

# Matrix Model of Forest Dynamics: An Overview and Outlook

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**Abstract:** The Matrix model uses transition matrices to predict future plant and animal population structures. Having been used to study the dynamics of forests all over the world, the Matrix model is thriving in forestry, with applications covering a wide array of areas. Despite its extensive application in forestry, the Matrix model is still suffering from a lack of due attention and appropriate understanding, especially on its advantages and limitations in comparison with those of other forest dynamics models. To facilitate further research and applications, a synthetic review of Matrix models is provided here with an emphasis on its mathematical properties and relationship with other forest dynamics models. In this article, we first introduce the general structure of Matrix models and its representation of forest dynamics components, i.e., upgrowth, mortality, and recruitment. Then, we summarize key properties of Matrix models, including basic assumptions, density dependence, size class width and time step, and the estimation of forest dynamics components will be summarized. Next, we evaluate advantages and limitations of the Matrix model and its relationship with other forest dynamics models. Finally, we share our perspective on the major challenges and future outlooks of Matrix models. *FOR. SCI.* 59(3):359–378.

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IT HAS BEEN SEVEN DECADES since the groundbreaking publications of Lewis (1942) and Leslie (1945), which, together with other pioneering works from a later era (e.g., Usher 1979, 1981), set the foundation for a state-of-the-art model that uses transition or probability matrices to predict future plant and animal population structures. Today, this model is thriving in many disciplines, especially in forestry in which it has been widely used to study the dynamics of almost all the forest types around the world (Table 1). The model is commonly named the transition matrix (hereafter “Matrix”) model, and, sometimes, it is also known as the matrix population model or matrix growth model.

Although it seems a natural application of Matrix models to predict dynamics of species-, age-, stage-, and/or size-structured forest populations, it has taken many dedicated scientists decades to achieve the conceptual soundness, predictive power, and broad applicability of the Matrix models we use today in forestry. Marking a pioneering effort to apply transition matrix models in forestry are the early fixed-parameter models (e.g., Usher 1966, Bosch 1971), in which dynamics are assumed to be independent of stand state. The instrumental study of Buongiorno and Michie (1980) was the first to address the effects of stand state on recruitment, which makes long-term projections more accurate and steady states more reasonable. With the development of numerous subsequent Matrix models (see Stationarity, Geospatial Dependence, and Density Dependence), further types of variability (e.g., spatial, sampling, and environmental variability) have been accounted for to make

Matrix models more accurate and robust for a wider range of applications. With these improvements, Matrix models have become increasingly popular, as shown in the steadily escalating number of publications on Matrix models over time (Figure 1).

In the typology classifying forest dynamics models depending on their level of description of the forest, Matrix models stand between stand models and individual tree models (Munro 1974, Vanclay 1994, Porté and Bartelink 2002). Stand models predict the temporal changes of population-level attributes such as basal area or tree density. Stand models are useful for monospecific even-aged stands, but become inappropriate for mixed or uneven-aged stands because they do not consider within-stand variability in individual size or species. Individual tree models (generally called “individual-based models” in the ecological literature (see Relational Position in Forest Dynamics Models) predict the temporal changes of each individual. Both Matrix models and individual tree models can deal with mixed uneven-aged stands, and the two approaches have developed in parallel (Peng 2000), with the first individual tree models (Stage 1973, Mitchell 1975) appearing shortly after the first Matrix models (Usher 1966, 1969). During the development of individual tree models, a subclassification has been introduced using the type of tree interactions as a classification key, leading to process-based models (often at the subtree level, see Isebrands et al. 1990), gap models (Botkin et al. 1972), tree-level distance-dependent models that use spatially explicit intertree competition metrics, and tree-level distance-independent models that use intertree competition

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**Table 1.** Existing matrix models of forest dynamics by country and forest type.

Continent/country (state/region)	Forest type	Publications
North America		
United States (Alaska)	Alaska boreal forest	Liang (2010, 2012), Liang and Zhou (2010), Liang et al. (2011)
United States (Wisconsin, Michigan)	Broadleaf temperate forest	Bruner and Moser (1973), Buongiorno and Michie (1980), Michie and Buongiorno (1984), Roberts and Hruska (1986), Kaya and Buongiorno (1987), Lu and Buongiorno (1993), Buongiorno et al. (1994), Lin et al. (1996), Lin and Buongiorno (1997), Lin and Buongiorno (1998), Kolbe et al. (1999), Buongiorno and Gilless (2003)
United States (Pennsylvania)	Oak-hickory temperate forest	Michie and McCandless (1986)
United States (Maine)	Northeastern temperate/boreal forest	Solomon et al. (1986)
United States (Georgia)	Longleaf pine temperate forest	Platt et al. (1988)
United States (Southeastern Coastal Plain)	Bottomland hardwood forest	Mengel and Roise (1990), Zhao et al. (2005)
United States (Southern states)	Loblolly and shortleaf pine forest	Lin et al. (1998), Schulte and Buongiorno (2004), Zhou and Buongiorno (2004, 2006)
United States (Oregon and Washington)	Douglas-fir temperate forest	Ralston et al. (2003a), Liang et al. (2005a), Zhou et al. (2008a, 2008b)
United States (Virginia)	Eastern hemlock temperate forest	Lamar and McGraw (2005)
United States (California)	Mixed-conifer and redwood forest	Bosch (1971), Liang et al. (2005b), Van Mantgem and Stephenson (2005)
United States (New York)	Temperate forest	Huenneke and Marks (1987), Sable and Rose (2008)
United States (Florida)	Mixed-hardwood forest	Batista et al. (1998)
Canada	Temperate forest	Bellefleur (1981), Tucker and Anand (2003), Lei et al. (2006), Yang and Kant (2008)
Mexico	Tropical dry and rain forest	Alvarez-Buylla and Slatkin (1991, 1993, 1994), Alvarez-Buylla and García-Barrios (1993), Alvarez-Buylla (1994), Olmsted and Alvarez-Buylla (1995), Alvarez-Buylla et al. (1996), Álvarez Aquino (2006)
South and Central America		
French Guiana	Tropical rain forest	Favrichon (1995, 1996, 1998a, 1998b), Gourlet-Fleury et al. (2005), Delcamp (2007), Picard et al. (2008a)
Bolivia	Tropical rain and dry forest	Sanquetta et al. (1999), Zuidema (2000), Boltz and Carter (2006), Ponce (2006)
Brazil	Tropical and subtropical forest	Higuchi (1987), Azevedo et al. (1994, 1995), Bom (1996), Arce et al. (1997), Pulz (1998), Hoffmann (1999), Pulz et al. (1999), Sanquetta (1999), Sanquetta et al. (1999, 2001), Spathelf and Durlo (2001), Cunha et al. (2002), Koehler (2002), Freckleton et al. (2003, 2006), Mendonça (2003), Austregésilo et al. (2004), Socher (2004), Nappo et al. (2005), Teixeira et al. (2005, 2007), Pereira Da Silva (2007), Stepka (2008), Castro de Barros (2009), Soares et al. (2009), Vasconcelos et al. (2009), Menon et al. (2010), Stepka et al. (2010), Fortini and Zarin (2011)
Panama	Tropical rain forest	Boscolo and Buongiorno (1997), Condit et al. (1998, 2004), Boscolo et al. (2001)
Puerto Rico	Tropical rain forest	Wadsworth (1977)
Argentina	Subtropical humid forest	Teresczuch et al. (2007)
Chile	Temperate and subtropical humid forest	Bustamante et al. (2005), Modrego et al. (2006)
Columbia	Tropical rain forest	González-Pérez (1996), Arango et al. (2010)
Costa Rica	Tropical rain forest	Súarez and Somarriba (2002)
Asia		
China	Mixed-species temperate forest	Hao et al. (2005a, 2005b, 2007), Wang et al. (2005), Qu and Hu (2006), Qu et al. (2007), Ma et al. (2011), Wei et al. (2011)
Japan	Mixed-species temperate forest	Nakashizuka (1991), Sanquetta et al. (1995, 1996)
Indonesia	Tropical rain forest	Mendoza and Setyarsa (1986), Favrichon and Cheol (1998), Sist et al. (2003)
Malaysia	Tropical rain forest	Ingram and Buongiorno (1996), Boscolo and Buongiorno (1997), Boscolo et al. (1997), Boscolo and Vincent (1998), and others
Vietnam	Tropical rain forest	Chien (2006), Zuidema (2006), Zuidema et al. (2010)

