

# 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
<b>North America</b>		
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 Gilles (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)
<b>South and Central America</b>		
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	Teresczczuch 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	Suárez and Somarriba (2002)
<b>Asia</b>		
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 Setyarso (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), Virgilietti 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 afro-montane 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 Atyi and Filius (1999), Eba'a Atyi (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)

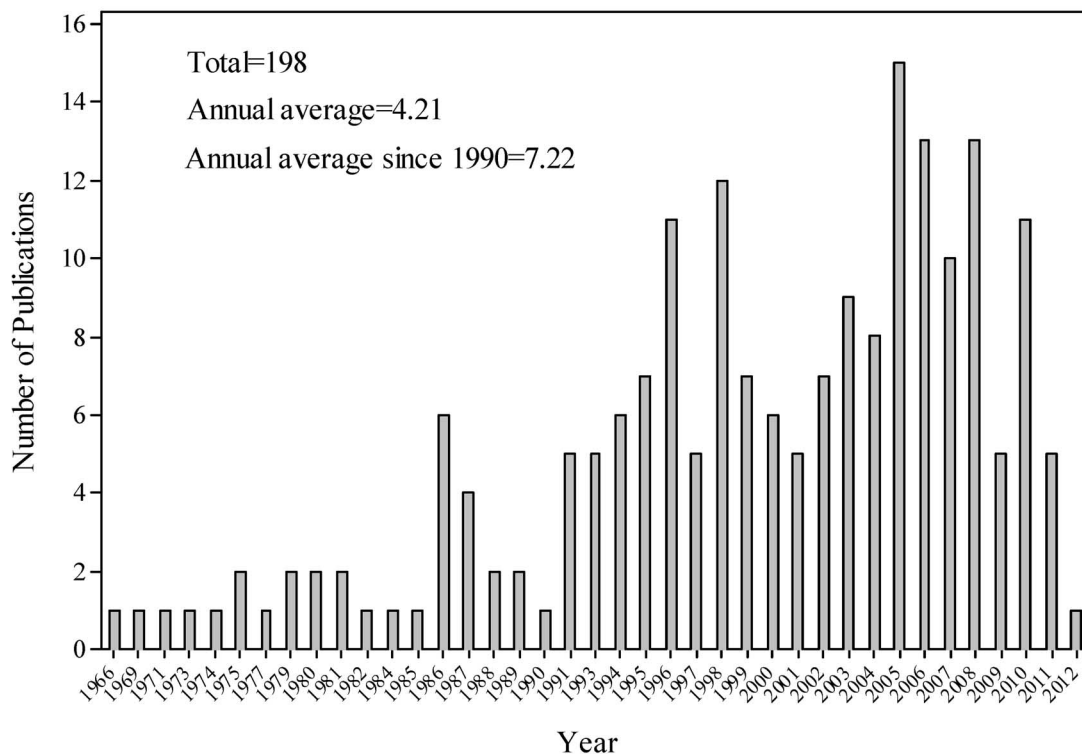
All the literature listed here is (1) published in or before 2012, (2) indexed in Google Scholar or Scopus, (3) is addressing the development and/or applications of one or more matrix models of forest dynamics, and (4) published in English, French, Chinese, Spanish, or Portuguese or with an abstract 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

$$\mathbf{G}_t = \begin{bmatrix} \mathbf{G}_{1t} & & & 0 \\ & \mathbf{G}_{2t} & & \\ & & \ddots & \\ 0 & & & \mathbf{G}_{mt} \end{bmatrix}, \quad \mathbf{G}_{it} = \begin{bmatrix} a_{i1t} & & & & 0 \\ b_{i1t} & a_{i2t} & & & \\ & \ddots & \ddots & & \\ & & b_{i,n-2,t} & a_{i,n-1,t} & \\ 0 & & & b_{i,n-1,t} & a_{int} \end{bmatrix} \quad (3)$$

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  $t + 1$

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

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

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

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 (Tuljapourkar and Orzack 1980, Tuljapourkar 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., Dalglish et al. 2010). Hence, there are some hyperparameters, collectively denoted as  $\boldsymbol{\varphi}$ , such that  $(\mathbf{G}, \mathbf{R})$  is randomly drawn according to  $\Lambda(\boldsymbol{\varphi})$ , 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:

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

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  $t$ .  $\varepsilon$  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  $\overline{\Delta D}_{ij}$  is the empirical mean of diameter increments of individuals of species  $i$  in class  $j$ , then the resulting increment estimator is

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

**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):

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

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  $\bar{f}$  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  $\bar{f}$ , the ratios  $f_{ij}/\bar{f}$  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 (Biging 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  $\mathbf{y}_i$  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, Bacaër 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  $j > 1$ ) 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 unthinkingly 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/).

