

A demographic study of the exponential distribution applied to uneven-aged forests

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Received 18 February 2016

A demographic approach based on a size-structured version of the McKendrick-Von Foerster equation is used to demonstrate a theoretical link between the population size distribution and the underlying vital rates (recruitment, mortality and diameter growth) for the population of individuals whose diameter distribution is negative exponential. This model supports the conclusion that the negative exponential distribution as applied to balanced natural uneven-aged stands is a stable equilibrium model under appropriate assumptions. These assumptions include constant recruitment of stems into the smallest class that balances total mortality, and a simple relation between per capita mortality and diameter growth. A simple maximum likelihood-based solution to parameter estimation in the inverse problem is developed allowing the estimation of recruitment and mortality given reasonable sample of diameters, along with an estimate of population size and diameter growth rate. Two sets of stand dynamics equations are developed that are based on (i) the form of the underlying negative exponential distribution, and (ii) more generally, from the derivation of the McKendrick-Von Foerster equation. Applications of the methods and their assumptions are discussed with regard to both managed and old growth uneven-aged stands. Stands or forests that are close to negative exponential structure and are judged to be reasonably close to steady state will have vital rates that support this model. In contrast, the negative exponential is likely more important and applicable as a pragmatic target distribution when used in managed forests.

Introduction

Uneven-aged stands and forests are characterized by the presence of trees of at least three different age classes or cohorts (Helms, 1998, p. 193). There is no commonly accepted standard with regard to what characterizes the cohorts in terms of age (e.g. 5-, 10-, 20-years), as it is dependent on a number of factors such as species composition and site. The important point is that the trees have not all originated from one or two events, creating for example, a simple two-layered (-aged) forest; rather, the differentiation in ages (and often species) tends to produce a more complex multi-layered vertical structure. One of the main characteristics of uneven-aged forests is the presence of some form of declining, reverse J-shaped diameter distribution. This was evidently first pointed out by de Liocourt (1898). Later, Meyer and Stevenson (1943) demonstrated that a scaled form of the negative exponential distribution would fit the diameter distribution from these stands and forests. Meyer (1952) subsequently expanded on this idea, and introduced the diminution quotient, q , based on a geometric progression of the number of trees by diameter class. He attributed this idea of constant q to de Liocourt, though a recent more thorough look at de Liocourt's analysis by Kerr (2014) rightly questions this lineage because the progression of number of trees in de Liocourt's data is not constant throughout all diameter classes.

Meyer's (1952) work can be considered seminal for two reasons. The first is the introduction of a constant q value with the link he made to the exponential distribution. This has become a standard in the management of uneven-aged stands where some combination of constant q , maximum stand diameter and residual basal area are chosen (the so-called BDq approach) as a target condition after harvest. But evidently it also applies in natural forests, such as the virgin northern hardwood-hemlock stands described in Meyer and Stevenson (1943), where their scaled exponential distribution approach fitted the observed diameter distributions well. Because of Meyer's inaccurate attribution of q to de Liocourt, it appears that the idea is actually due to Meyer himself.

The second classic idea reported by Meyer (1952) is the concept of balance in uneven-aged forests or stands. Meyer differentiates between managed and natural stands in his definition. A managed balanced uneven-aged forest 'is one in which the current growth can be removed annually or periodically while maintaining at the same time the structure and initial volume of the forest'. He goes on to illustrate this concept and gives appropriate formula based on the exponential- q assumption to aid foresters in achieving such target structures. A second definition of a balanced forest was also given by Meyer that pertains to old growth forests:

In a balanced virgin forest, the current growth is offset by current mortality, and the existing balance between growth and mortality makes it possible for such a forest to perpetuate itself indefinitely.

These two concepts, while similar in intent, are actually quite different in reality. In managed forests, balance comes via manipulation, the target diameter distribution is perpetuated by harvests, which artificially return it to the target structure. However, in virgin forests, there is no requirement for human involvement as the forest or stand appears to be in equilibrium. Indeed, it can be conjectured that any disturbance in such stands would at least temporarily upset this equilibrium, after which the original stand structure may or may not be reached again in the exact form as before disturbance, depending on its severity.

As noted above, Meyer's concept of balance as applied to natural old growth (virgin) stands is describing a form of equilibrium or steady-state condition as is commonly encountered in biology, chemistry and other branches of science. Another related concept from biology and demography is that of a stable distribution. As a classic demographic example, Keyfitz (1977, p. 47) in a discussion of age-class structure notes that 'the stable population has meaning as a set of proportions, not of absolute numbers'. This definition is echoed in the development of size-structured models (VanSickle, 1977a) to be discussed shortly. Thus, we can think of a constant form of probability density function (PDF) representing the diameter distribution as stable, if its shape does not change over time. However, this is only half of the definition, because we would like a criterion that allows us to determine whether the population size is growing, declining or staying constant (in equilibrium). A general definition of a population in equilibrium (Keyfitz, 1977, p. 170; Nisbet and Gurney, 1982, p. 22) is that input must equal output: births (regeneration) must equal deaths (whether from natural mortality or harvesting). It follows from this input-output balance that the population size, N , must be constant such that under exponential growth, $dN/dt = rN$ implies $r = 0$, the population size neither increases nor decreases over time (de Roos, 1997, p. 155; VanSickle, 1977a), where r is the intrinsic growth rate of the population. Thus, a stable equilibrium (steady state, stationary) distribution for a population is one where the shape of the distribution does not change over time, nor does the size of the population itself.

Meyer's concept of balance is similar in spirit then to the more well-defined idea of a stable equilibrium structure. Meyer failed to explicitly include recruitment (births) into the definition, though one could argue that he implicitly was including these in his 'current growth'. It will remain unknown whether he also had the idea of a constant population size, N , in mind; but we will conjecture that balance *sensu* Meyer, can be interpreted as equivalent to the stable equilibrium. Because these ideas constitute a balance law, they can be formalized mathematically into a dynamical system, not just one that relies on the resultant diameter distribution as will be shown shortly. The tools that allow one to do this for the negative exponential or any other distribution come from both demography and population biology, the two being closely linked in this area. They distinguish the vital rates of a population – recruitment, growth and mortality – as the critical parameters; and we assume that the vital rates of a population are known or can be estimated, similarly with the population size, N . In general, the vital rates can be modeled as functions of age

or size (or both). In particular, for diameter distributions in uneven-aged stands, size (physiological age, p -age, VanSickle, 1977a) is the appropriate attribute. Dynamical models that couple the vital rates of a population with the size structure are known as size-structured population models, and the distribution itself is referred to as the size-structured distribution (SSD) (Botsford *et al.*, 1994), or more generally, physiologically structured population models (de Roos, 1997; VanSickle, 1977a).

The theory of size-structured population models provides both a dynamical and equilibrium solution for the population distribution in terms of the vital rates. Thus, for example, providing a way to determine whether the negative exponential distribution is indeed a stable equilibrium distribution, and the conditions under which this is true. This is an important point to resolve as the stability of the exponential distribution has recently been questioned (Lopez Torres *et al.*, 2012). This paper concentrates on a partial differential equation (PDE) approach, because this method leads to a clear closed-form negative exponential solution, and provides other insights into the characteristics of the vital rates that are required for such a solution. It also provides related probabilistic results, such as the mortality probability density function, which is also linked to the vital rates. Matrix models are a complementary and often simpler approach, but lack the nice closed-form results that the PDE solution can provide; however, they are often simpler to work with in general. The main results and examples are given in the text, with derivations in Supplementary data. In what follows it is often convenient to drop the extra 'stable' qualifier when the context is obvious and simply speak in terms of an equilibrium, steady state or stationary condition as synonymous. In addition, the terms 'exponential distribution', 'negative exponential distribution' and 'q distribution' should be considered synonymous.

Demographic methods

Preliminaries

It was noted that the general model for the size-structure of a population can be defined in terms of a balance law, where inputs equal outputs, and growth moves the individuals through the diameter distribution. When the population is in a steady state, growth maintains the shape of the distribution, but prior to the population reaching a steady state, growth or changes in any of the vital rates may change the shape of the population distribution. The population distribution is given in terms of a continuous numbers density, $n(d, t)$, the number of individuals at time t of diameter d (number·cm⁻¹). Note that this is a loose interpretation, since the numbers density is akin to a scaled probability density (see, e.g. de Roos, 1997, p. 138) with, e.g.

$$N_{\mathcal{D},t} = \int_{d_l}^{d_u} n(d, t) dd \quad (1)$$

being the number of trees in the diameter interval $\mathcal{D} \in [d_l, d_u]$ at time t ; thus, $N_t = \int_{d_0}^{d_\infty} n(d, t) dd$, or at equilibrium, simply N .