**Table 1. (continued).**

Continent/country (state/region)	Forest type	Publications
Europe		
United Kingdom	Mixed-species temperate forest	Usher (1966, 1969), Maillette (1982)
France	Mixed-species temperate forest	Houllier (1986), Houllier and Lebreton (1986), Buongiorno et al. (1995), Rollin et al. (2005), Buongiorno (2007), Denis (2007), Sebert-Cuvillier et al. (2010)
Italy	Mixed-species temperate forest	Volin and Buongiorno (1996), Virgiliotti and Buongiorno (1997)
Spain	Mixed-species temperate forest	Orois and Soalleiro (2002), López Torres et al. (2008a and 2008b)
Norway	Mixed-boreal forest	Bollandsås et al. (2008)
Germany	Mixed-species temperate forest	Benabdellah et al. (2003), and others
Finland	Norway spruce forest	Pukkala and Kolström (1988), Kolström (1993), Tahvonen (2009), Tahvonen et al. (2010)
Russia	Mixed-boreal forest	Logofet and Lesnaya (2000), Korotkov et al. (2001)
Oceania		
Australia	Tropical and subtropical forest	Enright et al. (1995), Enright and Watson (1991), Johnson et al. (1991), Price and Bowman (1994)
Papua New Guinea	Tropical rain forest	Enright and Ogden (1979)
New Zealand	Temperate forest	Enright and Ogden (1979), Mason (2000)
Africa		
Ethiopia	Dry afromontane forest	Bekele (2000), Couralet (2004), Couralet et al. (2005)
Uganda	Tropical dry forest	Namaalwa et al. (2005)
Cameroon	Tropical rain forest	Debroux (1998), Debroux and Delvingt (1999), Eba'a Atiy and Filius (1999), Eba'a Atiy (2000)
West Africa	Tropical rain and dry forest	Gaoue and Ticktin (2010), Gaoue et al. (2011)
Central African Republic	Tropical rain forest	Lahoreau et al. (2002), Picard et al. (2008b)
South Africa	Afromontane forest	Hartshorn (1975), Manders (1987)
Nigeria	Tropical rain forest	Osho (1991, 1996)
General, or with unspecified region and forest type		García Vidal (1974), Usher (1979, 1981), van Hulst (1980), Harrison and Michie (1985), Getz and Haight (1989), Houllier et al. (1989), Silvertown et al. (1993), Batabyal (1996), Turner et al. (1998), Buongiorno (2001), Zetlaoui et al. (2006, 2007, 2008), Shimatani et al. (2007), Logofet (2008), Shimatani et al. (2008), Zhou and Buongiorno (2011)

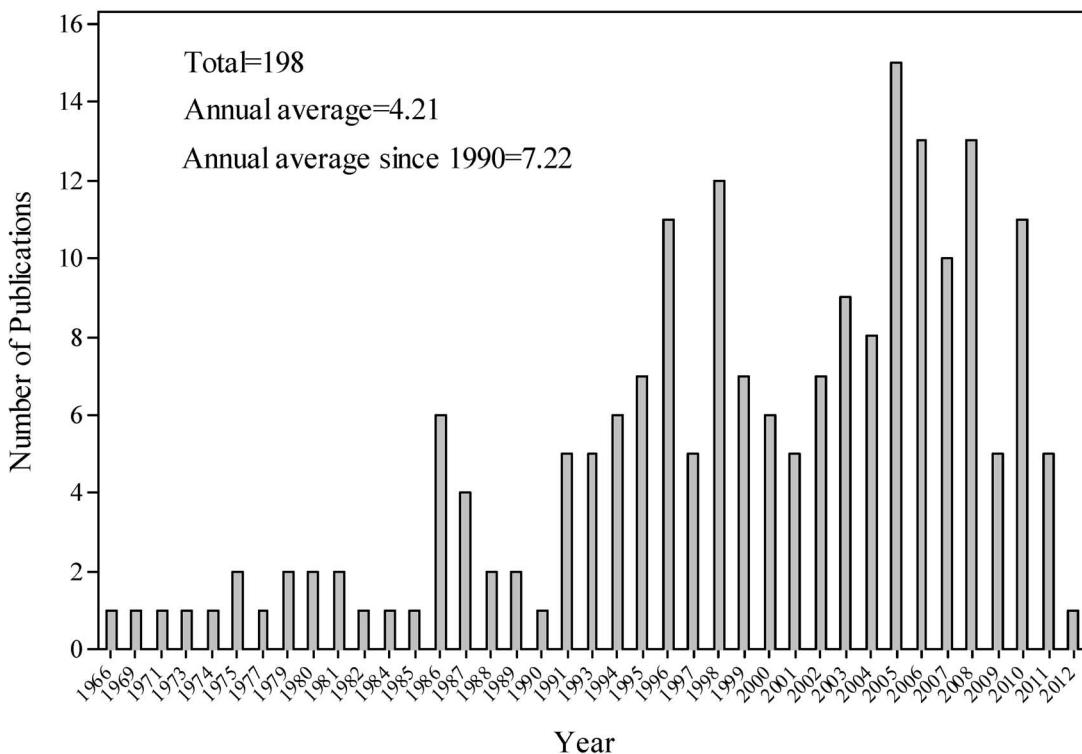
All the literature listed here is (1) published in or before 2012, (2) indexed in Google Scholar or Scopus, (3) is addressing the development and/or applications of one or more matrix models of forest dynamics, and (4) published in English, French, Chinese, Spanish, or Portuguese or with an abstract in English. To minimize repetition, publications that address multiple forest types/countries are arbitrarily categorized in one corresponding forest type/country. This table represents a majority but not the complete body of literature to date.

metrics without intertree distances (Biging and Dobbertin 1992, 1995).

Matrix models have been applied to almost all the subject areas of forestry. In forest ecology, Matrix models have been used to study the demography of natural succession (e.g., Huenneke and Marks 1987, Manders 1987, Alvarez-Buylla 1994, Liang et al. 2005a) and biodiversity dynamics (e.g., Lin et al. 1996, Liang and Zhou 2010) and the impacts of climate changes (Liang et al. 2011), natural disturbances (e.g., Price and Bowman 1994, Hoffmann 1999), and harvest (e.g., Schmidt et al. 2011). In forest management, Matrix models have been applied to evaluate economic outcomes (e.g., Buongiorno and Michie 1980, Ingram and Buongiorno 1996) and ecological impacts (e.g., Zhou et al. 2008a, Liang 2010) of various management regimes, including the impact on the habitat of endangered wildlife species (e.g., Zhou et al. 2008a, 2008b). Several Matrix model-based simulators (Schulte et al. 1998, Ralston et al. 2003b, Liang et al. 2004a, 2004b, 2006b) have been developed to facilitate forest management in the United States.<sup>1</sup> Most recently, Matrix models have been developed for

large-scale mapping of timber and biomass resources assuming constant climate (Liang and Zhou 2010, Liang 2012) and under climate change scenarios (Liang et al. 2011).

It has been brought to our attention that despite its extensive application in forestry (Table 1; Figure 1), the Matrix model is still suffering from a lack of due attention and appropriate understanding, especially regarding its advantages and limitations in comparison with other forest dynamics models. To facilitate further research and applications, in this article we aim to provide a review of the Matrix model with an emphasis on its mathematical properties and relationship with other forest dynamics models. This article is structured as follows: first, we introduce the general structure of the Matrix model and its representation of forest dynamics components, i.e., upgrowth, mortality, and recruitment. In the second section, key properties of the Matrix model, including basic assumptions, density dependence, size class width and time step, and the estimation of forest dynamics components will be summarized. Then, we evaluate advantages and limitations of the Matrix model and



**Figure 1.** Number of publications on forest matrix models through time (see Table 1). In total, 198 publications on forest matrix models were reviewed (for a total of 342 reviewed articles, the other articles dealing with nonmatrix forest models or with matrix models for plant or animal populations).

its relationship with other forest dynamics models. Finally, we share our perspective on the major challenges and future outlooks of the Matrix model.