## Literature Cited

- ÁLVAREZ AQUINO, C. 2006. Simulación experimental del impacto de la tala selectiva en la viabilidad de población de dos especies nativas de bosque mesófilo de montaña. *For. Veracruz* 8(2): 39–46.
- ALVAREZ-BUYLLA, E.R. 1994. Density dependence and patch dynamics in tropical rain forests: Matrix models and applications to a tree species. *Am. Nat.* 143:155–191.
- ALVAREZ-BUYLLA, E.R., AND R. GARCÍA-BARRIOS. 1993. Models of patch dynamics in tropical forests. *Trends Ecol. Evol.* 8(6):201–204.
- ALVAREZ-BUYLLA, E.R., R. GARCIA-BARRIOS, C. LARA-MORENO, AND M. MARTINEZ-RAMOS. 1996. Demographic and genetic models in conservation biology: Applications and perspectives for tropical rain forest tree species. *Annu. Rev. Ecol. Syst.* 27:387–421.
- ALVAREZ-BUYLLA, E.R., AND M. SLATKIN. 1991. Finding confidence limits on population growth rates. *Trends Ecol. Evol.* 6(7):221–224.
- ALVAREZ-BUYLLA, E.R., AND M. SLATKIN. 1993. Finding confidence limits on population growth rates: Monte Carlo test of a simple analytic method. *Oikos* 68(2):273–282.
- ALVAREZ-BUYLLA, E.R., AND M. SLATKIN. 1994. Finding confidence limits on population growth rates: Three real examples revised. *Ecology* 75(1):255–260.
- ANDERSON, T.W., AND L.A. GOODMAN. 1957. Statistical interference about Markov chain. *Ann. Math. Stat.* 28(1):89–110.
- ARAGON, Y. 1972. Sur l'estimation des probabilités de transition d'une chaîne de Markov à partir des données marginales. *Rev. Stat. Appl.* 20(2):79–94.
- ARANGO, D.A., Á.J. DUQUE, AND E. MUÑOZ. 2010. Dinámica poblacional de la palma Euterpe oleracea (Arecaceae) en bosques inundables del Chocó, Pacífico colombiano. *Rev. Biol. Trop.* 58(1):465–481.
- ARCE, J.E., W. PIZATTO, C.R. SANQUETTA, J.L.G. WENDLING, AND R. MAESTRI. 1997. Utilização das matrizes de transição na avaliação e simulação precoces do crescimento de povoamentos de *Pinus taeda* L. *Floresta* 27(1):83–98.
- ARTZY-RANDRUP, Y., AND L. STONE. 2010. Connectivity, cycles, and persistence thresholds in metapopulation networks. *PLoS Comp. Biol.* 6(8):e1000876.
- AUSTREGÉSILO, S.L., R.L. CARACIOLO FERREIRA, J.A. ALEIXO D. SILVA, A. LOPES D. SOUZA, I.M.J. MEUNIER, AND E. DE SOUZA SANTOS. 2004. Comparação de métodos de prognose da estrutura diamétrica de uma floresta estacional semidecidual secundária. *Árvore* 28(2):227–232.
- AZEVEDO, C.P., A.L. SOUZA, J.C. CHAGAS CAMPOS, AND G.G. PAULA JR. 1994. Predição da distribuição diamétrica da floresta Atlântica pelo emprego da matriz de transição. *Árvore* 18(3): 179–193.
- AZEVEDO, C.P., A.L. SOUZA, AND R.M. JESUS. 1995. Um modelo de matriz de transição para prognose do crescimento de um povoamento natural remanescente não manejado de mata Atlântica. *Árvore* 19(2):187–199.
- BACAËR, N., A. BAH, AND A. MAHAMANE. 2005. Fuelwood harvesting in Niger and a generalization of Faustmann's formula. *C. R. Biol.* 328(4):379–385.
- BATABYAL, A.A. 1996. On some aspects of the management of a stochastically developing forest. *Ecol. Model.* 89(1–3):67–72.
- BATISTA, W.B., W.J. PLATT, AND R.E. MACCHIAVELLI. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79(1):38–53.
- BEKELE, T. 2000. Plant population dynamics of *Dodonea angustifolia* and *Olea europea* spp. *cuspidata* in dry Afromontane forests of Ethiopia. *Acta Univers. Upsal.* 559:1–49.
- BELLEFLEUR, P. 1981. Markov models of forest-type secondary succession in coastal British Columbia. *Can. J. For. Res.* 11(1):18–29.
- BENABDELLAH, B., K.-F. ALBRECHT, V.L. POMAZ, E.A. DENISENKO, AND D.O. LOGOFET. 2003. Markov chain models for forest successions in the Erzgebirge, Germany. *Ecol. Model.* 159(2–3):145–160.
- BIGING, G.S., AND M. DOBBERTIN. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *For. Sci.* 38(3):695–720.
- BIGING, G.S., AND M. DOBBERTIN. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41(2):360–377.
- BOLLANDSÅS, O.M., J. BUONGIORNO, AND T. GOBAKKEN. 2008. Predicting the growth of stands of trees of mixed species and size: A matrix model for Norway. *Scand. J. For. Res.* 23(2): 167–178.
- BOLTZ, F., AND D.R. CARTER. 2006. Multinomial logit estimation of a matrix growth model for tropical dry forests of eastern Bolivia. *Can. J. For. Res.* 36(10):2623–2632.
- BOM, R.P. 1996. *Proposição de um sistema de manejo para floresta nativa objetivando a sustentabilidade da produção*. PhD thesis, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. 199 p.
- BOSCH, C.A. 1971. Redwoods: A population model. *Science* 172:345–349.
- BOSCOLO, M., AND J. BUONGIORNO. 1997. Managing a tropical rain forest for timber, carbon storage, and tree diversity. *Commonw. For. Rev.* 76(4):245–254.
- BOSCOLO, M., J. BUONGIORNO, AND R. CONDIT. 2001. A model to predict biomass recovery and economic potential of a neotropical forest. P. 585 in *Environment for growth in Central America: Environmental management for sustainability and competitiveness*, Panayotou, T. (ed.). Harvard University Press, Cambridge, MA.
- BOSCOLO, M., J. BUONGIORNO, AND T. PANAYOTOU. 1997. Simulating options for carbon sequestration through improved management of a lowland tropical rainforest. *Environ. Dev. Econ.* 2:241–263.
- BOSCOLO, M., AND J.R. VINCENT. 1998. *Promoting better logging practices in tropical forests: A simulation analysis of alternative regulations*. Development Discussion Paper, The Harvard Institute for International Development, Harvard University, Cambridge, MA. 53 p.
- BOTKIN, D.B., J.F. JANAK, AND J.R. WALLIS. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60:849–873.
- BRUNER, H.D., AND J.W. MOSER. 1973. A Markov chain approach to the prediction of diameter distributions in uneven-aged forest stands. *Can. J. For. Res.* 3(3):409–417.
- BUONGIORNO, J. 2001. Generalization of Faustmann's formula for stochastic forest growth and prices with Markov decision process models. *For. Sci.* 47(4):466–474.
- BUONGIORNO, J. 2007. Aménagement forestier: d'Une approche figée à un processus adaptatif. *Rev. For. Fran.* 59(3):272–275.
- BUONGIORNO, J., S. DAHIR, H.-C. LU, AND C.-R. LIN. 1994. Tree size diversity and economic returns in uneven-aged forest stands. *For. Sci.* 40(1):83–103.
- BUONGIORNO, J., AND J.K. GILLESS. 2003. *decision methods for forest resource management*. Academic Press, Amsterdam, The Netherlands. 439 p.
- BUONGIORNO, J., AND B.R. MICHIE. 1980. A matrix model of uneven-aged forest management. *For. Sci.* 26(4):609–625.

