. Existing trees thus produce offspring at a rate determined by their basal area (Strigul et al., 2004). Sub-models for regeneration are considered reflects the increased competition between 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).

Mortality occurs at a rate

\[ B(t) = f \int_{s} n(s, t) \frac{\pi s^2}{4} ds \] (5)

where \( f \) is the birth rate per m² basal area. The fecundity of trees and accurate quantification of seed establishment success is a long standing problem, due to the combination of seed production, dispersion, neighbourhood and environmental effects involved (Clark et al., 2004; Gratzer et al., 2004). Sub-models for regeneration are often used (e.g. Pacala et al., 1996), but for simplicity we remove this stage of the life cycle from the model by considering only individuals above a minimum size of 1 cm dbh. We assume that an individual takes y years to reach this size, and thus define a probability of seed establishment/survival:

\[ B(t) = (1 - (\mu_1 + \mu_2 \Phi(1, t)))^y \]

This ignores fluctuations in population state throughout the establishment period, but should be a good approximation in the steady state.

The evolution of the size distribution density \( n(s, t) \) is thus described by the equation

\[ \frac{dn(s, t)}{dt} + \frac{\partial(n(s, t)G(s, t))}{ds} = -M(s, t)n(s, t) \] (6)

with boundary condition \( n(1, t) = B(t)P_e(t) \). This dynamical model is similar to that discussed by Sinko and Streifer (1967) and Angulo
2.2. Equivalent spatial model

The model can be readily generalised to a Markovian stochastic birth–death–growth process in continuous (two-dimensional) space (Fig. 1). Individuals \( i = 1, \ldots, N \) are characterized by position and size, which jointly define the state space of the process.

Interaction (and hence growth, mortality and establishment) are not strictly governed by size as they are in the mean-field model, since now neighbourhood varies across individuals. To generalise the model to include spatial dependence, we rewrite the competition as

\[
\Phi_i(t) = \sum_{j \in \omega_i} f(s_j(t), s_i(t))g(\vec{x}_i, \vec{x}_j) \tag{7}
\]

where \( \omega_i \) is the set of all individuals excluding \( i, s_j \) is the size of tree \( i \) and \( \vec{x}_i \) its position. The effects of relative location and size are assumed to be independent; here we found that allowing the spatial scale of interaction to increase with competitor size did not noticeably alter behaviour (results not shown). Note that this is a sum over individuals, as opposed to the integral over the density function in Eq. (2).

Following Raghib-Moreno (2006) and Schneider et al. (2006), the spatial component of interaction is introduced with a Gaussian function of distance to neighbours

\[
g(\vec{x}_i, \vec{x}_j) = \frac{k_2^2}{\pi r^2} \exp \left( -\frac{k_2^2 |\vec{x}_i - \vec{x}_j|^2}{r^2} \right) \tag{8}
\]

where \( k_2 \) defines the decay of interaction with separation. Individual growth and mortality rates vary accordingly, by direct replacement of the interaction function.

The level of competition now varies between individuals of the same size, depending upon their spatial location in relation to others. Consequently, Eqs. (1) and (4) (respectively, the growth rate and mortality rate at a given size in the mean-field model) must instead be defined for each individual in the population. That is

\[
G_i(t) = s_i(t)(\alpha - \beta \ln(s_i(t)) - \gamma \Phi_i(t)) \tag{9}
\]

\[
M_i(t) = \mu_1 + \mu_2 \Phi_i(t) \tag{10}
\]

Reproduction is also computed on an individual basis (that is, \( B_i(t) = (f_r s_i^2)/4 \)). Dispersal of offspring from parents is considered in two generic forms: either randomly (with equal probability to any location in the population arena), or drawn from a Gaussian distribution (a dispersal kernel – as Eq. (8) but with parameter \( k_0 \)). Establishment uses \( P_r(t) \) as above, but with the spatial interaction function (7) in place of (2).