## Model Structure

Classified into  $n$  size classes, forest populations are often structured by individual size, dbh, although other individual characteristics such as crown area have occasionally been considered (Lamar and McGraw 2005). Conventional Matrix models (e.g., Buongiorno and Michie 1980) estimate stand diameter distribution at time  $t + 1$  based on that at time  $t$  represented by a  $mn \times 1$  column vector  $\mathbf{y}_t = [\mathbf{y}_{1t}, \dots, \mathbf{y}_{mt}]'$ , where  $\mathbf{y}_{it} = [y_{ijt}]$  is a  $n \times 1$  column vector of the diameter distribution of species  $i$  and  $y_{ijt}$  is the number of live individuals per unit of land area of species  $i$  ( $i = 1, 2, \dots, m$ , where  $m$  is the number of species) and diameter class  $j$  ( $j = 1, 2, \dots, n$ )

$$\mathbf{y}_{t+1} = \mathbf{G}_t(\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R}_t \quad (1)$$

where  $\mathbf{h}_t = [h_{ijt}]$  is a  $mn \times 1$  column vector representing the harvest per unit of land area and  $\mathbf{h}_t = 0$  if there is no harvest at time  $t$ .

The growth matrix  $\mathbf{G}_t$  describes how the individuals grow or die between  $t$  and  $t + 1$ .  $\mathbf{R}_t$  is a recruitment  $mn \times 1$  column vector representing the number of individuals naturally recruited in the smallest diameter class of each species between  $t$  and  $t + 1$ . An artificial regeneration extension (Liang 2010) enables prediction of stand diameter distribution under artificial regeneration

$$\mathbf{y}_{t+1} = \mathbf{G}_t(\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R}_t + \mathbf{A}_t \quad (2)$$

The  $mn \times mn$  growth matrix  $\mathbf{G}_t$  in conventional Matrix models (Equation 1) is defined as an  $m \times m$  block-diagonal matrix with  $n \times n$  matrices  $\mathbf{G}_{it}$  on its main diagonal

$$\mathbf{G}_t = \begin{bmatrix} \mathbf{G}_{1t} & & & 0 \\ & \mathbf{G}_{2t} & & \\ & & \ddots & \\ 0 & & & \mathbf{G}_{mt} \end{bmatrix},$$

$$\mathbf{G}_{it} = \begin{bmatrix} a_{11t} & & & & 0 \\ b_{11t} & a_{21t} & & & \\ & \ddots & \ddots & & \\ & & b_{i,n-2,t} & a_{i,n-1,t} & \\ 0 & & & b_{i,n-1,t} & a_{int} \end{bmatrix} \quad (3)$$

where  $a_{ijt}$  is the stasis rate representing the probability that an individual of species  $i$  and diameter class  $j$  stays alive in the same diameter class between  $t$  and  $t + 1$ .  $b_{ijt}$  is the upgrowth transition rate representing the probability that an individual of species  $i$  and diameter class  $j$  stays alive and moves up to class  $j + 1$  between  $t$  and  $t + 1$ .  $b_{int} = 0$  for the largest diameter class. The column sums of  $\mathbf{G}_{it}$  give the survival rates, or

$$a_{ijt} + b_{ijt} = 1 - m_{ijt} \quad (j = 1, \dots, n) \quad (4)$$

where  $m_{ijt}$  is the mortality rate representing the probability that an individual of species  $i$  and diameter class  $j$  died between  $t$  and  $t + 1$ . Individuals that survived cumulate those that stayed in the same class (stasis) and those that moved up to the next class (growth); hence, the left-hand side term in Equation 4.

In addition to Equation 1, other parameterizations of

Matrix models can be found (e.g., Alvarez-Buylla 1994, Hoffmann 1999, Caswell et al. 2004). The most commonly used one is

$$\mathbf{G}_{it} = \mathbf{S}_{it} \cdot \mathbf{P}_{it} \quad (5)$$

where  $\mathbf{S}_{it}$  is the  $n \times n$  diagonal matrix of survival rates for species  $i$  between  $t$  and  $t + 1$

$$\mathbf{S}_{it} = \begin{bmatrix} 1 - m_{i1t} & & & 0 \\ & 1 - m_{i2t} & & \\ & & \ddots & \\ 0 & & & 1 - m_{int} \end{bmatrix} \quad (6)$$

and  $\mathbf{P}_{it}$  is the  $n \times n$  stochastic matrix of conditional upgrowth rates for species  $i$  between  $t$  and  $t + 1$

$$\mathbf{P}_{it} = \begin{bmatrix} 1 - p_{i1t} & & & 0 \\ p_{i1t} & 1 - p_{i2t} & & \\ & \ddots & \ddots & \\ & & p_{i,n-2,t} & 1 - p_{i,n-1,t} \\ 0 & & & p_{i,n-1,t} & 1 \end{bmatrix} \quad (7)$$

Comparing Equations 4 and 7 shows that

$$p_{ijt} = \frac{b_{ijt}}{1 - m_{ijt}} \quad (j = 1, \dots, n) \quad (8)$$

$p_{ijt}$  can be interpreted as the conditional probability that an individual of species  $i$  and diameter class  $j$  moves up to class  $j + 1$  between  $t$  and  $t + 1$ , knowing that it stays alive.  $p_{int} = 0$  for the largest diameter class.

In some other studies (e.g., Usher 1979, Logofet and Lesnaya 2000, Korotkov et al. 2001, Benabdellah et al. 2003), Markovian matrices of transition probabilities are developed instead of the growth matrices (Equation 3) or conditional upgrowth matrices (Equation 7).

## Model Properties

### Basic Assumptions

Matrix models are primarily based on four assumptions: Markov property, Usher property, stationarity, and geospatial independence.

### Markov Property

Matrix models result from the aggregation at the population level of individual trajectories. The transition rates in  $\mathbf{G}$  represent individual stochastic transitions that correspond to a Markov chain. The states of the Markov chain are the  $n$  diameter classes, plus death as an absorbing state. The transitions of the Markov chain are

$$\begin{aligned} \Pr(x_{ijt} \rightarrow x_{ijt+1}) &= a_{ijt} \quad (j = 1, \dots, n) \\ \Pr(x_{ijt} \rightarrow x_{i,j+1,t+1}) &= b_{ijt} \quad (j = 1, \dots, n - 1) \\ \Pr(x_{ijt} \rightarrow \dagger) &= m_{ijt} = 1 - a_{ijt} - b_{ijt} \\ \Pr(x_{ijt} \rightarrow x_{ikt+1}) &= 0 \quad (k \neq j, j + 1) \\ \Pr(\dagger \rightarrow \dagger) &= 1 \end{aligned} \quad (9)$$

where  $x_{ijt} \rightarrow x_{ikt+1}$  is the event that a tree of species  $i$  and diameter class  $j$  moves to class  $k$  between  $t$  and  $t + 1$ , and  $\dagger$  denotes the death state. Given  $Y_{ijt}$  trees of species  $i$  in diameter class  $j$  at time  $t$ , where  $Y_{ijt} \in \mathbb{N}$  is an integer, and given that these trees independently follow the Markov chain, the number  $F_{i,j \rightarrow j,t}$  of trees of species  $i$  that stay alive in class  $j$ , the number  $F_{i,j \rightarrow j+1,t}$  of trees of species  $i$  that stay alive and grow up from class  $j$  to  $j + 1$ , and the number  $F_{i,j \rightarrow \dagger,t}$  of trees of species  $i$  and class  $j$  that die between  $t$  and  $t + 1$  are jointly distributed according to a multinomial distribution with parameters of the transition rates.

Most existing Matrix models are developed based on the first-order Markov assumption: the temporal evolution of an individual between  $t$  and  $t + 1$  only depends on its state at time  $t$  and is independent of the states that preceded it. The Markov assumption has been much discussed in the context of vegetation succession (e.g., Horn 1975, van Hulst 1980, Childress et al. 1998, Logofet and Lesnaya 2000, Korotkov et al. 2001, Benabdellah et al. 2003), and formal tests of the Markov assumption in matrix projection models have been proposed (Johnson et al. 1991, Picard et al. 2003a).

Second-order matrix models can be defined, such that the current transition rates depend both on the current state of an individual and on its previous transition (Picard et al. 2003a). Although this relaxes the Markov assumption, the gain in predictive performance of the model is often negligible (Picard et al. 2003a). Therefore, a first-order Markov model, although not exact, is a reasonable approximation to predict stand dynamics (Van Mantgem and Stephenson 2005).