- BUONGIORNO, J., J.L. PEYRON, F. HOULLIER, AND M. BRUCIAMACCHIE. 1995. Growth and management of mixed-species, uneven-aged forests in the French Jura: Implications for economic returns and tree diversity. *For. Sci.* 41(3):397–429.
- BUSTAMANTE, R.O., J.A. SIMONETTI, A.A. GREZ, AND J. SAN MARTÍN. 2005. Fragmentación y dinámica de regeneración del bosque Maulino: Diagnóstico actual y perspectivas futuras. P. 529–539 in *Historia, biodiversidad y ecología de los bosques costeros de Chile*, Smith-Ramírez, C., J.J. Armesto, and C. Valdovinos (eds.). Editorial Universitaria, Santiago, Chile.
- CASTRO DE BARROS, P. 2009. *Dinâmica de carbono de uma floresta primária na Resex Auatí-paraná, Fonte Boa, Amazonas*. MSc thesis, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil. 66 p.
- CASWELL, H. 2001. *Matrix population models: Construction, analysis and interpretation*. Sinauer Associates, Inc., Sunderland, MA. 722 p.
- CASWELL, H. 2010. Life table response experiment analysis of the stochastic growth rate. *J. Ecol.* 98(2):324–333.
- CASWELL, H., AND T. TAKADA. 2004. Elasticity analysis of density-dependent matrix population models: The invasion exponent and its substitutes. *Theor. Popul. Biol.* 65(4):401–411.
- CASWELL, H., T. TAKADA, AND C.M. HUNTER. 2004. Sensitivity analysis of equilibrium in density-dependent matrix population models. *Ecol. Lett.* 7(5):380–387.
- CHIEN, P.D. 2006. *Demography of threatened tree species in Vietnam*. PhD thesis, Utrecht University, Utrecht, The Netherlands.
- CHILDRESS, W.M., C.M. CRISAFULLI, AND E.J. RYKIEL JR. 1998. Comparison of Markovian matrix models of a primary successional plant community. *Ecol. Model.* 107(1):93–102.
- CONDIT, R., S. AGUILAR, A. HERNANDEZ, R. PEREZ, S. LAO, G. ANGEHR, S.P. HUBBELL, AND R.B. FOSTER. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.* 20(1):51–72.
- CONDIT, R., R. SUKUMAR, S.P. HUBBELL, AND R.B. FOSTER. 1998. Predicting population trends from size distributions: A direct test in a tropical tree community. *Am. Nat.* 152(4):495–509.
- COURALET, C. 2004. *Growth and population dynamics of Juniperus procera in an Ethiopian highland forest: Dendrochronology and matrix model*. MSc thesis, Wageningen University, Wageningen, The Netherlands. 109 p.
- COURALET, C., U. SASS-KLAASSEN, F. STERCK, T. BEKELE, AND P.A. ZUIDEMA. 2005. Combining dendrochronology and matrix modelling in demographic studies: An evaluation for *Juniperus procera* in Ethiopia. *For. Ecol. Manage.* 216(1–3):317–330.
- CUNHA, U.S., S.A. MACHADO, A. FIGUEIREDO FILHO, AND C.R. SANQUETTA. 2002. Predição da estrutura diamétrica de espécies comerciais de terra firme da amazônia por meio da matriz de transição. *Ciê. Flor.* 12(1):109–121.
- CUSHING, J.M. 1998. *An introduction to structured population dynamics*. SIAM, Philadelphia, PA.
- DALEY, D.J. 1979. Bias in estimating the malthusian parameter for Leslie matrices. *Theor. Popul. Biol.* 15(2):257–263.
- DALGLEISH, H.J., D.N. KOONS, AND P.B. ADLER. 2010. Can life-history traits predict the response of forb populations to changes in climate variability? *J. Ecol.* 98(1):209–217.
- DAVISON, R., H. JACQUEMYN, D. ADRIAENS, O. HONNAY, H. DE KROON, AND S. TULJAPURKAR. 2010. Demographic effects of extreme weather events on a short-lived calcareous grassland species: Stochastic life table response experiments. *J. Ecol.* 98(2):255–267.
- DE KROON, H., A. PLAISIER, J. VAN GROENENDAEL, AND H. CASWELL. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431.