In what follows $d_0 = 0$ and $d_\infty = \infty$ unless stated otherwise – or more generally an unattainable asymptotic maximum diameter (e.g. de Roos, 1997, p. 142) – to determine the theory, but in practice it would be some maximum diameter limit.

The vital rates are required for the determination of the model. Diameter growth, $dd/dt = g(d, t)$ ($\text{cm}\cdot\text{yr}^{-1}$) is assumed to be annual in time step, as is per-capita mortality $m(d, t)$ (yr^{-1}). The recruitment rate, R_t ($\text{number}\cdot\text{yr}^{-1}$), depends on the per capita birth rate, $b(d, t)$ (yr^{-1}), at which individuals of p -age d 'give birth' to those of p -age d_0 (VanSickle, 1977a) and is given by the renewal equation

$$R_t = \int_{d_{bl}}^{d_{bu}} b(d, t)n(d, t) dd \quad (2)$$

where R_t is total recruitment and $b(d, t) = 0$ for $d \notin [d_{bl}, d_{bu}]$, the diameter limits between which reproduction occurs. VanSickle shows that (2) can be recast to the boundary condition

$$R_t = g(d_0, t)n(d_0, t) \quad (3a)$$

or, at equilibrium, the recruitment is constant over time, i.e.

$$R = g(d_0)n(d_0) \quad (3b)$$

Regardless of the form (2)–(3b), recruitment is the required input into the system that counterbalances mortality and supplies the fresh pool of individuals to support the movement of trees through the distribution. A balance equation states that changes to the target state variable in the system (e.g. numbers, mass, volume) must come from known inputs (sources) and exit via known outputs (sinks) (Gurney and Nisbet, 1998, p. 10; Soetaert and Herman, 2009, p. 18). Using this concept, one can state a simple balance equation for the population growth rate as

$$\frac{dN}{dt} = \int_{d_{bl}}^{d_{bu}} b(d, t)n(d, t) dd - \int_{d_0}^{d_\infty} m(d, t)n(d, t) dd \quad (4)$$

At equilibrium ($r=0$ implies $dN/dt = 0$ under exponential population growth) this can be recast as a constraint on the system that ensures an exact balance between inputs and outputs; viz.,

$$\int_{d_{bl}}^{d_{bu}} b(d, t)n(d, t) dd = \int_{d_0}^{d_\infty} m(d, t)n(d, t) dd \quad (5)$$

or, under constant recruitment and mortality (M)

$$R = MN \quad (6)$$

Continuing with this concept of balance, one can derive a discrete balance equation for population size through diameter given the vital rates for the population. Let Δd be a very small increment in diameter, and similarly let Δt be a very small time increment. Then the balance equation for the net change – the difference between the number of trees at times t and $t + \Delta t$ in a class of width Δd – is (e.g. de Roos, 1997, p. 141)

$$\begin{aligned} n(d, t + \Delta t)\Delta d - n(d, t)\Delta d &= -m(d)n(d, t)\Delta d\Delta t \\ &+ [g(d_i)n(d_i, t) \\ &- g(d_i + \Delta d)n(d_i + \Delta d, t)]\Delta t \quad (7) \end{aligned}$$

Here, to make things simpler, the vital rates are assumed to be time-invariant, depending only on diameter. The relationship

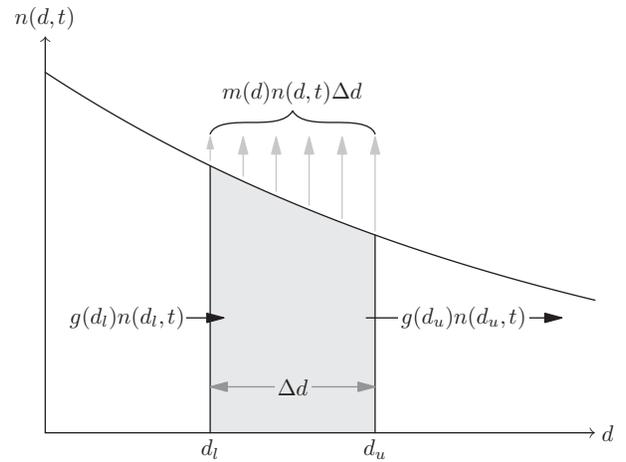


Figure 1 The flow through the system at a small time interval Δt ; as an example, the numbers density, $n(d, t)$, is given by the exponential distribution.

in (7) is illustrated in Figure 1; the change in the numbers density for a small increment of diameter is composed of movement into the class (ingrowth) and movement out (upgrowth) plus mortality. Finally, at equilibrium, (5) or (6) ensures that the system is in perfect balance, *sensu* Meyer. The discrete balance equation (7) has very practical applications, not the least of which is the coupling of population vital rates with the diameter distribution. Also slight algebraic rearrangement leads to an accounting equation used to grow stems in uneven-aged models as will be shown in the following sections.

The continuous size-structured model

The discrete balance equation (7) can be easily recast into the PDE (e.g. de Roos, 1997, p. 141) yielding the size-structured model of the flow of individuals first introduced by VanSickle (1977a)

$$\frac{\partial n(d, t)}{\partial t} + \frac{\partial [g(d, t)n(d, t)]}{\partial d} = -m(d, t)n(d, t) \quad (8)$$

A simplification of this equation was first suggested by McKendrick (1925) in the study of vital statistics for human populations. It was later independently introduced as a balance equation in the study of cell populations by Von Foerster (1959). In both cases, age was used so that $g(d, t) = 1$. Various forms of this equation are used in other fields where, for example, it is also known as the transport equation with decay (Olver, 2014, Ch. 2; Picard et al., 2010). Other variations to this model exist; for example, it has also been extended to two independent variables, age and size, by Sinko and Striefer (1967). Because mortality is a sink term there must be an accompanying boundary condition, e.g. (3a), as a source term for input into the system. Finally, an initial condition $n(d, 0) = n_0(d)$ can be specified when not working with the steady-state form, making this an initial-boundary value problem.

While the discrete form is convenient for understanding the genesis of (8) and for determining discrete projection equations, the PDE form allows the development of a more formal

mathematical analysis, particularly for the steady-state distribution. At equilibrium the time differential term $\partial n(d, t)/\partial t$ is zero, and applying the product rule to the size differential with some algebra yields the equilibrium numbers density in terms of the population vital rates

$$\begin{aligned} n(d) &= \frac{R}{g(d)} \exp\left(-\int_{d_0}^d \frac{m(d')}{g(d')} dd'\right) \quad d > d_0 \\ &= \frac{R}{g(d)} S(d) \end{aligned} \quad (9)$$

where recruitment is constant as in (6). Furthermore, the exponential term is a survival function, $S(d)$, giving the probability that a tree survives from size d_0 to size d (VanSickle, 1977a; de Roos, 1997, p. 133). In some cases, the survival integral can be determined analytically yielding a closed-form solution to the numbers density. In others, where either mortality or growth are more complicated functions, the integral is unyielding to analytic solution, but can be integrated numerically.

Finally, note from (1) that the population size is given by

$$N = \int_{d_0}^{d_\infty} n(d) dd \quad (10)$$

under the equilibrium distribution (9).

The negative exponential special case

Because our concern is with balance in uneven-aged stands under the exponential distribution model, it is natural to inquire what form the growth and mortality functions can take in order to yield an exponential distribution when applied to (9). In other words, we would like a resultant negative exponential numbers density

$$n(d) = N\psi \exp(-\psi d) \quad d \geq 0 \quad (11)$$

with corresponding PDF

$$p(d) = \psi \exp(-\psi d) \quad (12)$$

For example, Muller-Landau *et al.* (2006, their supplementary data) showed that when all vital rates are constant, i.e. $g(d) = G$, $m(d) = M$ and $R_t = R$, then the solution to (9) is the exponential distribution. However, there is a more general solution to the question, with constant rates being a special case. It is straightforward to demonstrate (Supplementary data section S.1) that given a diameter growth function $g(d)$, if the mortality function is constrained to the form

$$m(d) = \psi g(d) - g'(d) \quad (13)$$

where $g'(d) = dg(d)/dd$ (e.g. VanSickle, 1977a, 1977b, 1977c), then the resulting numbers density will be negative exponential in form with rate parameter ψ (Dr André M. de Roos, pers. comm.). Rearranging (13), we have in general that the rate parameter for the size-structured exponential distribution is

$$\psi = \frac{m(d) + g'(d)}{g(d)} \quad \forall d \quad (14)$$

which implies that the right-hand side is a constant for all d . It is trivial to show that in the case of constant rates, (14) reduces to

$$\psi = \frac{M}{G} \quad (15)$$

since $g'(d) = 0$ in this special case.