### Usher Property

According to the Usher assumption, between  $t$  and  $t + 1$ , an individual can either stay alive in the same class, stay alive and move up to the next class, or die; it cannot move up by more than one class or move backwards, i.e., the individual is free from diameter shrinkage. The Usher assumption ensures that the transition matrix  $\mathbf{G}_{it}$  has null entries everywhere except on its diagonal and subdiagonal. It corresponds to the fourth equality in Equation 9. Relaxing the Usher assumption is straightforward: allowing transitions from class  $j$  to class  $k$  (with  $k$  potentially different from  $j$  and  $j + 1$ ) will simply result in a non-null entry at the  $k$ th row and  $j$ th column of  $\mathbf{G}_{it}$ . In a general transition matrix, in which any transition between two classes is possible (Lefkovitch 1965), the number of parameters to estimate substantially increases. Matrix models most often comply with the Usher assumption to limit the number of parameters to estimate from data. An exception is Lamar and McGraw (2005), who used crown size classes with crown measurement by remote sensing, because of the uncertainty on crown measurements that brought many transitions between non-neighboring crown classes. However, consideration of shrinkage can be interesting in ecology to investigate size plasticity and demographic trade-offs (Salguero-Gómez and Casper 2010). By choosing an appropriate class width, the Usher assumption can often be verified with diameter classes of equal width.

## Stationarity

In the assumption of stationarity, transition matrices should be independent of time, other things being equal. A typical case of stationarity is constant transition rates for any point in time. Despite being a realistic assumption for short-term projections, this is not an acceptable assumption for long-term projections, in which transition rates are likely to change in response to environmental change, such as global climate change, for instance.

Most existing Matrix models assume constant environmental conditions; i.e., there are no natural disturbances, such as wildland fires, earthquakes, storm blowdown, and insects and diseases, and climate conditions remain constant. With the known effects of natural disturbances on forest growth (e.g., Turner et al. 1998) and the recent finding that global climate change may be affecting forests around the world (e.g., Serreze et al. 2000), this assumption is becoming impractical, especially for long-term projections. Two approaches used to address the variability in environmental conditions, stochastic elements and climate-sensitive models, will be discussed below.

**Natural Disturbances.**—Techniques of deterministic matrix models have been extended to environmental stochastic matrix models to account for natural disturbances. For instance, sensitivity and elasticity analyses (de Kroon et al. 1986, van Groenendaal et al. 1988, Caswell 2001) have been extended to the stochastic case (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, 1989, 1990). The life table response experiment (Caswell 2001) has also been extended to the stochastic case (Caswell 2010, Davison et al. 2010).

Three types of stochastic elements have been used to account for environmental variability (Fieberg and Ellner 2001, Kaye and Pyke 2003, Ramula and Lehtilä 2005): matrix resampling, parametric matrix distribution, and stochastic shocks.

Matrix resampling consists of randomly drawing  $\mathbf{G}$  and  $\mathbf{R}$  uniformly in a set  $((\mathbf{g}_1, \mathbf{r}_1), (\mathbf{g}_2, \mathbf{r}_2), \dots, (\mathbf{g}_E, \mathbf{r}_E))$  of  $E$  fixed transition matrices and recruitment vectors that correspond to  $E \in \mathbb{N}$  environments. The advantage of this method is that correlations between transition rates are preserved. The limitation is that  $E$  transition matrices have to be estimated in  $E$  environments, which may require many data because the environmental variability will be better described as  $E$  increases.

Parametric matrix distribution consists of assigning parametric distributions that reflect environmental variability to the transition rates (e.g., Dagleish et al. 2010). Hence, there are some hyperparameters, collectively denoted as  $\varphi$ , such that  $(\mathbf{G}, \mathbf{R})$  is randomly drawn according to  $\Lambda(\varphi)$ , where  $\Lambda$  is a given parametric distribution. It is often more convenient to use this approach in a Bayesian context, especially if there are several nested levels of environmental variations.

Stochastic shocks consist of adding a random noise to Equation 1

$$\mathbf{y}_{t+1} = \mathbf{G}(\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R} + \boldsymbol{\varepsilon}(t) \quad (10)$$

where the random  $m \times n$  vector  $\boldsymbol{\varepsilon}(t)$  represents natural disturbances and is often obtained by sampling randomly from a normal distribution of mean zero and the same

variance-covariance matrices as those of the observed shocks (Zhou and Buongiorno 2004).  $\boldsymbol{\varepsilon}(t)$  can be a white noise, which means that  $\text{Cov}[\boldsymbol{\varepsilon}(t), \boldsymbol{\varepsilon}(t')] = 0$  for  $t \neq t'$  if environmental variations are not correlated (e.g., Zhou and Buongiorno 2004, Rollin et al. 2005) or it can be a colored noise, which means that  $\text{Cov}[\boldsymbol{\varepsilon}(t), \boldsymbol{\varepsilon}(t')] \neq 0$  if environmental variations are correlated (e.g., Jiang and Shao 2004). The treatment of stochastic shocks is a key issue to address in stochastic Matrix models because natural disturbances are a pervasive and critical element of forest management and can drastically alter model projections (Zhou and Buongiorno 2004, 2006).

**Climate Change.**—Global climate change, strengthened by human-induced greenhouse gas emissions (Intergovernmental Panel on Climate Change 2007), is probably affecting forests around the world (e.g., Serreze et al. 2000). To address this change in climatic conditions, climate-sensitive Matrix models have been developed by accounting for the representative climate variables, such as temperature and precipitation, in upgrowth transition rates  $b_{ij}$ , mortality  $m_{ij}$ , and recruitment  $R_i$ . For instance, Liang et al. (2011) have calibrated a climate-sensitive matrix model for Alaska boreal forest, in which both the transition matrix and recruitment vector are functions of mean summer temperature ( $T$ ) and annual precipitation ( $P$ )

$$\mathbf{y}_{t+1} = \mathbf{G}(T_t, P_t) \cdot (\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R}(T_t, P_t) \quad (11)$$

The 100-year simulation of this model has revealed distinctive climate effects on forest dynamics, which cannot be detected with any conventional climate-insensitive Matrix models. The model is also capable of showing a significant difference in future forest states under various general circulation model climate change scenarios, which makes it a powerful tool to study forest dynamics and management under a changing climate.

## Geospatial Dependence

Most existing Matrix models assume that data are independent from the geographic locations and free of spatial autocorrelation. Recent studies (Legendre 1993) found that geospatial autocorrelation, a general property of most ecological attributes due to physical or community processes (Legendre 1993), is a key issue to address, especially in large-scale Matrix models (see Liang and Zhou 2010, p. 2351). When not accounted for, spatial autocorrelation may affect the statistical properties of model predictions because of its violation of the assumption of independence of most standard statistical procedures (Legendre 1993).

Spatial autocorrelation has been classified into “true” and “false” gradients (Legendre et al. 1990). Representing a spatial trend across the region is a “true” gradient, global trend, whereas a “false” gradient, autocorrelation represents a phenomenon in which observations at neighboring points are correlated with one another (Legendre et al. 1990). Different approaches have been used to address these two distinctive gradients. The true gradient has been accounted for mainly through trend surface (e.g., Gittins 1968, Kuuluvainen and Sprugel 1996) or controlled trend surface models (Liang and Zhou 2010). The false gradient has often

been addressed with geostatistical interpolation models, autoregressive models, and geographically weighted regression models (cf. Miller et al. 2007). Previous ecological models are mostly focused on either a true or false gradient, and little has been studied to simultaneously account for both gradients in a single model (Liang 2012).

Addressing geospatial variability often requires a spatially explicit geospatial matrix model (e.g., Liang 2010, Liang et al. 2011), in which Equation 1 is extended to recognize geospatial autocorrelation:

$$\mathbf{Y}_{t+1}(\mathbf{s}) = \mathbf{G}(\mathbf{s})\mathbf{Y}_t(\mathbf{s}) + \mathbf{R}(\mathbf{s}) + \boldsymbol{\varepsilon}, \quad \mathbf{s} = (\mathbf{x}, \mathbf{y})' \in \Delta \subset P^2 \quad (12)$$

where  $\mathbf{Y}_t(\mathbf{s}) = [y_{ijt}(\mathbf{s})]$  is a space-dependent column vector representing the number of live individuals per unit of land area of species  $i$  ( $i = 1, \dots, m$ ) and diameter class  $j$  ( $j = 1, \dots, n$ ) at location  $\mathbf{s}$  and at time  $t$ .  $\boldsymbol{\varepsilon}$  is a zero-mean, stationary process with known covariogram.  $\mathbf{x}$  and  $\mathbf{y}$  represent the plot coordinates within the region of interest  $\Delta$  of the plane ( $P^2$ ) (Liang 2012).