- DEANGELIS, D.L., AND K.A. ROSE. 1992. Which individual-based approach is most appropriate for a given problem? P. 67–87 in *Individual-based models and approaches in ecology—Populations, communities and ecosystems*, DeAngelis, D.L., and L.J. Gross (eds.). Chapman & Hall, New York.
- DEBROUX, L. 1998. *L'aménagement des forêts tropicales fondé sur la gestion des populations d'arbres: l'Exemple du moabi (Baillonella toxisperma Pierre) dans la forêt du Dja, Cameroun*. PhD thesis, Faculté Universitaire des Sciences Agronomiques de Gembloux, Gembloux, Belgique. 283 p.
- DEBROUX, L., AND W. DELVINGT. 1999. Perspectives pour un aménagement des forêts naturelles fondé sur la gestion des populations d'arbres: l'Exemple du moabi (*Baillonella toxisperma* Pierre) dans la forêt du Dja (Cameroun). In *La gestion des forêts denses africaines aujourd'hui: Actes du séminaire Forafri de libreville*, Nasi, R., I. Amsellem, and S. Drouineau (eds.). CIRAD-Forêt, Montpellier, France, Gabon.
- DELCAMP, M. 2007. *Groupes "fonctionnels" d'espèces et prédiction de la dynamique des peuplements d'arbres après perturbation en forêt dense tropicale humide: Exemple en Guyane française*. PhD thesis, Université Montpellier, Montpellier, France. 368 p.
- DENIS, M. 2007. *Analyse bayésienne de modèles d'évolution de ressources naturelles*. MSc thesis, Université Montpellier, Montpellier, France. 71 p.
- DEVENISH NELSON, E.S., S. HARRIS, C.D. SOULSBURY, S.A. RICHARDS, AND P.A. STEPHENS. 2010. Uncertainty in population growth rates: Determining confidence intervals from point estimates of parameters. *PLoS One* 5(10).
- EASTERLING, M.R., S.P. ELLNER, AND P.M. DIXON. 2000. Size-specific sensitivity: Applying a new structured population model. *Ecology* 81(3):694–708.
- EBA'A ATYI, R. 2000. *TROPFOMS: A decision support model for sustainable management of South-Cameroon's rain forests*. PhD thesis, Wageningen University, Wageningen, The Netherlands. 202 p.
- EBA'A ATYI, R., AND A.M. FILIUS. 1999. *Synthesis and significance of the results of the research in management and economics for the design of a forest management plan*. The Tropenbos-Cameroon Programme, Wageningen, The Netherlands. 9 p.
- ELLNER, S.P., AND M. REES. 2006. Integral projection models for species with complex demography. *Am. Nat.* 167(3):410–428.
- ENRIGHT, N.J., M. FRANCO, AND J. SILVERTOWN. 1995. Comparing plant life histories using elasticity analysis: The importance of life span and the number of life-cycle stages. *Oecologia* 104(1):79–84.
- ENRIGHT, N., AND J. OGDEN. 1979. Applications of transition matrix models in forest dynamics: Araucaria in Papua New Guinea and Nothofagus in New Zealand. *Aust. J. Ecol.* 4:3–23.
- ENRIGHT, N.J., AND A.D. WATSON. 1991. A matrix population model analysis for the tropical tree, *Araucaria cunninghamii*. *Aust. J. Ecol.* 16(4):507–520.
- FAVRICHON, V. 1995. *Modèle matriciel déterministe en temps discret. Application à l'étude de la dynamique d'un peuplement forestier tropicale humide (Guyane Française)*. PhD thesis, Université Claude Bernard—Lyon I, Lyon, France. 252 p.
- FAVRICHON, V. 1996. Modélisation en forêt naturelle: Les modèles à compartiments comme outils d'aide à l'aménagement forestier. *Bois For. Trop.* 249(3):23–32.
- FAVRICHON, V. 1998a. Apports d'un modèle démographique plurispécifique pour l'étude des relations diversité/dynamique en forêt tropicale guyanaise. *Ann. Sci. For.* 55(6):655–669.