The pool of possible diameter growth functions is large, though it is not immediately clear that any posited growth function would yield a mortality function constrained by (13) that is equally appropriate to the data. For this reason, and because constant rates are simple and can be validated with existing data, much of the remainder of this paper focuses on this special case, though an example with a more general growth model under (13) will be revisited later.

Under the constant rates scenario, the initial form of the solution to (9) is

$$n(d) = \frac{R}{G} \exp\left(-\frac{M}{G}d\right) \quad (16)$$

Integrating (16) over $[0, \infty)$ verifies (6), and substituting this result into (16) for R yields

$$n(d) = N\frac{M}{G} \exp\left(-\frac{M}{G}d\right) \quad (17)$$

or dividing through by N , the PDF is

$$p(d) = \frac{M}{G} \exp\left(-\frac{M}{G}d\right) \quad (18)$$

and finally, using (15) yields (11) and (12), respectively. These results lead directly to the following relationship for q under the size-structured model with constant rates

$$q = \exp\left(\frac{M}{G}w\right) \quad (19)$$

where w (cm) is the diameter class width.

Much like the survival term in (9), the interpretation of (17) with rate parameter (15) can intuitively be described in terms of a survival function. If mortality is small compared with growth, then ψ is small and the numbers density (17) will have a slow decline with a heavy tail since many trees survive to the larger diameter classes. Alternatively, if mortality is large compared with growth then so is ψ , consequently trees die quickly in the distribution, which is characterized by many small trees and few trees surviving to the larger size classes.

The inverse problem

Up to this point, it has been assumed that the vital rate parameters for a population are known, perhaps from permanent growth data. However, this will not always be the case, and estimates of both recruitment and mortality are more difficult to come by than those of annual growth, which can be deduced

from, e.g. increment cores. Therefore, it is of interest to look at the exponential version of the SSD (18) to see how one might estimate a subset of the vital rate parameters. This is often called the ‘inverse’ problem in the literature, because we are backing out the underlying dynamics from an observed distribution. The alternate ‘forward’ problem finds the distribution from the known dynamics (Banks *et al.*, 1991; Metz and Diekmann, 1986; van Straalen, 1986; Wood, 1997). In our case, the forward problem is known since we know the form of the equilibrium distribution, the inverse problem requires a method to estimate any unknown vital rate parameters.

Under the special case of constant rates, the relationship for the exponential rate parameter in (15) shows that one of the two rates, growth or mortality, must be known as there are infinitely many combinations of this ratio that will yield the same value of ψ . As noted above, it is assumed that growth has been estimated from field data because it is more readily obtainable in practice. Because (18) is a PDF, any statistical method that is useful for estimating parameters for densities can be used. In this case, maximum likelihood (ML) will be used to find a mortality estimator using the observed diameter distribution and the sample-based estimate of growth, \hat{G} .

In general, the ML estimator (MLE) for the negative exponential distribution is $\hat{\psi} = \bar{D}^{-1}$, where $\bar{D} = \sum_{i=1}^n d_i/n$ for a sample of n trees. Substituting this into (15) yields (Supplementary data section S.2)

$$\hat{M} = \frac{\hat{G}}{\bar{D}} \quad (20)$$

as an estimator for mortality given estimates of growth and average diameter. Similar reasoning can be employed for the more general case (14). That is, if ψ is estimated from the arithmetic mean of the sample diameters, then (13) provides the estimator for mortality based on ψ and some fitted growth function, where $g(d)$ and $m(d)$ share the same parameter values. In either case, mortality can be estimated from the growth function and sample average diameter for the population under study.

Now the steady-state balance equation (6) provides an estimator for recruitment as long as an estimate of the population size (e.g. number of trees ha^{-1}), \hat{N} , is available; i.e. $\hat{R} = \hat{M}\hat{N}$. The growth estimate will normally contain some uncertainty but for simplicity, we will assume that the effects on the estimate of mortality and recruitment are negligible as these errors would presumably be minor in relation to the error in \bar{D} from a sample of small n ; and a rigorous assessment of the effects of these sources of error is beyond the scope of the current study. The extension of this estimator for recruitment under the more general assumption (13) is given in Supplementary data section S.5, and demonstrated in the examples.

Discrete movement equations

The general form of discrete movement or accounting equations for uneven-aged stand projection in terms of numbers have been known for decades (e.g. Adams and Ek, 1974).

Given diameters partitioned into discrete classes, then from (1) let

$$N_{i,t} = \int_{d_{li}}^{d_{ui}} n(d, t) dd \quad (21)$$

be the number of trees in the i th diameter class $[d_{li}, d_{ui}]$ of width w at time t . Then the general discrete movement equations for the time interval $[t, t + \Delta t]$ (i.e. $\Delta t \equiv 1$ for annual growth) follow

$$N_{i,t+1} = N_{i,t} + \text{ingrowth} - \text{upgrowth} - \text{mortality} \quad (22)$$

for all diameter classes $i = 1, \dots, n_d$. Here ‘ingrowth’ is growth in number of trees into the i th class from class $i - 1$ and is equivalent to recruitment, R , for the lowest class. Likewise, ‘upgrowth’ is the growth in number of trees from class i to $i + 1$. Note that we assume without loss of generality that a tree will not grow more than one diameter class during the growth period: i.e. $G\Delta t \leq w$. This assumption is in accordance with Usher (1966) for the matrix approach.

There are at least two different specific solutions to the movement equations (22) based on direct partitioning of the density, or on the discrete balance equation (7). In the following, the distribution is assumed to be in steady state, so the time-invariant numbers density, $n(d)$ replaces $n(d, t)$. As a consequence, the stand at time $t + 1$ will exactly equal the stand at time t if the movement equations are correct.

Movement via density partitioning

Note that when the growth rate is constant, every tree will grow $G\Delta t$ cm per year. Thus, in each diameter class i , the only trees that can move up one class are those in the interval $[d_{Gi}, d_{ui}]$ where $d_{Gi} = d_{li} - G\Delta t$ (Figure 2a). Since the steady-state PDF is known up to an estimate of the vital rates, the number of trees in this interval is given by

$$\begin{aligned} N_{i,t}^{\text{pdf}} &= N_t \int_{d_{Gi}}^{d_{ui}} p(d) dd & i = 1, \dots, n_d \\ &= \int_{d_{Gi}}^{d_{ui}} n(d) dd & i = 1, \dots, n_d \end{aligned} \quad (23)$$

where N_t is the total number of trees in the stand at time t . Therefore, the accounting equations (22) become

$$\begin{aligned} N_{i,t+1} &= N_{i,t} + R - N_{i,t}^{\text{pdf}} - MN_{i,t} & i = 1 \\ &= N_{i,t} + N_{i-1,t}^{\text{pdf}} - N_{i,t}^{\text{pdf}} - MN_{i,t} & i = 2, \dots, n_d \end{aligned} \quad (24)$$

The type of movement given in (23) has evidently been recognized previously (e.g. Kohyama and Takada, 1998; Picard *et al.*, 2008). In what follows, we will refer to (23) and (24) as the approximate accounting/movement equations.