This type of geospatial matrix model mainly accounts for the spatial structure of the environment. However, it is also possible with geospatial matrix models to account for demographic spatial effects such as dispersal and migration (Neubert and Caswell 2000, Lutscher and Lewis 2003, Garnier and Lecomte 2006).

## Model Estimation

Transition rates of the matrix  $\mathbf{G}_t$ , which are empirically estimated from observed data, are not known with certainty. The estimates of transition rates come with an estimation error that reflects both the amount and variability of the data. The estimation error of the transition rates propagates through the model, so that any prediction of the model has also an associated prediction error (Daley 1979, Rago and Dorazio 1984, Meyer et al. 1986, Devenish Nelson et al. 2010). This variability in model predictions is called sampling variability. Alvarez-Buylla and Slatkin (1991) and Picard et al. (2009) have reviewed three methods for computing sampling uncertainty on matrix model predictions: the analytic method, the Monte Carlo method, and resampling methods.

Sampling variability raises a related question: what is the best estimator of transition rates that brings the lowest error? Many estimators of the transition rates for matrix models have been defined and studied since the seminal review by Michie and Buongiorno (1984). We do not intend here to give an exhaustive review of all estimators for transition rates but shall rather present a general classification of upgrowth, mortality, and recruitment estimators.

## Upgrowth and Mortality

**Proportion Estimator.**—Given a data set of  $N$  observations, where an observation consists of the classes of an individual at times  $t$  and  $t + 1$ , the proportion estimator  $\hat{b}_{ij}$ ,  $\hat{m}_{ij}$ , and  $\hat{a}_{ij}$  simply estimates the transition rates as the proportions of individuals in the total population  $y_{ij}$  that

stayed in the same class ( $F_{ij \rightarrow j}$ ), moved up to the next class ( $F_{ij \rightarrow j+1}$ ), or died ( $F_{ij \rightarrow \dagger}$ ), as defined in Equation 9

$$\hat{b}_{ij} = \frac{F_{ij \rightarrow j+1}}{y_{ij}}, \quad \hat{m}_{ij} = \frac{F_{ij \rightarrow \dagger}}{y_{ij}}, \quad \hat{a}_{ij} = \frac{F_{ij \rightarrow j}}{y_{ij}} = 1 - \hat{b}_{ij} - \hat{m}_{ij} \quad (13)$$

This estimator corresponds to the maximum likelihood estimator of the Markov chain defined by Equation 9 (Anderson and Goodman 1957, Zetlaoui et al. 2006).

**Increment Estimator.**—The proportion estimator uses discrete information, such as whether the individuals stayed alive, stayed in the same class, or moved up to the next class. When an observation consists of the diameters of an individual at time  $t$  and  $t + 1$ , which makes continuous information on diameter increment available, the proportional estimator corresponds to a loss of information (Picard et al. 2007). When the data set includes diameter measurements at  $t$  and  $t + 1$ , the upgrowth transition rates may rather be estimated as

$$\hat{b}_{ij} = \frac{\Delta D_{ij}}{\delta_j} \quad (14)$$

where  $\delta_j$  is the width of diameter class  $j$ , and  $\Delta D_{ij}$  is the average diameter increment between  $t$  and  $t + 1$  of species  $i$  in diameter class  $j$  (e.g., Buongiorno et al. 1995, Liang et al. 2005a, Namaalwa et al. 2005). The expression of  $\Delta D_{ij}$  depends on the growth curve for species  $i$  through Equation 14 on the regression  $\phi_i = E(\Delta D_i | D_i)$  of diameter increments with respect to diameter for species  $i$ . Depending on  $\phi_i$ , different types of increment estimators will be obtained (Picard et al. 2008b). In particular, if  $\phi_i$  is a step function whose breakpoints are the bounds of the diameter classes, and  $\bar{\Delta D}_{ij}$  is the empirical mean of diameter increments of individuals of species  $i$  in class  $j$ , then the resulting increment estimator is

$$\hat{b}_{ij} = \frac{\bar{\Delta D}_{ij}}{\delta_j} \quad (15)$$

**Indirect Estimators.**—The proportion estimator and the increment estimator are direct, in the sense that they estimate the transition rates from directly observed transitions or diameter growth. Indirect estimators use predicted quantities of Matrix models to infer transition rates. The most commonly found indirect estimator uses the relationship between transition rates and the stationary diameter distribution,  $y_{i\infty}$ , of species  $i$  (Michie and Buongiorno 1984, Houllier and Lebreton 1986):

$$\begin{cases} b_{i,n-1} = & m_{in} \frac{y_{in\infty}}{y_{i,n-1,\infty}} \\ b_{i,n-2} = (m_{i,n-1} + b_{i,n-1}) \frac{y_{i,n-1,\infty}}{y_{i,n-2,\infty}} & \dots \\ \dots & \dots \\ b_{i1} = & (m_{i2} + b_{i2}) \frac{y_{i2\infty}}{y_{i1\infty}} \\ R_i = & (m_{i1} + b_{i1}) y_{i1\infty} \end{cases} \quad (16)$$

Hence, if the observed diameter distribution of species  $i$  is taken as its stationary diameter distribution, and given estimated mortality rates, estimators of the upgrowth transition rates and of the recruitment rate are obtained by plugging these estimates into Equation 16.

Alternatively, if the observed diameter distribution of species  $i$  is taken as its stationary diameter distribution, and given estimated upgrowth transition rates, an estimator of mortality rates can be obtained. In particular, if the observed diameter distribution conforms to an exponential distribution with parameter  $\mu$  and if all classes have the same width  $\delta = u_{j+1} - u_j$ ,

$$\frac{y_{ij\infty}}{y_{i,j-1,\infty}} = \exp(-\mu\delta) \quad (17)$$

This type of indirect estimator has occasionally been used in Matrix models (Houde and Ledoux 1995, Ingram and Buongiorno 1996, Lahoreau et al. 2002).

**Choosing the Best Estimator.**—Indirect estimators rely on the assumption that the observed diameter distribution is a stationary distribution. This strong assumption may lead to overfitting. Indirect estimators should thus be avoided, unless data are too scarce for other estimators to produce reliable predictions (Ingram and Buongiorno 1996).

The proportion estimator is unbiased (Picard et al. 2007). Moreover, because it is the maximum likelihood estimator of the Markov chain (Equation 9), it is the estimator with the lowest asymptotic variance when only discrete information on transitions is available. However, when continuous information on diameter growth is available, the proportion estimator is no longer the maximum likelihood estimator. Its asymptotic variance in that case is actually elevated compared with that of other estimators (Picard et al. 2007, 2008b).

The increment estimator, despite being potentially biased depending on sample distribution, has a low asymptotic variance compared with that of the proportion estimator (Picard et al. 2007, 2008b). Hence, in terms of quadratic error, the proportion estimator should be preferred when sample size  $N$  is high, whereas the increment estimator should be preferred when sample size  $N$  is low. The threshold sample size where the proportion estimator becomes superior to the increment estimator is often elevated (Picard et al. 2008b), so that in most situations the increment estimator should be preferable.

Estimators may also be assessed on the basis of their robustness, i.e., sensitivity to outliers or abnormal data (Hampel 1974, Hampel et al. 1986, Logofet 2008). The proportion estimator is more robust than the increment estimator, which also provides guidance to deal with data that violate the Usher assumption (Zetlaoui et al. 2007). Previous studies have also addressed the estimation of transition rates from marginal counts of individuals  $\mathbf{y}_t, \mathbf{y}_{t+1}$  (Aragon 1972), the maximum likelihood estimator when a temporal sequence of observations is available (Denis 2007), changing the time step of the matrix model (Harrison and Michie 1985), or changing the dimensionality of the matrix (Hooley 1990).

## Recruitment

Recruitment, as a major forest growth component, has important implications for the properties of Matrix models. We now focus on the mathematical properties of two major distinctive approaches to estimate recruitment.