- FAVRICHON, V. 1998b. Modeling the dynamics and species composition of tropical mixed-species uneven-aged natural forest: Effects of alternative cutting regimes. *For. Sci.* 44(1):113–124.
- FAVRICHON, V., AND K.Y. CHEOL. 1998. Modelling the dynamics of a lowland mixed dipterocarp forest stand: Application of a density-dependent matrix model. P. 229–248 in *Silvicultural research in a lowland mixed dipterocarp forest of East Kalimantan—The contribution of STREK project*, Bertault, J.G., and K. Kadir (eds.). CIRAD-Forêt, Montpellier, France.
- FIEBERG, J., AND S.P. ELLNER. 2001. Stochastic matrix models for conservation and management: A comparative review of methods. *Ecol. Lett.* 4(3):244–266.
- FORTINI, L.B., AND D.J. ZARIN. 2011. Population dynamics and management of Amazon tidal floodplain forests: Links to the past, present and future. *For. Ecol. Manage.* 261(3):551–561.
- FRECKLETON, R.P., D.M.S. MATOS, M.L.A. BOVI, AND A.R. WATKINSON. 2003. Predicting the impacts of harvesting using structured population models: The importance of density-dependence and timing of harvest for a tropical palm tree. *J. Appl. Ecol.* 40(5):846–858.
- FRECKLETON, R.P., D. NOBLE, AND T.J. WEBB. 2006. Distributions of habitat suitability and the abundance-occupancy relationship. *Am. Nat.* 167(2):260–275.
- FREEDMAN, B., AND T. KEITH. 1996. Planting trees for carbon credits: A discussion of context, issues, feasibility, and environmental benefits. *Environ. Rev.* 4(2):100–111.
- GAOUE, O.G., C.C. HORVITZ, AND T. TICKTIN. 2011. Non-timber forest product harvest in variable environments: Modeling the effect of harvesting as a stochastic sequence. *Ecol. Appl.* 21(5):1604–1616.
- GAOUE, O.G., AND T. TICKTIN. 2010. Effects of harvest of non-timber forest products and ecological differences between sites on the demography of African mahogany. *Conserv. Biol.* 24(2):605–614.
- GARCÍA VIDAL, O. 1974. *On mathematical stand models*. Management section, Forestry Division, Santiago, Chile. 22 p.
- GARNIER, A., AND J. LECOMTE. 2006. Using a spatial and stage-structured invasion model to assess the spread of feral populations of transgenic oilseed rape. *Ecol. Model.* 194:141–149.
- GETZ, W.M., AND R.G. HAIGHT. 1989. *Population harvesting. Demographic models of fish, forest and animal resources*. Princeton Univ. Press, Princeton, NJ. 391 p.
- GITTINS, R. 1968. Trend-surface analysis of ecological data. *J. Ecol.* 56(3):845–869.
- GONZÁLEZ-PÉREZ, H. 1996. Planteamiento de un modelo matricial para el análisis de la dinámica de poblaciones de árboles. *Crón. For. Med. Amb.* 11(1).
- GOODMAN, L.A. 1967. On the reconciliation of mathematical theories of population growth. *J. Roy. Stat. Soc.* 130(4):541–553.
- GOURLET-FLEURY, S., G. CORNU, S. JÉSEL, H. DESSARD, J.G. JOURGET, L. BLANC, AND N. PICARD. 2005. Using models for predicting recovery and assessing tree species vulnerability in logged tropical forests: A case study from French Guiana. *For. Ecol. Manage.* 209(1–2):69–85.
- GRIMM, V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecol. Model.* 115(2–3):129–148.
- GRIMM, V., AND S.F. RAILSBACK. 2005. *Individual-based modeling and ecology*. Princeton Univ. Press, Princeton, NJ. 480 p.
- GROSS, K., B.A. CRAIG, AND W.D. HUTCHISON. 2002. Bayesian estimation of a demographic matrix model from stage-frequency data. *Ecology* 83(12):3285–3298.
- GUÉDON, Y., Y. CARAGLIO, P. HEURET, E. LEBARBIER, AND C. MEREDIEU. 2007. Analyzing growth components in trees. *J. Theor. Biol.* 248(3):418–447.
- HAMPEL, F.R. 1974. The influence curve and its role in robust estimation. *J. Am. Stat. Assoc.* 69:383–393.
- HAMPEL, F.R., E.M. RONCHETTI, P.J. ROUSSEUW, AND W.A. STAHEL. 1986. *Robust statistics: The approach based on influence functions*. John Wiley & Sons, New York. 502 p.
- HAO, Q., F. MENG, Y. ZHOU, AND J. WANG. 2005a. Determining the optimal selective harvest strategy for mixed-species stands with a transition matrix growth model. *New For.* 29(3):207–219.
- HAO, Q., F. MENG, Y. ZHOU, AND J. WANG. 2005b. A transition matrix growth model for uneven-aged mixed-species forests in the Changbai Mountains, northeastern China. *New For.* 29(3):221–231.
- HAO, Z., J. ZHANG, B. SONG, J. YE, AND B. LI. 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. *For. Ecol. Manage.* 252(1–3):1–11.
- HARA, T. 1988. Dynamics of size structure in plant populations. *Trends Ecol. Evol.* 3(6):129–133.
- HARA, T., AND T. WYSZOMIRSKI. 1994. Competitive asymmetry reduces spatial effects on size-structure dynamics in plant populations. *Ann. Bot.* 73:285–297.
- HARA, T., AND M. YOKOZAWA. 1994. Effects of physiological and environmental variations on size-structure dynamics in plant populations. *Ann. Bot.* 73(1):39–51.
- HARRISON, T.P., AND B.R. MICHIE. 1985. A generalized approach to the use of matrix growth models. *For. Sci.* 31(4):850–856.
- HARTSHORN, G.S. 1975. A matrix model of tree population dynamics. P. 41–51 in *Tropical ecological systems—Trends in terrestrial and aquatic research*, Golley, F.B., and E. Medina (eds.). Springer-Verlag, Berlin.
- HENSON, S.M. 1998. Leslie matrix models as “stroboscopic snapshots” of McKendrick PDE models. *J. Math. Biol.* 37(4):309–328.
- HIGUCHI, N. 1987. *Short-term growth of an undisturbed tropical moist forest in the Brazilian Amazon*. PhD thesis, Michigan State University, East Lansing, MI. 129 p.
- HOFFMANN, W.A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: Matrix model projections. *Ecology* 80(4):1354–1369.
- HOOLEY, D.E. 1990. Collapsed matrices with (almost) the same eigenstuff. *Coll. Math. J.* 31(4):297–299.
- HORN, H.S. 1975. Markovian properties of forest succession. P. 196–211 in *Ecology and Evolution of Communities*, Harvard Univ. Press, New York.
- HOUE, L., AND H. LEDOUX. 1995. Modélisation en forêt naturelle: Stabilité du peuplement. *Bois For. Trop.* 245(3):21–26.
- HOULLIER, F. 1986. *Echantillonnage et modélisation de la dynamique des peuplements forestiers. Application au cas de l'inventaire forestier national*. PhD thesis, Université Claude Bernard—Lyon I, Lyon, France. 267 p.
- HOULLIER, F., AND J.D. LEBRETON. 1986. A renewal-equation approach to the dynamics of stage-grouped populations. *Math. Biosci.* 79:185–197.
- HOULLIER, F., J.D. LEBRETON, AND D. PONTIER. 1989. Sampling properties of the asymptotic behavior of age- or stage-grouped population models. *Math. Biosci.* 95(2):161–177.
- HIRONENKO, N., Y. YATSENKO, R.U. GOETZ, AND A. XABADIA. 2008. Maximum principle for a size-structured model of forest and carbon sequestration management. *Appl. Math. Lett.* 21(10):1090–1094.
- HUENNEKE, L.F., AND P.L. MARKS. 1987. Stem dynamics of the shrub *Alnus Incana* ssp. *rugosa*: Transition matrix models. *Ecology* 68(5):1234–1242.
- HUSTON, M.A., D.L. DEANGELIS, AND W.M. POST. 1988. New computer models unify ecological theory. *Bioscience* 38(10):682–691.