Movement via the PDE

A second version of (22) can be derived directly from the balance equation (7), which will yield the exact dynamics when the diameter distribution is in equilibrium. First, let

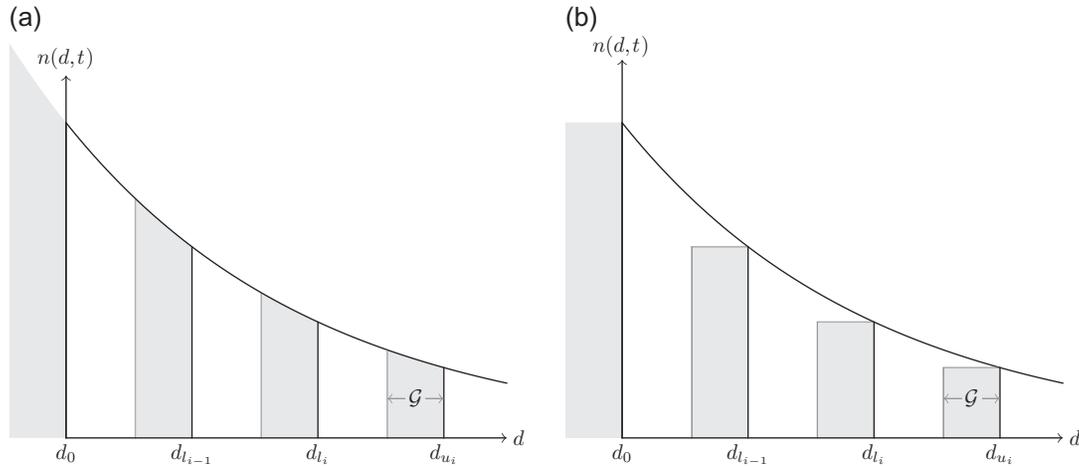


Figure 2 An illustration of growth projection using (a) approximate and (b) exact rules for the numbers density, $n(d, t) \equiv n(d)$, for the system in equilibrium as given by the exponential distribution. The shaded areas of width $G = G\Delta t$ show the density that shifts from one class to the next due to growth under the two projection methods (refer to the text for more explanation).

$$N_{i,t}^{\text{pde}} = G\Delta t \cdot n(d_{u_i}) \quad i = 0, \dots, n_d \quad (25)$$

then

$$N_{i,t+1} = N_{i,t} - MN_{i,t} + N_{i-1,t}^{\text{pde}} - N_{i,t}^{\text{pde}} \quad i = 1, \dots, n_d \quad (26)$$

where recruitment is given by (3b) when $i = 0$, since $d_{u_0} \equiv d_0$. The quantity defined in (25) is a rectangle of width $G\Delta t$ and height given by the point estimate of the numbers density at the upper limit of the class. These dynamics are illustrated in Figure 2b. Note that only a portion of the density in a particular block of width $G\Delta t$ is shown to move as compared with (23) and Figure 2a.

The approximate dynamics intuitively may seem correct at first glance. This is because the same geometric progression of trees given by q that preserves the density relationship from one class to the next also preserves any portion of density; for example, $N_{i,t}^{\text{pdf}} \equiv q_G \int_{d_{i+1}}^{d_{i+1}+G\Delta t} n(d) dd$, where q_G is the diminution coefficient for a ‘class’ of width $w = G\Delta t$. From this the recruitment for the approximate method is given by $\tilde{R} = q_G \int_{d_0}^{d_0+G\Delta t} n(d) dd$. However, $\tilde{R} > R$, where R is given by (3b), which is the correct amount of recruitment to balance mortality $M = R/N$ from (6). As a consequence of the balance in (5) and (6), if recruitment is given by \tilde{R} , then a new estimate of mortality is required to balance the source–sink relationship of the system; this is given by $\tilde{M} = \tilde{R}/N$ yielding $\tilde{M} > M$. However, this now leads to a new exponential distribution with rate parameter $\tilde{\psi} = \tilde{M}/G$ as in (15). Thus, while the dynamics given by (24) are now balanced for the original exponential distribution, the required vital rates \tilde{R} and \tilde{M} now apply to an exponential distribution with rate $\tilde{\psi}$ and not the original distribution with rate ψ in (15). The conclusion is that too much recruitment is required for the equilibrium distribution to be in balance using the approximate dynamics as illustrated in Figure 2a. However, because the amount of recruitment given

in (3b) is proportionately the same (with appropriate q adjustment) as the ingrowth into each class, and because recruitment balances with mortality (6), the system is exactly balanced and remains so when projected using (26). All of this can be deduced geometrically by careful examination of Figure 2. It should be noted that the differences $(\tilde{R} - R)$ and $(\tilde{M} - M)$ may be small in practice, depending on the population, yielding small differences in growth. In addition, for a distribution that is not in equilibrium and does not exactly follow the negative exponential, either of the two systems may project better than the other.

A conservation law: The fact that equations (26) define the exact movement of trees is no mathematical coincidence. The systems (5) and (8) define a conservation law with source–sink balance in general, not only in the case of constant rates. The PDE (8) gives the differential form of the conservation law, which is at equilibrium when the time differential is zero as previously mentioned; this latter case applies to the exponential distribution. The integral form of the conservation equation with source–sink terms assuming time-invariant vital rates is (LeVeque, 2002, p. 22).

$$\frac{d}{dt} \int_{d_l}^{d_u} n(d, t) dd = - \int_{d_l}^{d_u} \frac{\partial}{\partial d} g(d) n(d, t) dd - \int_{d_l}^{d_u} m(d) n(d, t) dd \quad (27)$$

This equation states that the change in the numbers density between any d.b.h. limits $[d_l, d_u]$ is equal to minus the flux through the endpoints minus the mortality (sink). In Supplementary data section S.3 it is demonstrated that this equation leads directly to the ‘master’ movement equation (22) and provides the link between this and (26) with general growth equation component to the flux, leading to (25) in the special case of constant growth. It is important to understand that the equilibrium system definition given here for the exponential distribution means that individuals are conserved through time because of the source–sink balance (5). This again corresponds to the intrinsic rate of increase being zero as previously noted.

The mortality density

It may seem reasonable to posit the assumption that if the mortality and growth functions are exactly proportional over all diameters, then the result is a negative exponential distribution that can be used to model the tree diameter distribution. In other words, let

$$\psi = \frac{m(d)}{g(d)} \quad d \geq d_0 \quad (28)$$

be the negative exponential rate parameter under this assumption. Then, this result leads immediately to the probability density

$$p(d) = \frac{m(d)}{g(d)} \exp\left(-\frac{m(d)}{g(d)}d\right) \quad (29)$$

which is equivalent to (12) under (28), with a presumed numbers density following from multiplication by N as in (11).

However, it will be demonstrated in what follows that the interpretation of (29) leading to a numbers density is incorrect in general under the assumed dynamics in (8) for two reasons. First, (28) only satisfies (14) in the case where mortality and growth are constant (i.e. $g'(d) = 0$). Second, under the size-structured vital rate dynamics, the density in (29) is a special case of the probability density for mortality under assumption (28). Thus, it would be erroneous to infer a numbers density from this PDF in the sense of (9), again with the exception of the special case of constant vital rates.

Most sources on survival methods derive the mortality density from the survival function in terms of age-structured population models (Keyfitz, 1977, p. 5; Elandt-Johnson and Johnson, 1980, p. 50). However, de Roos (1997, p. 134) has expanded this derivation to size-structured models, with survival $S(d)$, yielding the general form of the probability density for mortality

$$m(d) = \frac{m(d)}{g(d)} \exp\left(-\int_{d_0}^d \frac{m(d')}{g(d')} dd'\right) \quad (30)$$

It is important to note that $m(d)$ is the general form for the mortality density for any growth and mortality function regardless of whether assumption (28) holds or not; i.e. it is not necessary for mortality and growth to be proportional, proportionality is a special case yielding a negative exponential mortality density of the form (29). In other words, (30) applies equally to vital rates that do not give rise to negative exponential distributions; i.e. when (14) does not hold. The mortality density arises from the dynamics for the survival function, $dS(d)/dt$ (e.g. de Roos, 1997, p. 134), while the equilibrium numbers density arises from (8) with time differential zero; the different respective dynamics underlying the two densities reinforces that they can not be equivalent in general. Thus, the vital rate dynamics will not, in general, support (29) as an equilibrium density useful in modeling the diameter distribution. Because of this lack of correspondence at the most basic level, it is straightforward to devise examples with vital rates that follow (28) and produce numbers densities that are

not negative exponential, but whose mortality densities are (Supplementary data section S.4).