**Recruitment Proportional to Stem Density.**—For Matrix models with a proportional recruitment model (e.g., Manders 1987, Orois and Soalleiro 2002), there is an  $nm \times nm$  matrix  $\mathbf{F}$  such that

$$\mathbf{R}_t = \mathbf{F}_t(\mathbf{y}_t - \mathbf{h}_t) \quad (18)$$

where

$$\mathbf{F}_t = \begin{bmatrix} \mathbf{F}_{1t} & & & 0 \\ & \mathbf{F}_{2t} & & \\ & & \ddots & \\ 0 & & & \mathbf{F}_{mt} \end{bmatrix}, \quad \mathbf{F}_{it} = \begin{bmatrix} f_{i1t} & \cdots & f_{int} \\ 0 & \cdots & 0 \\ \vdots & & \vdots \\ 0 & \cdots & 0 \end{bmatrix} \quad (19)$$

$f_{ijt}$  is the fecundity rate representing the number of offspring entering the first diameter class produced between  $t$  and  $t + 1$  by an individual of species  $i$  and diameter class  $j$ . Plugging Equation 18 into Equation 1 gives

$$\mathbf{y}_{t+1} = \mathbf{U}_t(\mathbf{y}_t - \mathbf{h}_t) \quad (20)$$

where  $\mathbf{U}_t = \mathbf{G}_t + \mathbf{F}_t$  is an  $nm \times nm$  block-diagonal Usher projection matrix, in which each block is an  $n \times n$  projection matrix similar to  $\mathbf{G}_{it}$ , except that its first row now contains the fecundities  $f_{i1t}, \dots, f_{int}$ , with the first entry being  $a_{i1t} + f_{i1t}$ .

Because it is often not possible to know the size of the individual that gave birth to a newly recruited individual (unless genetic markers are used to identify its parents), most often a mean fecundity  $f$  is estimated as the ratio of the number of newly recruited individuals between  $t$  and  $t + 1$  over the number of live individuals at time  $t$ . Logofet (2008) proposed an indirect estimator of the  $f_{ij}$  in this case: given the estimate of the mean fecundity  $f$ , the ratios  $f_{ij}/f$  are obtained by maximizing with respect to the dominant eigenvalue of the transition matrix. This relies on the assumption that the distribution of fecundities across size classes maximizes the fitness of the species.

The mathematical behavior of Equation 20 has been thoroughly described by Caswell (2001) in the common case of time-independent transition rates (then  $\mathbf{U}_t$  does not depend on  $t$  and the subscript can be dropped). In particular, when there is no harvest ( $\mathbf{h}_t \equiv 0$ ), the asymptotic behavior of the forest stand is determined by the eigenvalues and eigenvectors of  $\mathbf{U}$ . The dominant eigenvalue of  $\mathbf{U}$  is denoted  $\lambda$  and represents the asymptotic population growth rate. If  $\lambda > 1$ , the population grows to infinity; if  $\lambda < 1$ , the population declines to zero; and if  $\lambda = 1$ , the population converges to an equilibrium. The asymptotic diameter distribution is defined by the eigenvector of  $\mathbf{U}$  associated to  $\lambda$ .

In some Matrix models (e.g., Buongiorno and Michie 1980, Liang et al. 2005a, 2011), recruitment has also been estimated as functions of stand basal area and site attributes such as productivity and climate conditions. For these extended proportional recruitment models, convergence of population, despite being a much more complicated issue,

serves a good indicator of model robustness and soundness of long-term projections.

**Recruitment Independent of Stem Density.**—For Matrix models with a recruitment independent of stem density (e.g., Usher 1969, Osho 1991), a common case being when recruitment is constant, the mathematical behavior of Matrix models (Equation 1) is then much simpler than Equation 20. When there is no harvest ( $\mathbf{h}_t \equiv 0$ ) and when transition rates are time-independent, the diameter distribution converges toward the equilibrium distribution defined by

$$\mathbf{y}_\infty = (\mathbf{I} - \mathbf{G})^{-1} \mathbf{R} \quad (21)$$

where  $\mathbf{I}$  is the  $nm \times nm$  identity matrix and the  $t$  subscript of  $\mathbf{R}$  has been dropped to underline that the recruitment is constant. Thus, a constant recruitment without harvest ensures a steady state equivalent to the ecological climax state.

Because constant and proportional recruitment approaches imply different asymptotic behavior of the Matrix model, the type of recruitment modeling has to be chosen carefully, especially if long-term predictions are to be made. Proportional recruitment implies that all offspring are produced in proportion to the modeled population; recruitment is null when  $\mathbf{y}_t \equiv 0$ , which corresponds to an isolated population without any external inflow of seeds. Constant recruitment, on the other hand, implies that recruitment is not null even when there is no population, which corresponds to a subpopulation within a larger population with external inflow of seeds.

Any combination of proportional and constant recruitment can also be used. For instance,

$$\mathbf{R}_t = \mathbf{F}_t(\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R}_0 \quad (22)$$

where  $\mathbf{R}_0$  is constant, and  $\mathbf{R}_t$  is a mixture of a proportional part and a constant part. This is often used with density-dependent matrix models (e.g., Maillette 1982, Huenneke and Marks 1987). In ecology, this is also often used to model metapopulation dynamics (e.g., Artzy-Randrup and Stone 2010), where the proportional part corresponds to population self-recruitment and the constant part corresponds to migration fluxes between populations.

### Density Dependence

Early Matrix models were based on the assumption that the temporal evolution of an individual tree is independent from that of the other individuals. However, trees compete for resources in intertree and tree-plant competition, so that the growth of an individual depends on its neighborhood. Density-dependent matrix models (e.g., Buongiorno and Michie 1980, Picard and Franc 2001, Zhao et al. 2005), in which the transition rates are dependent on the diameter distribution of the forest stand, have been developed to overcome this limitation and are now commonly used.

For a density-dependent matrix model, the transition matrix  $\mathbf{G}$  and the recruitment vector  $\mathbf{R}$  depend on the diameter distribution  $\mathbf{y}_t$ ,

$$\mathbf{y}_{t+1} = \mathbf{G}(\mathbf{y}_t) \cdot (\mathbf{y}_t - \mathbf{h}_t) + \mathbf{R}(\mathbf{y}_t) \quad (23)$$

The resulting model is nonlinear and can theoretically exhibit all kinds of dynamic behaviors, including equilibrium,

cycles, pseudocycles, and chaos (Caswell 2001, Caswell and Takada 2004, Zetlaoui et al. 2008). However, realistic parameter values most often (if not always) lead to an equilibrium in the stationary state (Buongiorno and Michie 1980, Houllier et al. 1989, Favrichon 1998b).

Density dependence is mostly modeled through classic distance-independent competition indices such as total stand density or stand basal area (Biring and Dobbertin 1992). With density-dependent matrix models, the transition probabilities of individuals are linked. However, conditionally on the forest stand at time  $t$ , the transition of individuals is independent of each other. Hence, density dependence consists of conditional independence.

### Class Width and Time Step

Two different approaches have been designed to address the question of matrix dimensionality and class width. The first approach (Vandermeer 1978, Moloney 1986) considers that diameters are sampled from a continuous size distribution. Discretizing the size in classes increases a prediction bias but reduces the sampling variability. Hence, a tradeoff between bias and variance is sought for the optimal class width. This algorithm was discovered to be flawed, and a corrected version has been proposed (Picard et al. 2010a).

The second approach (Shimatani et al. 2007, 2008) consists of using a very fine division into size classes and then penalizing the standard likelihood of observations with a term that accounts for the smoothness of estimates. With this approach, the concern of choosing class width is translated into the concern of choosing an appropriate smoothing parameter for the very thin class estimates.

Although the question of discretization has mainly focused on the width of size classes, it cannot be disconnected from the choice of time step. It has long been known that too long time steps can bring biased estimates of recruitment and mortality rates (Sheil et al. 1995, Sheil and May 1996, Kubo et al. 2000, Lewis et al. 2004) and the convergence of the matrix model toward partial differential equations requires that both the class width and the time step simultaneously tend to zero (Henson 1998, Picard et al. 2010c). If the time interval is too large with respect to the class width, the Usher assumption may be violated so that transitions across distant classes occur.