The mean-field model (Eq. (6)) may be derived directly from a differential equation approximating the spatial model described above, making the assumption that the pair density of individuals with sizes \( s \) and \( s' \) separated by distance \( r \), \( n(s,s',r) \), can be approximated as \( n(s)n(s') \) (Adams, 2010).

2.3. Statistics and simulation

Community structure is tracked using various metrics: density (number of individuals per m²), total basal area (mean field: \( \int s(s) \pi s^2/4 \) ds, spatial: \( \sum s \pi s^2/4 \)), size and age density distributions, and pair correlation (PCF) and mark correlation (MCF) functions. Here, a value of 1 indicates that the average density (PCF) or size multiple (MCF) of pairs of individuals with a given separation is equal to the overall population average. Deviation from 1 indicates the level of spatial aggregation of individuals (PCF) or biomass (MCF), relative to a spatially random pattern (Penttinen et al., 1999; Law et al., 2009). All presented spatial model results presented have mean and standard deviation (in figures, lines within grey envelopes), which are computed from 50 repeat simulation runs. The simulation arena represents a 1 ha plot (100 m × 100 m). Periodic boundary conditions are used to remove edge effects. Due to the scale of the kernels used, results are not significantly altered by increasing arena size.

The mean-field model is integrated using an explicit forward-difference numerical scheme, with a size step of 0.1 cm and a time step of 0.2 years. The spatial model is integrated numerically in continuous time by means of the Gillespie algorithm (Cox and Miller, 1965; Gillespie, 1977); this generates a series of events (that is, growths, births, deaths) and inter-event times. After any given event, the rate \( (t_{\text{event}}) \) of every possible event that could occur next is computed. The time to the next event is drawn from an exponential distribution with rate \( R = \sum t_{\text{event}} = \sum (B_i(t) + G_i(t) + M_i(t)) \); the probability of a particular event occurring is \( t_{\text{event}}/R \).

2.4. Parameterisation for Caledonian Scots Pine

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). The plantation datasets (6 > 1.0 ha stands) from Glenmore (Highland, Scotland) incorporate location and size information, which allows comparison of basic statistics at a single point in time (stand age approximately 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 1.0 m height) for four 0.8 ha stands in the Black Wood of Rannoch (Perth and Kinross, Scotland) allows estimation of growth and interaction parameters. Location and size measurements (in 1997) from a 1.0 ha semi-natural stand in Glen Affric (Highland, Scotland) provide another basis for later comparison.

Our simulations use a dispersal kernel with identical spatial scale to the interaction kernel, and an establishment time \( (y) \) of 20 years, in accordance with field studies of Scots Pine regeneration (Sarah Taylor, unpublished data). 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 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 A. Mean values for \( \alpha \) and \( \beta \) are used for simulation, though large variation between individuals was observed. Clark (2010) identifies the potential importance of such individual variation to species coexistence, but this is outside the scope of this article. \( \gamma \) was difficult to estimate from the semi-natural data, its standard deviation being larger than its mean; a consequence of the fact that interaction does not explain a majority of variation in individual growth (see Appendix B). However, it has a large effect on the simulated “plantation” size distribution (Appendix C). 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.

\( k_b \) was selected to provide an interaction neighbourhood similar to previous authors (e.g. Canham et al., 2004). (1) Determines early plantation size distribution, and was selected accordingly; it has minimal effect on long-run behaviour. Parameter values used for model Scots Pine populations are shown in Table 1. Sensitivity to

and Lopez-Marcos (2000), but additionally incorporates a population state dependent interaction effect in the functions \( G(s,t) \) and \( M(s,t) \).
parameter variation over broad intervals was also tested (Appendix C).

A standard planting regime implemented in Scots Pine plantations is a 2 m square lattice, typically on previously planted ground. Old stumps and furrows prevent a perfectly regular structure being created, so our initial condition has 1 cm dbh trees with small random deviations from exact 2 m square lattice sites, which more closely resembles observed planting positions. With such tuning, it is found that the model is able to replicate key patterns observed in both plantation and semi-natural data stands (see Appendix A). The generic aspects of model behaviour, how these are affected by the inclusion of local spatial effects, and specific differences between its behaviour and that observed in real forests, are outlined below.