- INGRAM, D., AND J. BUONGIORNO. 1996. Income and diversity tradeoffs from management of mixed lowland dipterocarps in Malaysia. *J. Trop. For. Sci.* 9(2):242–270.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2007. Climate change 2007: Synthesis report. P. 104 in *Contribution of working groups I, II, and III to the fourth assessment report of the Intergovernmental Panel on Climate Change*, Team, C.W., R.K. Pachauri, and A. Reisinger (eds.). Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- ISEBRANDS, J.G., H.M. RAUSCHER, T.R. CROW, AND D.J. DICKMANN. 1990. Whole-tree growth process models based on structure—Functional relationships. P. 96–112 in *Forest growth: Process modeling of responses to environmental stress*, Dixon, R., R. Meldahl, G. Ruark, and W. Warren (eds.). Timber Press, Portland, OR.
- JIANG, L., AND N. SHAO. 2004. Red environmental noise and the appearance of delayed density dependence in age-structured populations. *Proc. Roy. Soc. Lond.* 271(1543):1059–1064.
- JOHNSON, S.E., I.S. FERGUSON, AND L. RONG-WEI. 1991. Evaluation of a stochastic diameter growth model for mountain ash. *For. Sci.* 37(6):1671–1681.
- KAYA, I., AND J. BUONGIORNO. 1987. Economic harvesting of uneven-aged northern hardwood stands under risk: A Markovian decision model. *For. Sci.* 33(4):889–907.
- KAYE, T.N., AND D.A. PYKE. 2003. The effect of stochastic technique on estimates of population viability from transition matrix models. *Ecology* 84(6):1464–1476.
- KEYFITZ, N. 1967. Reconciliation of population models: Matrix, integral equation and partial fraction. *J. Roy. Stat. Soc.* 130:61–83.
- KOEHLER, H.S. 2002. *Sistema computacional de dinâmica para florestas naturais*. PhD thesis, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. 192 p.
- KOHYAMA, T. 1989. Simulation of the structural development of warm-temperate rain forest stands. *Ann. Bot.* 63(6):625–634.
- KOHYAMA, T. 1991. Simulating stationary size distribution of trees in rain forests. *Ann. Bot.* 68(2):173–180.
- KOHYAMA, T. 1993. Size-structured tree populations in gap-dynamic forest—The forest architecture hypothesis for the stable coexistence of species. *J. Ecol.* 81:131–143.
- KOHYAMA, T., E. SUZUKI, T. PARTOMIHARDJO, AND T. YAMADA. 2001. Dynamic steady state of patch-mosaic tree size structure of a mixed dipterocarp forest regulated by local crowding. *Ecol. Res.* 16(1):85–98.
- KOKKILA, T., A. MÄKELÄ, AND A. FRANC. 2006. Comparison of distance-dependent and distance-independent stand growth models. Is perfect aggregation possible? *For. Sci.* 52(6):623–635.
- KOLBE, A.E., J. BUONGIORNO, AND M. VASIEVICH. 1999. Geographic extension of an uneven-aged, multi-species matrix growth model for northern hardwood forests. *Ecol. Model.* 121(2–3):235–253.
- KOLSTRÖM, T. 1993. Modelling the development of an uneven-aged stand of *Picea abies*. *Scand. J. For. Res.* 8(1):373–383.
- KOROTKOV, V.N., D.O. LOGOFET, AND M. LOREAU. 2001. Succession in mixed boreal forest of Russia: Markov models and non-Markov effects. *Ecol. Model.* 142(1–2):25–38.
- KUBO, T., T. KOHYAMA, M.D. POTTS, AND P.S. ASHTON. 2000. Mortality rate estimation when inter-census intervals vary. *J. Trop. Ecol.* 16(5):753–756.
- KUULUVAINEN, T., AND D.G. SPRUGEL. 1996. Examining age- and altitude-related variation in tree architecture and needle efficiency in Norway spruce using trend surface analysis. *For. Ecol. Manage.* 88:237–247.
- LAHOREAU, G., N. PICARD, AND S. GOURLET-FLEURY. 2002. Grouping species to model forest dynamics: A case study of a forest in the Central African Republic. *Bois For. Trop.* 271(1):89–100.
- LAMAR, W.R., AND J.B. MCGRAW. 2005. Evaluating the use of remotely sensed data in matrix population modeling for eastern hemlock (*Tsuga canadensis* L.). *For. Ecol. Manage.* 212(1–3):50–64.
- LEFKOVITCH, L.P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18.
- LEGENDRE, P. 1993. Spatial autocorrelation: Trouble or new paradigm? *Ecology* 74(6):1659–1673.
- LEGENDRE, P., N.L. ODEN, R.R. SOKAL, A. VAUDOR, AND J. KIM. 1990. Approximate analysis of variance of spatially autocorrelated regional data. *J. Classif.* 7:53–75.
- LEI, X., C. PENG, Y. LU, AND X. ZHANG. 2006. A matrix growth model of natural spruce-balsam fir forest in New Brunswick, Canada. P. 231–235 in *2006 International symposium on plant growth modeling, simulation, visualization and applications*, Peng, C., Y. Lu, and X. Zhang (eds.). IEEE Computer Society, Los Alamitos, CA.
- LESLIE, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33(3):183–212.
- LEWIS, E.G. 1942. On the generation and growth of a population. *Sankhya* 6(1):93–96.
- LEWIS, S.L., O.L. PHILLIPS, D. SHEIL, B. VINCETI, T.R. BAKER, S. BROWN, A.W. GRAHAM, ET AL. 2004. Tropical forest tree mortality, recruitment and turnover rates: Calculation, interpretation and comparison when census intervals vary. *J. Ecol.* 92(6):929–944.
- LIANG, J. 2010. Dynamics and management of Alaska boreal forest: An all-aged multi-species Matrix growth model. *For. Ecol. Manage.* 260(4):491–501.
- LIANG, J., J. BUONGIORNO, A. HUBBELL, AND B. SCHULTE. 2004a. *NorthPro: A spreadsheet program for the management of uneven-aged northern hardwood stands*. Univ. of Wisconsin-Madison, Madison, WI. 36 p.
- LIANG, J., J. BUONGIORNO, AND R.A. MONSERUD. 2004b. *CalPro: A spreadsheet program for the management of California mixed-conifer stands*. USDA For. Serv., Pacific Northwest Research Station, Portland, OR. 32 p.
- LIANG, J., J. BUONGIORNO, AND R.A. MONSERUD. 2005a. Growth and yield of all-aged Douglas-fir/western hemlock stands: A matrix model with stand diversity effects. *Can. J. For. Res.* 35(10):2369–2382.
- LIANG, J., J. BUONGIORNO, AND R.A. MONSERUD. 2006a. Bootstrap simulation and response surface optimization of management regimes for Douglas-fir/western hemlock stands. *For. Sci.* 52(5):579–594.
- LIANG, J., J. BUONGIORNO, AND R.A. MONSERUD. 2006b. *WestProPlus: A stochastic spreadsheet program for the management of all-aged Douglas-fir/western hemlock forests in the Pacific Northwest*. USDA For. Serv., Pacific Northwest Research Station, Portland, OR. 42 p.
- LIANG, J., J. BUONGIORNO, R.A. MONSERUD, AND J. FRIED. 2005b. Estimation and application of a growth and yield model for uneven-aged mixed conifer stands in California. *Int. For. Rev.* 7(2):101–112.
- LIANG, J., AND M. ZHOU. 2010. A geospatial model of forest dynamics with controlled trend surface. *Ecol. Model.* 221(19):2339–2352.
- LIANG, J., M. ZHOU, D. VERBYLA, L. ZHANG, A.L. SPRINGSTEEN, AND T. MALONE. 2011. Mapping forest dynamics under climate change: A matrix model. *For. Ecol. Manage.* 262:2250–2262.
- LIANG, J. 2012. Mapping large-scale forest dynamics: a geospatial approach. *Land. Ecol.* doi: 10.1007/s10980-012-9767-7.