No efficient algorithm for optimizing the time step for the matrix model has been designed yet. Use of integral projection models to solve the question of class width, as has sometimes been proposed (Easterling et al. 2000, Ellner and Rees 2006, Zuidema et al. 2010), does not address the question of the time step. If discretization is really an issue, then a full continuous approach such as partial differential equations could be more useful for now. For empirical Matrix models, the best time step should be consistent with the interval between remeasurements, and it needs to be recognized that any other time steps will be an approximation subject to additional errors.

### Relational Position in Forest Dynamics Models

In Matrix models, both size and time are often discrete. When time is discrete but size is continuous, an integral

projection model is more appropriate; when time is continuous, a partial differential equation is more appropriate if size is continuous and a continuous-time Markov chain is more appropriate if size is discrete (Table 2). Apart from population dynamics models, a connection with individual-based models can also be established (Picard et al. 2002, Pfister and Stevens 2003, Sable and Rose 2008). Understanding the connections between the Matrix model and other closely related models will help model selection for future applications and also justify the selection of some transition estimators (see Model Estimation). We now explore these relationships and discuss the advantages and limitations of Matrix models in comparison with other forest dynamics models. The continuous-time Markov chain models, having rarely been used in forestry except, e.g., by Batabyal (1996), will not be discussed here.

### *Relationship with Partial Differential Equations*

The equivalent of the vector  $\mathbf{y}_{it}$  when both size and time are continuous is a  $\mathbb{R}^2$ -valued function  $f_i$  such that  $f_i(x, t) dx dt$  gives the number of individuals of species  $i$  per unit of land area with a diameter equal to  $x \pm dx/2$  at time  $t \in \mathbb{R}$ .  $f_i$  thus is the (continuous) diameter distribution for species  $i$ . For simplicity, let us focus on a given species and drop the  $i$  index. The temporal evolution of  $f$  is most often described by a Liouville partial differential equation with a sink term

$$\frac{\partial f}{\partial t}(x, t) = -\frac{\partial}{\partial x}[b(x)f(x, t)] - m(x)f(x, t) \quad (24)$$

with boundary condition  $b(x_0)f(x_0, t) = r(t)$ , where  $x_0$  is the minimum diameter of an inventory,  $b$  is the diameter growth rate,  $m$  is the mortality rate, and  $r$  is the recruitment rate. This type of model for size-structured populations has been extensively used in forestry (e.g., Hara 1988, Kohyama 1989, 1991, 1993, Hara and Yokozawa 1994, Kohyama et al. 2001, Bacaér et al. 2005, Hritonenko et al. 2008). A second-order diffusion term is sometimes added to the right-hand side of Equation 24, making it a Fokker-Planck equation to account for the variability of growth (e.g., Suzuki and Umemura 1974, Hara and Wyszomirski 1994).

The relationship between the matrix model and partial differential equations has long been investigated (Goodman 1967, Keyfitz 1967, García Vidal 1974.). First, it can be shown that, as the class width and the time step jointly tend to zero while population size approaches infinity, an Usher matrix model converges toward a partial differential equation (Equation 24). This has been first demonstrated for the Leslie matrix model for age-structured populations that

converge toward a McKendrick partial differential equation (Cushing 1998, Henson 1998) and extended to the Usher matrix model for size-structured populations (Uribe 1993).

Second, schemes to solve Equation 24 numerically can lead to an Usher matrix model. Numerical schemes to solve partial differential equations are based on a discretization of size and time (see Press et al. 1992, chap. 19). Let  $\tau$  be an infinitesimal time step, and let  $\delta$  be an infinitesimal size step. Let  $x_j = x_0 + j\delta$  and  $t_k = k\tau$  for every integer  $j$  and  $k$ . Finally, let  $b_j = b(x_j)$ ,  $m_j = m(x_j)$ , and  $f_{jk} = f(x_j, t_k)$  be the discretized values for  $b$ ,  $m$ , and  $f$ , respectively. An explicit scheme to solve Equation 24 numerically using forward Euler differencing (Press et al. 1992) is

$$\frac{f_{j,k+1} - f_{jk}}{\tau} = -\frac{c_j f_{jk} - c_{j-1} f_{j-1,k}}{\delta} - m_j f_{jk} \quad (25)$$

If we denote  $\mathbf{f}_k$  as the vector whose  $j$ th element is  $f_{jk}$ , then this numerical scheme can be synthesized as  $\mathbf{f}_{k+1} = \mathbf{G}\mathbf{f}_k$ , where  $\mathbf{G}$  is an Usher transition matrix of which the  $j$ th element on the main diagonal (with  $i > 1$ ) is  $1 - c_j\tau/\delta - m_j\tau$ , and the  $j$ th element on the subdiagonal is  $c_j\tau/\delta$  (Picard et al. 2010c). Hence, a matrix model can be seen as a discretization of a partial differential equation.

### *Relationship with Integral Projection Models*

Like partial differential equations, integral projection models are based on a continuous size distribution  $f_{it}(x)$ , such that  $f_{it}(x) dx$  gives the number of individuals of species  $i$  per unit of land area with a diameter equal to  $x \pm dx/2$  at time  $t \in \mathbb{N}$ . Notice that time is now discrete and indexed by an integer. Let us focus on a given species and drop the  $i$  index. The temporal evolution of  $f_t$  is given by

$$f_{t+1}(x) = \int_0^\infty P(x, y) f_t(y) dy \quad (26)$$

where  $P$  is a transition kernel such that  $P(x, y)$  gives the probability that an individual with diameter  $y$  at time  $t$  has diameter  $x$  at time  $t + 1$ .  $P$  can be seen as the continuous version of the transition matrix  $\mathbf{G}$ .

Integral projection models have raised interest quite recently and are becoming increasingly used (Easterling et al. 2000, Ellner and Rees 2006, Metcalf et al. 2009, Ramula et al. 2009, Salguero-Gómez and de Kroon 2010, Salguero-Gómez and Plotkin 2010, Zuidema et al. 2010). They are supposed to solve one issue with matrix models: model predictions are sensitive to the number and width of diameter classes (see Class Width and Time Step).

### *Relationship with Individual-Based Models*

Although individual-based models predict each individual as a unique entity, whereas Matrix models simulate the temporal changes of forest population, both models are fundamentally the same in the way that forest dynamics are simulated on the basis of recruitment, upgrowth, and mortality from extensive and detailed analysis of individual data. In the limit where the number of individuals goes to infinity, a space-independent individual-based model with

**Table 2.** Typology of population dynamics models for size-structured populations depending on the time and size representations.

Size	Time	
	Continuous	Discrete
Continuous	Partial differential equation	Integral projection model
Discrete	Continuous-time Markov chain	Matrix model

growth rate  $b$  and mortality rate  $m$  is equivalent to the partial differential equation (Equation 24) (Picard and Franc 2001, Verzelen et al. 2006). The partial differential equation is itself the continuous limit of the matrix model; thus, individual-based models and the matrix model are also equivalent under some limit.

This equivalence paves the way for connecting individual growth rates to probabilities of transition between classes. Assuming constant diameter increment and uniform diameter distribution in class  $j$ , we have (Picard et al. 2007)

$$b_j = \frac{\Delta D}{\delta_j} \quad (27)$$

where  $\delta_j$  is the width of the diameter class  $j$ ,  $\Delta D$  is the diameter increment, and  $b_j$  is the transition rate from class  $j$  to  $j + 1$ . This expression relates the individual increment  $\Delta D$  to the upgrowth transition rate and is the basis of transition rate estimators of recent Matrix models (e.g., Namaalwa et al. 2005, Liang 2010). Because  $b_j$  represents a probability, it must be lower than 1 and hence  $\Delta D \leq \delta_j$ . The computation of  $\Delta D$  using an individual-based growth model has been specified by Rogers-Bennett and Rogers (2006).

Predictions of Matrix models depend on the number and width of the diameter classes (e.g., Hooley 1990, López Torres et al. 2008a, Silvertown et al. 1993, Zuidema et al. 2010). Although this dependence disappears in the limit where matrix models converge to the continuous case, the class width and the time step of the matrix models have to be carefully chosen.