3. Results

3.1. Qualitative model behaviour

The generic behaviour of the mean-field and spatial models is very similar, and we discuss here features common to both. Starting from the plantation configuration, model populations pass through several stages, an overview of which is given by Fig. 2: (i) an initial growth dominated period, during which the plantation structure largely remains, and the canopy closes; (ii) a period of high density-dependent mortality as the impact of interactions begins to be felt; (iii) gap creation together with an increase in regeneration; (iv) the long-run meta-stable state, during which stand structure is more irregular and determined by the levels of mortality and birth. These stages effectively mirror those of various qualitative models of forest stand development discussed by Franklin et al. (2002).

The plantation structure initiated by forest management has a higher density than a natural self-regenerating forest. Initially, reproduction is low, due to individuals’ small size. Rapid growth of the immature trees means that basal area increases rapidly (see Fig. 3a). Individual density falls equally quickly due to high levels of density-dependent mortality. Stochastic variation in growth and asymmetric competition lead to a gradual spread of sizes of individuals (the initial size distribution is a delta peak at $s = 1$ cm). 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 early stages of stand development: it is almost independent of any other parameter, or even starting spatial configuration (see Table B1, Appendix B). The period described above contains the cohort establishment, canopy closure and biomass accumulation stages of Franklin et al. (2002).

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. Density-dependent mortality remains high, but is overtaken by density-independent (intrinsic) mortality, which opens gaps in the canopy (represented by reduction in overall density of large trees in the mean-field model). During this period, a real stand would also see the accumulation of woody debris (in large part arising through heightened mortality seen in our model). This is the maturation stage of Franklin et al. (2002).

In many real populations the generic properties of the observed state are substantially determined by external disturbances (and the relationship between their extent and frequency), as opposed to demographic properties alone (Turner et al., 1993), bringing into question the utility of the terms “old-growth” or “equilibrium” in describing natural systems. Indeed, Oliver and Larson (1996) point out that due to external catastrophic disturbances, true old growth is rarely reached by many temperate forest communities. In the long run (and in the absence of external disturbance), the model reaches a steady state where fecundity, mortality and growth are in balance. Fig. 3b (dotted lines) shows the typical size structure present in the long run. Only a small proportion of juveniles attain canopy size, but individuals of all sizes are present, and the asymptotic nature of growth means that individuals accumulate in the higher size classes as the system approaches equilibrium, where the size distribution stabilizes. This is a consequence of the ability of trees to survive during periods when they are not growing. Caledonian Scots Pine does not readily establish in low light conditions, and consequently produces a fairly open forest. Growth is also very much limited by shading from other trees, but in many cases old stunted trees are observed in Scottish stands (the implication being that shading affects growth more than it does survival). In the model, local reductions in canopy density thus allow trees that have stunted growth to increase in size, refilling gaps.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
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</thead>
<tbody>
<tr>
<td>$f$</td>
<td>Reproduction per m² basal area</td>
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</tr>
<tr>
<td>$\mu_1$</td>
<td>Baseline mortality</td>
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<td>Gompertz $b$</td>
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<tr>
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<td>$\gamma$</td>
<td>Growth interaction</td>
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<tr>
<td>$k_0$</td>
<td>Size asymmetry</td>
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<td>$k_{d1}$</td>
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</tr>
<tr>
<td>$k_{d2}$</td>
<td>Dispersal distance decay</td>
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</tr>
</tbody>
</table>