The mortality density (30) should be compared with the equilibrium numbers density in (9), where the recruitment scale factor (constant) in the latter has been replaced by the mortality (shaping) function. Integrating (30) gives the probability of a tree dying in, e.g., a given size range as

$$\mathfrak{M}(d_l, d_u) = \int_{d_l}^{d_u} m(d) dd \quad (31)$$

The relation between total mortality, \mathcal{M} , as determined from the numbers density, the density for mortality, (30), and recruitment is given in general as

$$\begin{aligned} \mathcal{M} &= \int_{d_0}^{d_\infty} m(d)n(d) dd \\ &= R \int_{d_0}^{d_\infty} \frac{m(d)}{g(d)} S(d) dd \\ &= R \times \mathfrak{M}(d_0, d_\infty) \\ &= R \end{aligned} \quad (32)$$

where the support for diameter is $d \in [d_0, d_\infty)$, and d_∞ can be finite as will be demonstrated shortly. Once again, there is conservation of individuals through the balance between total mortality and recruitment in this general (not necessarily negative exponential) case.

Application examples

The examples that follow illustrate many of the concepts presented in the previous sections. The equations that have been presented for the discrete version of the PDE and the corresponding matrix formulation discussed later (Supplementary data section S.7) can be shown to be equivalent, and therefore yield the same results when applied to data, either simulated or actual. Therefore, only one set of results encompassing both methods is presented.

Exact exponential

In this section, the results are applied to known exponential distributions in order to explore the estimation of vital rates and application of growth dynamics.

Effects of sample size on estimation of vital rates

First, a set of simulations were designed to demonstrate the convergence of the MLE for mortality under constant rates as sample size, n , increases given the assumption stated earlier that growth rate and population size are assumed known. The results for recruitment will parallel these, since recruitment is estimated as $\hat{R} = \hat{M}N$. Figure 3a presents three different exponential distributions all with the same vital rates with the exception of mortality. As noted earlier, higher mortality naturally leads to a steeper decline in the density, all else being equal. Figure 3b illustrates the convergence of (20) with increasing sample size. Likewise, the relative root mean square error

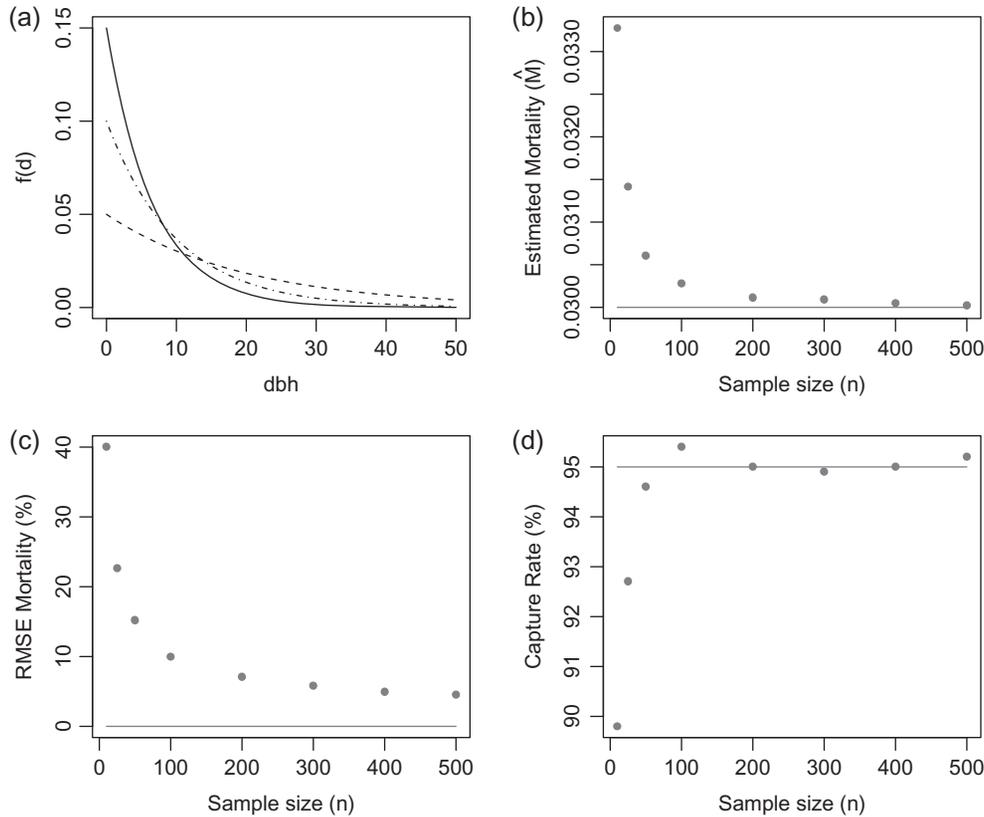


Figure 3 The effect of sample size, n , on the MLE of mortality, \hat{M} with true $M = 0.03$, $G = 0.5$ and $R = 62$ for all panels. Panel (a) illustrates three exponential distributions with $M = 0.03$ (solid), 0.01 (dashed), 0.02 (dot-dashed). Panels (b) and (c) show estimated mortality and relative RMSE, respectively. Lastly, the confidence interval capture rates are shown in (d). Panels (b)–(d) are based on 1000 Monte Carlo draws for each n .

(RMSE % = $\frac{100}{M} \sqrt{\sum_{i=1}^n (\hat{M}_i - M)^2 / n}$), is given in Figure 3c, with a minimum of $\sim 4.5\%$ at $n = 500$. The final panel, Figure 3d, shows the percentage capture rate for confidence intervals around the exponential mean (15). Because the only estimated parameter in the mean is \hat{M} , these results can be applied to mortality. The convergence results for \hat{M} and the confidence interval convergence seem to suggest that a sample size of at least $n = 100$ is necessary to estimate mortality with 95% coverage, while $n = 200$ would be better, and this estimate would have an associated error estimate of $\sim 7\text{--}10\%$ of the true unknown mortality for the tract (Figure 3c). These results are the same for all three exponential distributions depicted, and thus will be consistent for any other (constant) vital rates chosen. However, it should be noted that somewhat different results will occur in repeated simulation runs, and depend on the number of Monte Carlo samples drawn, so these figures should be used simply as rough but reasonable guidelines.

Stand projection comparisons

The exact and approximate dynamics as computed from (26) and (24), respectively, are compared in Table 1. The RMSE for the exact dynamics is zero, while that for the approximate dynamics is 0.3 trees ha^{-1} (for the classes shown). Note the slight underestimation of number of trees in the smallest diameter class under the approximate dynamics. This is attributable to the

amount of recruitment (6), which is exact for exact dynamics, but slightly too small for approximate dynamics, as noted earlier. This slight underestimation affects only the first diameter class, the remaining classes are overestimated due to the extra trees coming into the class (Figure 2) until the difference between the methods becomes very small in the largest classes. This example illustrates the small magnitude of the differences overall between the two approaches. Therefore, if the diameter distribution follows an exact exponential with constant vital rates, either method could be used to project the stand in practical applications.

Virgin hardwoods

Meyer and Stevenson (1943) studied virgin beech–birch–maple–hemlock (northern hardwood) stands in northern Pennsylvania. They presented growth increment data by diameter class for six different tracts ranging in size from ~ 6 to 60 ha. These authors also presented diameter distributions for eight different ‘structural types’, which were not necessarily equivalent with the original six tracts (Meyer and Stevenson, 1943, p. 480). However, as noted by the authors the growth data were only slightly different for the six tracts; therefore, for illustration of the methods, in the following analysis the growth for stands A–F was applied to the average diameter distributions for structural types A–F as if they were indeed from the same areas. Hereafter

the tract-structural type combinations are referred to simply as stands.

The relevant stand attributes and parameter estimates are presented in Table 2. Attributes based on diameters such as average diameter, \bar{D} , and all estimated parameters such as \hat{M} , were calculated by shifting the diameter distribution such that the lower limit of the smallest class aligned to zero. The growth data were digitized from Meyer and Stevenson’s figure 4 and an average diameter growth, \hat{G} , was calculated for both hardwood and hemlock components for each stand in accordance with

Table 1 Number of trees per hectare by 4-cm diameter class for a stand with $q \approx 1.5$, $N = 1240$, $G = 0.5$, $M = 0.05$ and $R = 65$

d.b.h. (cm)	N_t	N_{t+1} exact	N_{t+1} approximate
2	408.80	408.80	407.75
6	274.03	274.03	274.38
10	183.69	183.69	183.92
14	123.13	123.13	123.29
18	82.54	82.54	82.64
22	55.33	55.33	55.40
26	37.09	37.09	37.13
30	24.86	24.86	24.89
34	16.66	16.66	16.68
38	11.17	11.17	11.18
42	7.49	7.49	7.50
46	5.02	5.02	5.03
50	3.36	3.36	3.37
54	2.26	2.26	2.26
58	1.51	1.51	1.51
62	1.01	1.01	1.01

Note: The larger diameter classes totaling three trees are not shown for clarity.