### **Advantages and Limitations**

Because the matrix model, partial differential equations, integral projection models, and space-independent individual-based models are equivalent to some extent, the best model for an application should be the one that is the most consistent with modeling purposes while making the fewest assumptions according to the law of parsimony (Occam's razor). With growth considered as a continuous process, which may actually be questioned when one is focusing on very short intervals (Guédon et al. 2007), the continuous approaches such as partial differential equations and integral projection models may seem preferable. The discretization of these models introduces a bias in predictions. However, this discretization also better accounts for prediction variance. To make a parallel with the estimation of (continuous) distribution density, one may think about the difference between the histogram and a continuous density estimator. Although many methods are now available to estimate continuous densities, such as variable bandwidth kernels or all kinds of wavelet thresholding, the histogram is still a popular method, and, for irregularly shaped distributions, the histogram can often be more accurate. All continuous smoothing techniques generally end up with the same general shape of the estimated distribution density, with differences only in details, depending on the amount of available data. The details that vary are related to the sampling error and are not meaningful. The aim of the histogram, similar to that of the matrix model, is to keep

only the meaningful features of the distribution in a discrete way.

The connection between individual-based models and the Matrix model as defined by Equation 27 enables one to fit indifferently an individual-based growth model or an Matrix model. This will be particularly useful to model the growth response to environmental conditions (see Stationarity) and for parameter estimation but most often a choice will have to be ultimately made between these two modeling approaches. Individual-based models have the advantage of mimicking reality in an intuitive and tangible way, because individuals are handled, and the interactions between them can be modeled in a way that reflects their perceivable interactions in the field (Huston et al. 1988, Grimm and Railsback 2005). Individual-based models also have the advantage of explicitly accounting for the spatial location of individuals. They can thus integrate spatial heterogeneity in a simple and intuitive way (DeAngelis and Rose 1992). However, individual-based models require handling of a much larger amount of information than Matrix models (Grimm 1999). The risk to be overcome by the amount of simulated data, with a model complexity that approaches the complexity of the real world, is much more elevated with individual-based models than with Matrix models (Van Nes and Scheffer 2005). When such is the case, especially for large-scale studies, understanding the behavior of the individual-based model becomes impossible, and even intensive simulations cannot bring insight into all possible outcomes.

Although conceptually more complex than individual-based models, Matrix models are actually simpler from a computational and analytical point of view. Because most forest studies focus on the dynamics of a forest rather than on the growth of an individual tree, individual-based models in most applications are actually assessed and validated at the population level, just like Matrix models. When the two approaches make predictions of similar quality, Occam's razor favors parsimonious Matrix models (Gourlet-Fleury et al. 2005, Kokkila et al. 2006, Sable and Rose 2008).

To choose an appropriate model, a distinction has to be made between the target population for which the dynamics are to be predicted and the sample population used to calibrate a model. These two populations can be unnecessarily confounded. When the predicted population has few individuals, demographic random fluctuations are likely to play an important role in the population dynamics (see Tuljapurkar et al. 2009). Then models that are able to project individual trajectories, such as individual-based models, are preferable. When the predicted population has many individuals, individual trajectories are not meaningful and modeling the size distribution at the population level is the main matter. In this case, matrix models are much more useful.

### **Challenges and Outlook**

In this section, we summarize the major challenges Matrix models are facing in terms of model development and application. We also give an outlook on some of the ways to address these challenges so future Matrix models could be

more useful especially in dealing with contemporary issues in forestry.

As a major challenge for the development of Matrix models and other forest dynamics models in general, the difficulty of estimating recruitment and mortality has been documented in many studies (e.g., Buongiorno and Michie 1980, Liang et al. 2005a, Picard et al. 2008a). Compared with transition rates between different diameter classes, recruitment and mortality are often main sources of error in empirical forest growth models, primarily because of the nature of recruitment and mortality data. The numbers of recruitments and dead cannot be negative; therefore, recruitment and mortality data are always truncated at zero. Non-linear functions have been fitted to abnormally distributed recruitment and mortality data (e.g., Ralston et al. 2003a, Liang et al. 2005a), but the poor goodness of fit suggests that a large proportion of variation in recruitment and mortality still remains unaddressed. Because of the importance of recruitment and mortality in shaping forest dynamics, it is recommended that future efforts to improve Matrix models be focused on the estimation of recruitment and mortality.

It is also a challenging task in the development of Matrix models to justify the classification of species groups. Despite being a commonly adopted solution to investigate species-rich forests, use of species groups instead of species in Matrix models introduces a bias in the predictions (Picard et al. 2003b, 2010b). Species groups can be defined independently for Matrix models, using an *a priori* classification based on any relevant specific traits (Favrichon 1998b, Liang et al. 2005a). However, a more relevant approach consisting of simultaneously defining species groups and fitting the Matrix model (Picard et al. 2010b) can be achieved using a finite mixture of Matrix models (McLachlan and Peel 2000). It is, however, even more difficult to define species groups for species-rich forests in such a way that species diversity information could be preserved. The distribution of species abundance in tropical rain forests is often unbalanced, with few abundant species and many rare species. Fitting a transition matrix  $G_i$  for each species may unmindfully inflate the variance of predictions or is even impossible for the rarest species. This issue is not specific to Matrix models but is common to all models of forest dynamics (Gourlet-Fleury et al. 2005).

Yet another challenge is to develop Matrix models in a Bayesian context. Bayesian statistics are useful to deal with environmental variations. A Bayesian matrix model can break down a problem into hierarchical components and is suitable for incorporating *a priori* biological knowledge. Bayesian matrix models have largely been developed in animal ecology (e.g., Gross et al. 2002) but are still lacking due attention in forestry.

A major contemporary issue and one of the greatest challenges in forest management is optimization while simultaneously accounting for an array of risk in natural disturbances, catastrophic events, timber and biomass prices, and interest rates. In the section Stationarity, we reviewed how Matrix models could be developed to address natural disturbances and catastrophic events. To optimize for management objectives with economic components, risk in timber and biomass prices and interest rates also needs to

be taken into account (e.g., Zhou and Buongiorno 2011), but the high level of complexity imposed by multiple stochastic factors renders direct optimization almost impossible. Therefore, the dynamics of forest growth, timber and biomass prices, and interest rates have to be simplified to their essentials. To this end, a response surface model (Liang et al. 2006a) and Markov decision process (MDP) models (Buongiorno 2001) have been developed for optimization under multiple risk. Supported by a large number of studies (e.g., Kaya and Buongiorno 1987, Getz and Haight 1989, Lin and Buongiorno 1998, Hao et al. 2005a, Zhou and Buongiorno 2006, Buongiorno 2007, Zhou et al. 2008b, Tahvonen 2009, Tahvonen et al. 2010, Zhou and Buongiorno 2011), Matrix models provide a very useful forest dynamics basis for the development of MDP models because Matrix models project structured populations, making it more convenient to estimate transition probabilities between forest states in MDP models.

Quickly adapting to emerging topics of forest sciences, the Matrix model has shown great potential to support forest dynamics mapping and carbon management. With the recent developments in geographical information systems (GISs) and computer technology, digital maps of forest resources are emerging as a useful research and management tool. Conventional forest dynamics models predict future forest stand states on an individual basis (Monserud 2003), whereas digital maps of forest dynamics integrate future stand-state estimates throughout the region into GIS layers, so that forest dynamics and carbon offset values could be instantly georeferenced for research and management purposes. Pioneered by the studies of Liang and Zhou (2010) and Liang (2012) and powered by an increasing demand from academia and industry, the application of Matrix models in mapping the dynamics of forest resources is of great potential.

As an international effort to reduce greenhouse gases emissions, Cap and Trade programs have been ratified in conjunction with the Kyoto Protocol. With these programs being established worldwide (Stavins 2001), managing forests as carbon reservoirs is becoming a plausible and potentially profitable option (Marland 1988, Freedman and Keith 1996). The Matrix model, because of its accuracy, simplicity, and quick adaptation to new forestry applications, could be useful to project carbon credits or sequestration.

Last, but not least, we wish to echo Occam's razor in the development and applications of future Matrix models. To maintain their usefulness to end users, there must be a continuous to push for simplicity in model development and easy access in model application with auxiliary tools such as computer simulation programs (e.g., Schulte et al. 1998, Liang et al. 2006b). After all, it is the end users, not the modelers themselves, who will determine the value of a model.

### ***Endnote***

1. The simulators are available online at [fwe.wisc.edu/facstaff/Buongiorno/](http://fwe.wisc.edu/facstaff/Buongiorno/).

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