* Spatial model only.
3.2. The effect of localised interaction

Space has been noted as having a sometimes subtle but important impact on population dynamics (Law and Dieckmann, 2000; Pacala et al., 1996). Both our mean-field and spatial models produce a bimodal size distribution, with peaks at the smallest size (juveniles) and just below $s^* = \exp(\alpha/\beta)$ (“canopy” individuals). However, “individuals” in the mean-field model experience competition based solely upon their size. This leads to a sharply peaked canopy density in the size distribution, as the entire canopy population has an identical asymptotic size at the steady state (a result replicated by a stochastic version of the mean-field interaction model; Adams, 2010). In the spatial model, the variation in competition over space leads to a blurring in size of the canopy, represented by a lower density, higher variance peak. However, under the Scots Pine parameterisation shown in Table 1, the effect of space on individual density and basal area (a surrogate for population biomass) is fairly minor – the trajectories of density for mean-field and spatial models are almost indiscernible (Fig. 3a), while basal area at equilibrium is around 10% lower in the mean-field model. Such relatively small discrepancies between spatial and mean-field models are commonly observed in temperate forest ecology (Deutschman et al., 1999; Busing and Mailly, 2004) and may be significant in some applications.

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 in early population structure (Fig. 3c, 80 years – peaks are at multiples of the lattice spacing). 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), but does not provide a great deal of useful information due to the regular pattern of trees (Fig. 3d, 80 years). On the other hand, our semi-natural Scots pine data stands demonstrate generic features of the spatial structure induced by natural processes in more mature stands: (i) a suppressed MCF at short ranges and (ii) a heightened PCF at short ranges (Appendix B). The mean-field model cannot replicate either feature, but the spatial model can reproduce the suppressed MCF when local interaction is implemented (Fig. 3d, 800 years).

3.3. The effect of localised dispersal

Local dispersal of seedlings leads to an increased PCF at short ranges (Fig. 3c), while the MCF is somewhat reduced at short ranges, due to the effect of interaction on growth. If dispersal is long-ranged (random) both size and frequency of adjacent pairs is lowered, leading to reduced PCF and MCF (see below). In line with the expectation of Murrell (2009), we find that interaction is sufficiently strong, and fecundity and growth sufficiently high, to cause a decrease in clustering with size. Computing the cross-correlation function of juveniles and mature trees for the semi-natural stand data shows that indeed there is either zero or negative correlation between their locations (not shown). Some authors (e.g. Barbeito et al., 2008) have noted that regeneration sometimes occurs in explicitly clustered patterns, and that this is not necessarily a consequence of local dispersal. The apparent contradiction between the model's
steady state spatial correlation functions and the data suggests that the clustering seen in the data stands is partly due to management history, or environmental heterogeneity (though a reduced density of juveniles in comparison with real stands may partly explain this discrepancy; Adams, 2010). In reality, spatial structure is also generated by disturbance (for example due to treefall during mortality).

3.4. The importance of fine-scale spatial effects

In the spatial model, low reproduction at early stages means that spatial structure is governed by the starting configuration. Over time, more substantial regeneration begins to occur in model populations (gaps between more mature trees increase in size, while high basal area ensures a large seed source) and a much broader age/size structure begins to develop. The initial regular spatial structure is erased through mortality, regeneration and differential growth. This change is apparent in maps of the stand at 300 years (Fig. 2).

Although we found here that for the Scots’ Pine parameterisation spatial heterogeneity has a limited impact on first-order quantities (see Section 3.2), an important question is: under what circumstances do spatial effects become more important? In very dense populations (under either low mortality or high fecundity, Fig. 4a and b), the effect of explicit spatial interactions remains fairly similar to that of mean-field interactions (in line with the results of Pacala and Silander, 1990). On the other hand, in low density populations, the difference between the two models increases (with density/basal area in the mean-field model being comparatively higher, Fig. 4a and b) – an effect of finite area. Spatial interactions only directly affect the realised density when the overall effect of interaction is relatively strong in relation to basic population rates (the last term in each of Eqs. (1), (4), (9) and (10) is large). That is to say, increasing $\gamma$ (the effect of interaction upon growth) or $\mu_2$ (the effect of interaction upon mortality) both widen the gap between simulated spatial and mean-field populations (mean-field populations having the lower density/basal area – Fig. 4d and e). Increasing $k_d$ (localisation of interaction in the spatial model) reduces the effective neighbourhood size and as a consequence leads to an increase in density and basal area (not shown). Aside from very low density scenarios, the only case in which our mean-field simulations produce a higher density and basal area than spatial simulations is when greatly increased strength of competitive interactions ($\gamma, \mu_2$) are combined with relatively short range dispersal ($k_b > k_d$, not shown).