Table 2 Stand parameters and estimated vital statistics for six virgin northern hardwood stands from Meyer and Stevenson (1943) (see Figure 4)^a

Parameters	Stand					
	A	B	C	D	E	F
Area (ha)	10.20	5.83	30.19	17.00	42.90	58.60
N (ha^{-1})	199.17	211.28	220.42	225.36	222.89	208.06
\bar{D} (cm)	14.14	15.28	16.52	17.98	19.59	21.37
\hat{G} (cm yr^{-1})	0.31	0.20	0.27	0.24	0.32	0.22
\hat{M} (yr^{-1})	0.02	0.01	0.02	0.01	0.02	0.01
\hat{R} ($\text{ha}^{-1} \text{yr}^{-1}$)	4.32	2.78	3.54	3.00	3.64	2.19
$\hat{\psi}$ (cm^{-1})	0.07	0.07	0.06	0.06	0.05	0.05
RMSE N^{pdf} (ha^{-1})	0.01	0.01	0.01	0.01	0.02	0.02
RMSE N^{pde} (ha^{-1})	0.01	0.01	0.01	0.01	0.02	0.02

Note: The table entries are rounded, therefore calculating $\hat{R} = N\hat{M}$ from the entries will only approximate the given value (true, also rounded) in each stand.

^aParameters are based on shifted diameters where applicable (see text for details).

the theory presented previously. It should be noted that the growth data for both species components of each stand were essentially constant with minor random fluctuations by diameter class. A weighted mean of the species components of growth was used for the analysis in each stand based on the percentage of hemlock in the structural type (Meyer and Stevenson, 1943, their table 7). The RMSE values presented in Table 2 clearly demonstrate that both the approximate and exact dynamics are able to reproduce the original stand distribution to a degree of accuracy in the hundredths of a tree per hectare. This is corroborated graphically in Figure 4, where the difference between the original stand data and the projected stands is indistinguishable. Note that the negative exponential distribution estimated from the parameters in Table 2 is also presented for reference. Stands A–C are quite close to the theoretical q distribution, while stands D–F are slightly less so. However, since the RMSE’s are of the same magnitude for all stands, it is encouraging that both sets of dynamics are able to project the stand to a reasonable degree of accuracy even when they are not necessarily exponential, but only close. This analysis further demonstrates that the estimation of mortality by the MLE (20), and subsequently recruitment, from empirical average growth rates and diameter distributions is reasonable for stands of the nature described here, and is therefore valid not only for data that conform to an exact exponential distribution as presented in the previous section, but for empirical data that are close to exponential. There are two extra sources of error in this analysis beyond those normally associated with such data (e.g. measurement, sampling): the first is the arbitrary matching of tract growth with structural type distributions, the

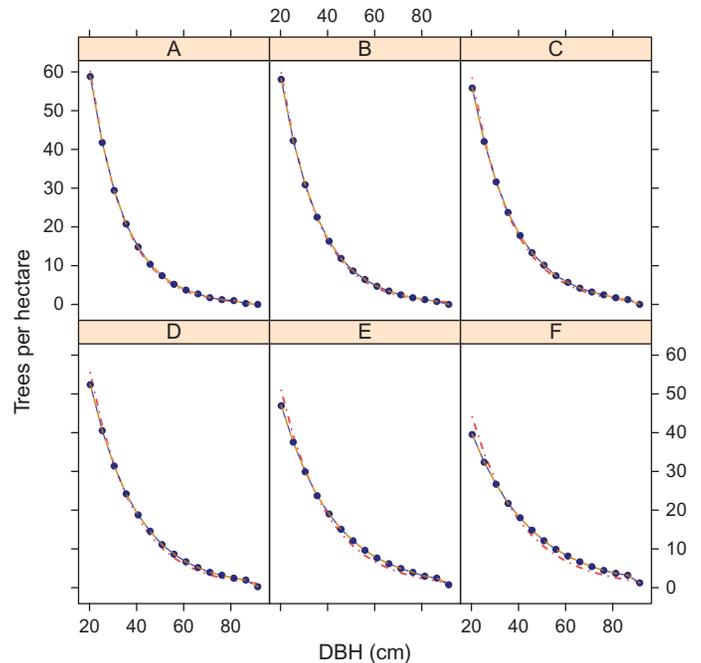


Figure 4 Observed diameter distributions (dots) for six virgin northern hardwood stands from Meyer and Stevenson (1943) with approximate (solid) and exact (dashed) dynamics applied based on the parameters in Table 2. The ML fit to each stand are shown for comparison (dot-dashed).

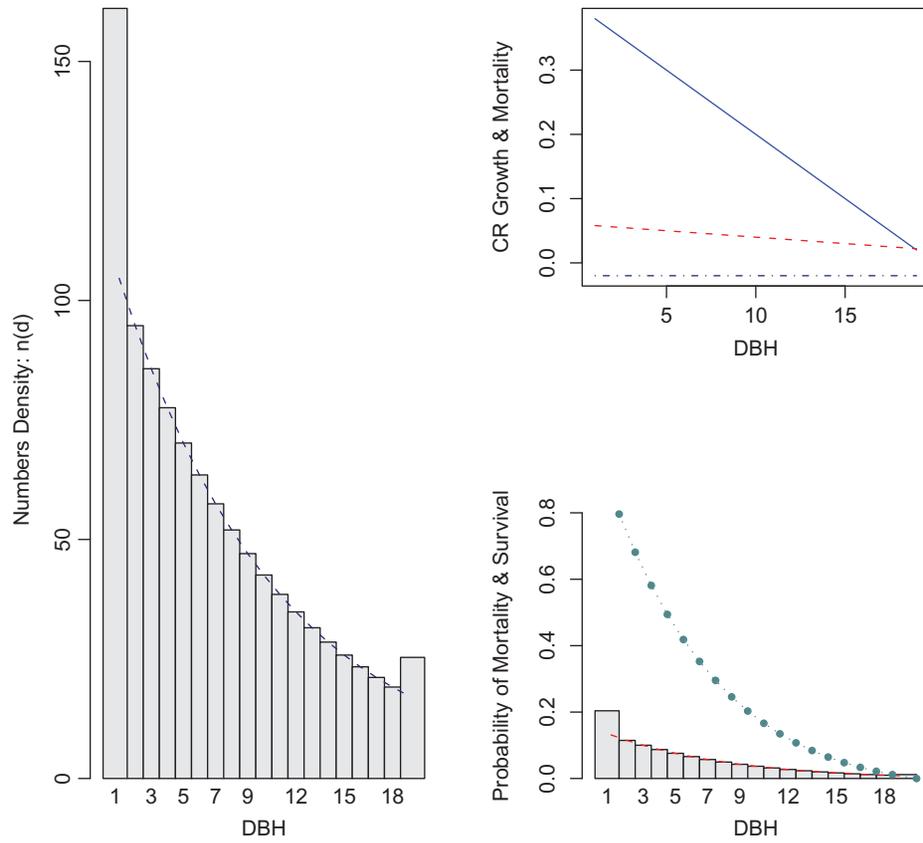


Figure 5 The equilibrium numbers density (left) with $N = 1000$, $R \approx 46.3$, $\psi = 0.1$, $m = 0$, $\gamma = 0.02$, $\eta = 0.4$ and $d_\infty = 20$ under assumption (13) – a truncated negative exponential numbers density; and (top right) the driving CR growth (solid), mortality (dashed) and growth derivative (dot-dashed) functions, with (bottom right) probability of survival (dotted) denoted at the upper limit of each diameter class (solid dots) and probability density for mortality (bar/dashed) (note that the first and last d.b.h. classes carry more density in both histograms because they are wider than the other classes).

second is digitization error associated with the growth trends. The accuracy of the model results, even with these two extra sources of error, hints at a reassuring robustness with respect to the equilibrium modeling approach.