- LIN, C.R., AND J. BUONGIORNO. 1997. Fixed versus variable-parameter matrix models of forest growth: The case of maple-birch forests. *Ecol. Model.* 99(2–3):263–274.
- LIN, C.R., AND J. BUONGIORNO. 1998. Tree diversity, landscape diversity, and economics of maple-birch forests: Implications of Markovian models. *Manage. Sci.* 44:1351–1366.
- LIN, C.R., J. BUONGIORNO, J. PRESTEMON, AND K. SKOG. 1998. Growth model for uneven-aged loblolly pine stands. Simulations and management implications. USDA For. Serv., Forest Products Laboratory, Madison, WI. 13 p.
- LIN, C.R., J. BUONGIORNO, AND M. VASIEVICH. 1996. A multi-species, density-dependent matrix growth model to predict tree diversity and income in northern hardwood stands. *Ecol. Model.* 91(1–3):193–211.
- LOGOFET, D.O. 2008. Convexity in projection matrices: Projection to a calibration problem. *Ecol. Model.* 216(2):217–228.
- LOGOFET, D.O., AND E.V. LESNAYA. 2000. The mathematics of Markov models: What Markov chains can really predict in forest successions. *Ecol. Model.* 126(2–3):285–298.
- LÓPEZ TORRES, I., C. FULLANA BELDA, S.F. ORTUÑO PÉREZ, AND A.J. MARTÍN FERNÁNDEZ. 2008a. Choosing *Fagus sylvatica* L. matrix model dimension by sensitivity analysis of the population growth rate with respect to the width of the diameter classes. *Ecol. Model.* 218(3–4):307–314.
- LÓPEZ TORRES, I., S.F. ORTUÑO PÉREZ, Á.J. MARTÍN FERNÁNDEZ, AND C. FULLANA BELDA. 2008b. Estimación del aprovechamiento máximo sostenible y distribución diamétrica estable de masas irregulares de *Pinus nigra* mediante modelos matriciales. *Interciencia* 33(11):789–794.
- LU, H.C., AND J. BUONGIORNO. 1993. Long- and short-term effects of alternative cutting regimes on economic returns and ecological diversity in mixed-species forests. *For. Ecol. Manage.* 58(3–4):173–192.
- LUTSCHER, F., AND M.A. LEWIS. 2003. Spatially-explicit matrix models. *J. Math. Biol.* 48(3):293–324.
- MA, W., C. SHEN, X. LEI, S. DUFOUR, AND F.D. COLIGNY. 2011. Development of matrix growth model for larch-spruce-fir forest based on CAPSIS platform. *J. Northeast. For. Univ.* 39(9):1–4 (in Chinese).
- MAILLETTE, L. 1982. Structural dynamics of silver birch. II. A matrix model of the bud population. *J. Appl. Ecol.* 19(1): 219–238.
- MANDERS, P.T. 1987. A transition matrix model of the population dynamics of the Clanwilliam cedar (*Widdringtonia cedarbergensis*) in natural stands subject to fire. *For. Ecol. Manage.* 20(1–2):171–186.
- MARLAND, G. 1988. *The prospect of solving the CO<sub>2</sub> problem through global reforestation*. US Department of Energy, Oak Ridge, TN. 66 p.
- MASON, E.G. 2000. Evaluation of a model of beech forest growing on the West Coast of the South Island of New Zealand. *N. Z. J. For.* 44(4):26–31.
- MCLACHLAN, G., AND D. PEEL. 2000. *Finite mixture models*. John Wiley & Sons, New York. 456 p.
- MENDONÇA, A.C.A. 2003. *Caracterização e simulação dos processos dinâmicos de uma área de Floresta Tropical de Terra Firme utilizando matrizes de transição*. MSc thesis, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. 92 p.
- MENDOZA, G.A., AND A. SETYARSO. 1986. A transition matrix forest growth model for evaluating alternative harvesting schemes in Indonesia. *For. Ecol. Manage.* 15(3):219–228.
- MENGEL, D.L., AND J.P. ROISE. 1990. A diameter-class matrix model for Southeastern US coastal plain bottomland hardwood stands. *South. J. Appl. For.* 14:189–195.
- MENON, M.U., A.F. FILHO, AND L.F. WATZLAWICK. 2010. Matriz de transição para predição da distribuição diamétrica em Floresta Ombrófila Mista na flona de Irati (PR). *Ambiência* 6(2):271–280.