We also investigated the impact that the dispersal kernel has on stand dynamics. Bolker and Pacala (1999) found that species’ relative scale of dispersal affects their ability to invade one another. In our single species “Scots pine” populations altering the scale (distance $1/k_b$) of dispersal relative to the interaction kernel affects the spatial structure of the population (increasing $k_b$ producing a more clustered pattern), but does not affect the resulting population density as the effect of interaction is too weak (Fig. 5a). In more competitive populations (for example, increasing $\mu_2$ by one order of magnitude – Fig. 5b), longer range dispersal has a qualitatively similar, but more pronounced effect on spatial structure. It also allows offspring to escape the shade of their parents, and consequently increases both individual density and stand basal area (as found by Bolker and Pacala, 1997). Strong local ordering can arise for this model, but not under the Scots pine parameterisation. However, in no case did we observe development of structure at a larger scale than that of the interaction and dispersal kernels (it is not a possible outcome of the model, and neither could we
4. Discussion

Both mean-field and spatial models are in qualitative agreement with real communities, showing the same generic behaviour as the forest matures. However, the same Caledonian Scots Pine parameterisation results in a 10% lower basal area in the mean-field model compared with the fully spatial process, and a more sharply peaked “canopy” in the size distribution, due to the lack of variation in competitive neighbourhood. The spatial model also represents second-order (e.g. PCF MCF) characteristics not possible in the mean-field model. However, in this case (by virtue of the parameterisation) the effect of including spatial heterogeneity may be considered relatively weak. However, numerical exploration demonstrates that for highly competitive populations (or those in which interaction is very localised), the explicit treatment of space has a much larger effect on computed density or biomass (first-order quantities). Increasing γ, μ2 or k_d for example, all widen the gap between the mean-field and spatial model behaviour. An example would be a pioneer species that cannot tolerate any level of shading/interaction, particularly in a larger-scale patchy distribution amongst individuals of a late-successional (or high-shading) species. In all cases the density and biomass of spatially interacting populations was higher.

The structure of simulated and real 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 which appears to produce a stable canopy, with no evidence of cyclical variation in structural characteristics. The inclusion of a non-random dispersal kernel recreates the clustered pattern seen in data stands, and at the level of interaction present in Scots Pine stands does not greatly affect density or basal area (which it would do in more dense/competitive populations). However, it also weakens the signal of inhibition in the MCF, due to an increase in the number of parent offspring pairs at close separations. This discrepancy with

![Fig. 4. The effect of space – sensitivity of the discrepancy between mean-field and spatial model density (dashed line) and basal area (solid line) to model parameters (keeping all others equal). The thick vertical line in each panel shows the “Scots Pine” parameter value (Table 1). Altering growth entails altering both α and β, fixing their ratio (the value of α is shown). A mortality change entails altering both μ1 and μ2 fixing their ratio (the value of μ1 is shown). The most significant differences are seen on alteration of interaction parameters μ2 and γ.](image)

![Fig. 5. The relative scale of dispersal – altering k_d (random dispersal, solid; k_d = 0.1, dashed; k_d = 0.2, dotted) while fixing k_b = 0.1. Insets show the change Δ in density (dashed) and basal area (solid) as a result of changing k_d (k_d/k_b small = relatively short range dispersal). (a) Behaviour at the “Scots Pine” parameterisation – spatial structure changes, but density and basal area do not. (b) With stronger interaction (μ2 = 0.0002), spatial structure changes more dramatically, and density/basal area also increase as dispersal becomes more global.](image)
data, and significant differences between real stands, suggest environmental (e.g. Gravel et al., 2008; John et al., 2007) or management influences. Plant/tree establishment has traditionally proven difficult to quantify accurately (Clark et al., 2004), and is certainly deserving of further work.