Generalized growth and mortality example

This section presents an example using the general growth and mortality relation (13) where growth follows a Chapman-Richards (CR) model. The CR function for diameter growth is given by (Pienaar and Turnbull, 1973)

$$g(d) = \eta d^m - \gamma d \quad 0 \leq d < d_\infty = \left(\frac{\eta}{\gamma}\right)^{\frac{1}{m-1}} \quad (33)$$

with derivative

$$g'(d) = \eta m d^{m-1} - \gamma \quad (34)$$

where m , η and γ are model parameters to be estimated from the data. The CR model has an asymptotic maximum diameter limit $d_\infty \ll \infty$ given above, which will therefore yield a numbers density in the form of a truncated exponential distribution. It is important to note that not all parameter combinations for (33)

are valid under the constraint (13) because mortality must be positive. Therefore, any parameter combinations that result in $g'(d) > \psi g(d)$ are inadmissible. The class of admissible forms under CR appears quite restricted. Moreover, it is difficult to determine exactly what parameter values will fulfill this constraint for the CR model due to the interaction of the parameters. However, trial and error shows that a decreasing slightly curvilinear or linear function are possible special cases (along with constant rates), where the linear case is demonstrated below.

Figure 5 shows the results of a simple example where mortality is determined by (13) with $\psi = 0.1$. The CR parameters for the example are $m = 0$, $\gamma = 0.02$, $\eta = 0.4$, yielding $d_\infty = 20$ cm. These parameter values result in the following two linear equations for growth and mortality

$$\begin{aligned} g(d) &= \eta - \gamma d = 0.4 - 0.02d \\ m(d) &= \psi \eta + \gamma - \psi \gamma d = 0.06 - 0.002d \end{aligned}$$

The first and last diameter classes shown in both histograms are wider than the nominal $w = 1$ cm width for the other classes, and hence there is more density shown in each of these classes.

Recruitment can not be calculated from relation (6), since mortality is not constant in this example. However, it can be

shown (Supplementary data section S.5) that for any growth and mortality model an analogous result is that

$$R = N\tilde{m} \quad (35)$$

where \tilde{m} is defined as an expected mortality rate in the Supplementary data. In this example, one can verify that $R \approx 46.3$ stems $\text{ha}^{-1}\text{yr}^{-1}$ when the population size is $N = 1000$ stems ha^{-1} .

Discussion

The subject of this paper was introduced with a discussion of the two different, generally accepted concepts of balance in uneven-aged forests or stands, and how the stricter definition of this concept can be interpreted in the more general sense of a stable steady-state structure. The subsequent demographic analysis showed that the negative exponential distribution does indeed fulfill the requisite assumptions for this type of structure. However, the analysis also demonstrates that the exponential distribution is also a strict model in terms of the underlying dynamics: (i) one recruited tree must replace each tree lost to mortality due to the equilibrium assumption, (ii) mortality rate must follow (13), which implies a possible restriction on more flexible growth model forms such as the CR. Now, of course, forest stands are not exactly deterministic systems, so the inputs and outputs may not balance exactly each year, rather on average this needs to be true. Likewise, as we have demonstrated with the virgin northern hardwood data, the diameter growth does not need to be exactly equal among size classes in the constant rate case in order for the theory to work, some reasonable amount of variability is allowed (Meyer and Stevenson's figure 4), but any departure from the mean that does not fulfill the mortality constraint (13), would lead to a non-exponential (though perhaps still reverse J-shaped) structural model based on (9). Indeed, due to the rigidity of the exponential assumptions with regard to vital rates, it is somewhat reassuring that it does indeed seem to apply to actual virgin stands such as those in Meyer and Stevenson (1943). Thus, we have demonstrated that, even with the restrictive assumptions in vital rates, the negative exponential distribution can be a valid model for natural undisturbed stands. In addition, knowing diameter growth with a reasonably large sample of diameters alone on such forests is evidently sufficient information to estimate the remaining vital rates of mortality and recruitment, the latter provided a good estimate of population size, N , is also available.

Managed stands

The negative exponential or q distribution is simply a mathematical model. This model has been used extensively in uneven-aged management, presumably in large part due to its simplicity, and the idea that managed uneven-aged stands should structurally mimic natural undisturbed stands that are found to be in equilibrium. However, Meyer (1952) clearly distinguished two different conceptualizations of 'balanced' uneven-aged stands as discussed earlier. The elucidation of the model in terms of the coupled dynamics and

structural component discussed to this point have been in terms of a stable steady-state distribution where there has been no option for harvest, since the balance is maintained through three components to the flux: inflow from recruitment, outflow from mortality and flow through the size classes due to growth (Figure 1). Intervention into the stand in terms of harvesting is not accommodated in the PDE model presented thus far. If we adopt Meyer's definition of balance for managed stands, then there is nothing more to be done, because one would simply pick a target structure and harvest the growth as previously discussed. This is the pragmatic view of uneven-aged management, but the stand is not balanced in the sense of conservation of individuals and therefore departs from the mathematical ideals of a theoretical conservation equation, unlike the equilibrium setting. Indeed, in the stable-steady state, there are no extra trees to harvest.

It is, however, possible to extend the results presented thus far to incorporate harvest into the model, and this may be of some interest, even if only for pedantic reasons. This can be done in a way that does conform to a stable steady-state balance model. However, as will be demonstrated, to retain the balance the model must be precisely followed (with some leeway for stochasticity as mentioned above) to keep the stand in this equilibrium state. The numbers density model formulation extending the stable equilibrium theory to harvesting is shown below, details for several other components to the overall model are found in Supplementary data section S.6. Again, the following concentrates on the special case of constant vital rates as a tractable example.

In the special case of constant vital rates harvest, $h(d, t)$, is also a constant per capita rate, just like mortality, i.e. $h(d, t) = H$. Adding harvest, the equilibrium numbers density, (9) and (17), becomes

$$n(d) = N \frac{M+H}{G} \exp\left(-\int_{d_0}^d \frac{M+H}{G} dd'\right) \quad (36)$$

$$= N \frac{M+H}{G} \exp\left(-\frac{M+H}{G}d\right) \quad (37)$$

respectively. The integral form in (36) is presented to reinforce that harvest, like mortality, is a component in the survival function. Thus, if it is not constant, then it is diameter-dependent, $h(d)$, and therefore must effectively 'steal' some trees from mortality while both retaining the same form in (13) in order to preserve the negative exponential model.

To further illustrate, take the simplest case where trees less than a prescribed diameter limit are not harvested, while larger trees are. That is, define the indicator function

$$I(d) = \begin{cases} 0 & \text{if } d < d_H \\ 1 & \text{if } d \geq d_H \end{cases} \quad (38)$$

where d_H is the lower diameter limit for harvesting. Then the numbers density (36) can be written as

$$n(d) = N \frac{M + \mathcal{I}(d)H}{G} \exp\left(-\int_{d_0}^d \frac{M + \mathcal{I}(d')H}{G} dd'\right) \quad d > d_0$$

$$= \begin{cases} N \frac{M}{G} \exp\left(-\frac{M}{G}d\right) & \text{if } d < d_H \\ N \frac{M+H}{G} \exp\left(-\frac{M+H}{G}d\right) & \text{if } d \geq d_H \end{cases}$$

This result is simply (17) for unmerchantable trees and (37) for merchantable stems. These are both exponential distributions, but with potentially differing mortality rates (compare (20) and (S.18)) and q values (compare (19) and (S.17)). Of course, growth could also be different between the two components. Thus, the indicator approach is the same as using two different q values, unless M/G for unmerchantable stems happened to equal $(M + H)/G$ for merchantable stems. And if we chose to enlarge on the number of classes to more than two, in the limit the step function goes to a continuous function $h(d)$, in which case the more general approach would apply as mentioned above.

Thus, for a managed stand to conform to the stable steady-state concept of balance, the harvest rate must be of the same form as mortality, effectively taking trees that would otherwise die. Such strict adherence to the exponential in managed forests may be unreasonable in practice as, for example, under constant rates where this demands that all size classes must be cut at exactly the same rate H , even the unmerchantable diameter classes. Therefore, the pragmatic approach as defined by Meyer would appear to be the preferred approach to management. Even though the exponential is just a residual structure rule for cutting in this case, it is still a reasonable and simple target distribution. Used in this context, the negative exponential model may not be optimal; however, there are numerous optimization studies that have demonstrated how vital rates can be linked to an optimal diameter distribution and cutting rule that are available as alternative methods (e.g. Adams and Ek, 1974; Getz and Haight, 1989, Ch. 5; Gove and Ducey, 2014).

Stability

It has been maintained throughout that the equilibrium solution (9) is also a stable distribution. VanSickle (1977a) first presented the asymptotic stability analysis for size-structured populations as an extension of the renewal approach for age-structured populations (e.g. Lotka, 1956, Ch. 9 and Keyfitz, 1977, Ch. 5), where the vital rates were assumed time-invariant. de Roos (1997, p. 155) provides a similar derivation and either source should be consulted for the details. Because the stationarity of (9) couple with the balance of recruitment and mortality (5) guarantees that $r = 0$, the negative exponential distribution is a stable steady-state distribution.

Recently Lopez Torres et al. (2012) presented a matrix analysis that questioned the stability of the exponential distribution. They used a different parameterization of the CR model (33) for growth and assumed constant recruitment and mortality. This model for mortality does not fit the necessary condition given in (13) for the form of the mortality function under CR growth to result in an exponential distribution. Indeed, it can be shown that the equilibrium numbers density solution to (9) with constant

recruitment R , constant mortality M , and CR growth (33) is given as

$$n(d) = \frac{R}{\eta d^m - \gamma d} \left(\frac{d^{m-1} (\eta d_0^{m-1} - \gamma)}{d_0^{m-1} (\eta d_0^{m-1} - \gamma)} \right)^{\frac{M}{\gamma(m-1)}} \quad 0 < d \leq \left(\frac{\gamma}{\eta} \right)^{\frac{1}{m-1}} \quad (39)$$

This density is clearly not negative exponential in form; however, it is reverse J-shaped for certain combinations of parameter values for $g(d)$ in (33) and mortality (however, it can be shown that the negative exponential distribution is a limiting special case of this density). As such, it presents an interesting possible alternative to the negative exponential distribution that allows a flexible model for diameter growth and simple mortality assumption. The equilibrium solution given in (39) is similar to that given by Zavala et al. (2007), who used yet another different parameterization of the CR function for diameter growth. In addition to reverse-J, the range of shapes covered by (39) also include both positively and negatively skewed, uniform, concave, gentle rotated-sigmoid and U-shaped, among others. The latter two forms result in part from a decreasing mortality rate relative to growth, allowing trees to accumulate in the larger diameter classes, a point that was also noted by Zavala et al. (2007). In general, however, the shape of this distribution depends on the interplay between both the shape of the underlying growth curve and the mortality rate, while recruitment acts as a scale factor on the numbers density.

Other models

There are other modeling approaches that can be adopted as methods that couple the individual vital rate dynamics and resulting size-structured numbers density, specifically of negative exponential form. These approaches include, but are not limited to, matrix and diffusion models as discussed below. Optimization models already mentioned provide a numerical approach to the problem.

Matrix models

A matrix approach (Caswell, 2001) can be adopted to model the dynamics under the exponential distribution. It can be shown in general (e.g. Caswell et al., 1997; Caswell, 2001, Ch. 8; Uribe, 1993) that the matrix approach is a discrete time-size analog to the PDE approach presented. Thus, if the model is constructed in a compatible manner, it should yield comparable results. Matrix models are often easier to work with and understand, but they suffer from the potential drawback that one cannot arrive at an actual closed-form algebraic solution to the equilibrium distribution; however, a matrix analysis can be used to show that the numerical solution is of the same character. It should be noted that the PDE approach does not always yield a closed-form solution to the survival integral in $S(d)$, and may also require numerical methods to solve the numbers density; however, the cases where analytical solutions are available are often enlightening. A matrix model for the negative exponential distribution under the special case of constant vital rates is given in Supplementary data section S.7.

Diffusion models

The diffusion approach was evidently first introduced to forestry by Suzuki and Umemura (1974), while Hara (1984) formalized the ideas in a more concrete and understandable manner. The diffusion equation extends (8) by adding a second-order term with $\mathcal{D}(d, t)$ that has the interpretation of the variance in d.b.h. growth (Hara, 1984). The general form of the diffusion equation is given by

$$\frac{\partial n(d, t)}{\partial t} = \frac{1}{2} \frac{\partial^2 [\mathcal{D}(d, t)n(d, t)]}{\partial d^2} - \frac{\partial [g(d, t)n(d, t)]}{\partial d} - m(d, t)n(d, t) \quad (40)$$

where the diffusion term allows for modeling the variability in d.b.h. growth by diameter over time.

As with (8), it is possible to find at least one solution to (40) that is a negative exponential distribution by assuming constant growth, associated variance, and mortality. The details are given in Supplementary data section S.8. The solution given there shows that the exponential rate parameter is of the form

$$\psi_{\mathcal{D}} = \frac{\sqrt{G^2 + 2\mathcal{D}M} - G}{\mathcal{D}}$$

while the MLE for mortality is found to be given by

$$\hat{M}_{\mathcal{D}} = \frac{\mathcal{D} + 2G\bar{D}}{2\bar{D}^2}$$

where setting $\mathcal{D} = 0$ reduces to (20). As noted in Section S.8.1, the variance term should generally play a minor role in the estimation of mortality via ML, since \mathcal{D} will probably be small in comparison to $2G\bar{D}$. A more in-depth analysis of this model and how it compares to the PDE-based results are required to determine the sensitivity of mortality to the variance and is beyond the scope of this paper. However, the example with the Meyer and Stevenson (1943) virgin hardwood data suggests that the addition of a small variance term would not change the MLE for mortality in such a way that it would make any practical improvement on the fit of the numbers distribution for these data. Interested readers should consult Kohyama and Hara (1989) or Takada and Hara (1994) in addition to the above references for forestry applications, and the general reference Okubo and Levin (2001) for more details on diffusion applications in general.

Summary and concluding remarks

This work has demonstrated the link between the structural form of a negative exponential distribution and the generative form of its underlying vital rates leading to a stable steady-state population model. While we have shown that small departures from the assumed vital rates will still produce dynamics equations that closely reproduce the original reverse J-shaped structure, it is also true that too radical a departure in the form of vital rates will lead to other structural models, such as (39). When Meyer's pragmatic balance approach to management is used in uneven-aged stands that depart from

the assumptions of the model, the excess growth resolved into harvest in such stands results from a decoupling of the observed vital rates and the negative exponential. Simply put, stands so managed are not stable (the distribution shape changes), nor are they in equilibrium (enough new trees are added to allow a harvest: $r > 0$), so the vital rates of the stand produce excess growth that can be harvested. This happens because a cutting rule was imposed on the stand that is not in accord with its underlying demographic parameters; hence, the stand is escaping from the overly restrictive exponential form to one that is more natural to its underlying vital rates. Through numerous cutting cycles, the stand so manipulated may indeed become adjusted so that it can be managed as a theoretically balanced system with constant harvest, but it would take careful planning to adjust the vital rates to this model. Where a long-run equilibrium structure is not the goal, the q distribution under the pragmatic approach reduces simply to a convenient marking guide, potentially with little or no biological or economic justification.

For stands that do approximate a q distribution in shape, we have shown that it is a relatively simple matter to solve the inverse problem. With a stand inventory providing a reasonable estimate for the population size, and diameter growth data from increment cores with a sample size of diameters in accordance with Figure 3, mortality and recruitment can be estimated using (20) and (6), respectively, under the constant rates case. In the more general case, the MLE $\hat{\psi} = 1/\bar{D}$ can be used in cooperation with (13) for estimating mortality given an appropriate growth model, while recruitment is then estimated by (35).

The negative exponential distribution and Meyer's pragmatic concept of balance will likely remain a useful approach to management in uneven-aged stands and forests, not the least because of its simple form and ubiquitous current applications. This paper has noted the theoretical shortcomings of such an approach in light of the assumptions necessary for Meyer's stable equilibrium concept of balance in virgin or old-growth stands. While we have carefully demonstrated the theoretical shortcomings of a steady-state interpretation to the q distribution applied to managed stands, the two forest conditions are obviously quite different, and Meyer (1952) was quite justified in expounding his dual definition of balance.

Supplementary data

Supplementary data are available at *Forestry* Online.

Acknowledgements

My thanks to John C. Brissette, André M. de Roos, Mark J. Ducey, William B. Leak, Thomas B. Lynch, Harry T. Valentine and the referees for their helpful comments, suggestions and encouragement on this manuscript, with special thanks to the Editor, Gary Kerr.

Conflict of interest statement

None declared.

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