It is worth bearing in mind the growth information for most populations is generally not available with the level of detail of our Scots pine data. While the model's interaction-limited growth is consistent with field observations, our model parameterisation and tuning found significant variation in growth trajectories between individual trees, which is impossible to explain fully by recourse to interaction (even when this is allowed to accumulate over time – Adams, 2010). While the basic growth, birth and death parameters could be taken as constant for all trees, it proved necessary for the maximum size (determined by $\beta$) to be drawn from a distribution. This may represent either genetic diversity (Provan et al., 1998) or a variation in the ability of a given location to support a tree, but we do not have relevant data for the stands in question. The robustness of model behaviour to the inclusion of such variation (see Appendix B) suggests that the results that we have obtained should generalise to multi-species communities (provided that the questions being asked relate to bulk properties such as basal area, as opposed to species composition, for example). Further, the detailed data combined with our sensitivity analysis affords us some confidence in the region of parameter space in which we are interested.

In modelling complex real-world systems in ecology a common approach is to develop detailed application specific models (Botkin et al., 1972; Busing and Mailly, 2004). While this can be successful, such models are often difficult to parameterise given the available data, and by their nature tend to focus on system-specific features. In contrast, generic models are of great interest to theoretical ecology because they facilitate understanding of common or universal properties of ecosystems (Bolker et al., 2003; Law et al., 2009; Weiner et al., 2001). Here we have shown that generic dynamic models enable investigation of the importance of different factors and components of the life-history of a target species on population dynamics, and can be informed by empirical models. Moreover, simple generic models may also have practical advantages when applied to specific systems because they typically require relatively few parameters and, with sparse data, are less prone to over-fitting than complex models. It is inevitable that such simple models (and indeed any model) will not capture every aspect of real world systems. However, often much of this additional variability can be represented via stochasticity, implicit or explicit spatial heterogeneity and intra-individual variation in parameters.

The speed of approach to an equilibrium state is affected by disturbances (which were not implemented in this manuscript). If these are regular and major, a persistent low density state will prevail. However, small scale disturbance can benefit a stand by encouraging heterogeneity in size (through the light environment), and more rapid development of an uneven-aged structure (through regeneration, Adams et al., 2011).

5. Conclusions

Here we applied generic models of reproduction, competition, growth and mortality (Bolker and Pacala, 1997; Sinko and Streifer, 1967) to real single-species population dynamics using detailed and long-term data on Caledonian Scots Pine stands. This approach was able to reproduce known qualitative and measured quantitative features of the transition from plantation to old growth stands. For such stands we found that the inclusion of explicit spatial interactions did not explain a majority of individual variation in growth, and furthermore did not have a profound effect on overall density with respect to a mean-field model. By consideration of a much wider parameter space, however, the model allowed useful generic insights into the importance of the explicit treatment of space in size-structured models of population dynamics. That they do not greatly affect the overall density and biomass of a typical modelled temperate forest population suggests that the application of mean-field models (or better, those accounting for space implicitly, e.g. Purves et al., 2008) to global issues, such as carbon and nutrient cycling, may be appropriate. However, stand level models such as ours are important for many smaller-scale goals: while our emphasis has been on understanding the mechanisms and dynamics of a population in its approach to a steady state, models of this type can also be used to investigate management strategies (Adams, 2010; Comas, 2005), covering diverse goals such as plantation transformation (Adams et al., 2011), conservation, or maximum production of timber. In conclusion, we hope that this study will prompt renewed theoretical and applied interest in dynamic models of populations structured in size and space.

Acknowledgements

We would like to acknowledge the support from the Scottish Government and the EPSRC funded NANIA network (grants GRT11777 and GRT11753). This work made use of resources provided by the Edinburgh Compute and Data Facility (ECDF) (http://www.ecdf.ed.ac.uk/). The ECDF is partially supported by the eDIKT initiative (http://www.edikt.org.uk). We are grateful for the comments of anonymous referees, which helped to significantly improve the manuscript.

Appendix A. Supplementary data


References