- METCALF, C.J.E., S.M. MCMAHON, AND J.S. CLARK. 2009. Overcoming data sparseness and parametric constraints in modeling of tree mortality: A new nonparametric Bayesian model. *Can. J. For. Res.* 39(9):1677–1687.
- MEYER, J.S., C.G. INGERSOLL, L.L. McDONALD, AND M.S. BOYCE. 1986. Estimating uncertainty in population growth rates: Jack-knife vs. bootstrap techniques. *Ecology* 67(5):1156–1166.
- MICHIE, B.R., AND J. BUONGIORNO. 1984. Estimation of a matrix model of forest growth from re-measured permanent plots. *For. Ecol. Manage.* 8:127–135.
- MICHIE, B.R., AND F.D. MCCANDLESS. 1986. A matrix model of oak-hickory stand management and valuing forest land. *For. Sci.* 32(3):759–769.
- MILLER, J., J. FRANKLIN, AND R. ASPINALL. 2007. Incorporating spatial dependence in predictive vegetation models. *Ecol. Model.* 202:225–242.
- MITCHELL, K.J. 1975. Dynamics and simulated yield of Douglas fir. *For. Sci. Monogr.* 17:1–39.
- MODREGO, F., O. MELO, AND H. GILABERT. 2006. Los bosques de araucaria en Chile: Manejo sostenible, el costo de la sostenibilidad y las restricciones técnicas a su manejo. *Econ. Agr.* 10:73–82.
- MOLONEY, K.A. 1986. A generalized algorithm for determining category size. *Oecologia* 69:176–180.
- MONSERUD, R.A. 2003. Evaluating forest models in a sustainable forest management context. *For. Biometry Model. Inform. Sci.* 1:35–47.
- MUNRO, D.D. 1974. Forest growth models: A prognosis. P. 7–21 in *Growth models for tree and stand simulation*, Fries, J. (ed.). Royal College of Forestry, Department of Forest Yield Research, Stockholm, Sweden.
- NAKASHIZUKA, T. 1991. Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. *J. Veg. Sci.* 2(3):413–418.
- NAMAALWA, J., T. EID, AND P. SANKHAYAN. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *For. Ecol. Manage.* 213:312–327.
- NAPPO, M.E., J.J. GRIFFITH, S.V. MARTINS, P. DE MARCO JR., A.L. DE SOUZA, AND A.T. DE OLIVEIRA FILHO. 2005. Dinâmica da estrutura diamétrica da regeneração natural de espécies arbóreas e arbustivas no sub-bosque de povoamento puro de *Mimosa scabrella* Benth. em área minerada, em Poços de Caldas, MG. *Árvore* 29(1):35–46.
- NEUBERT, M.G., AND H. CASWELL. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81(6):1613–1628.
- OLMSTED, I., AND E.R. ALVAREZ-BUYLLA. 1995. Sustainable harvesting of tropical trees: Demography and Matrix models of two palm species in Mexico. *Ecol. Appl.* 5(2):484–500.
- OROIS, S.S., AND R.R. SOALLEIRO. 2002. Modelling the growth and management of mixed uneven-aged maritime pine—Broadleaved species forests in Galicia, north-western Spain. *Scand. J. For. Res.* 17(6):538–547.
- OSHO, J.S.A. 1991. Matrix model for tree population projection in a tropical rain forest of south-western Nigeria. *Ecol. Model.* 59(3–4):247–255.
- OSHO, J.S.A. 1996. Modelling the tree population dynamics of the most abundant species in a Nigerian tropical rain forest. *Ecol. Model.* 89(1–3):175–181.
- PENG, C. 2000. Growth and yield models for uneven-aged stands: Past, present and future. *For. Ecol. Manage.* 132:259–279.
- PEREIRA DA SILVA, R. 2007. *Alometria, estoque e dinâmica da*

- biomassa de florestas primárias e secundárias na região de Manaus (AM). PhD thesis, Universidade Federal do Amazonas, Manaus, Amazonas, Brazil. 152 p.
- PFISTER, C.A., AND F.R. STEVENS. 2003. Individual variation and environmental stochasticity: Implications for matrix model predictions. *Ecology* 84(2):496–510.
- PICARD, N., L.N. BANAK, S. NAMKOSSERENA, AND Y. YALIBANDA. 2010a. The stock recovery rate in a Central African rain forest: An index of sustainability based on projection matrix models. *Can. J. For. Res.* 39(11):2138–2152.
- PICARD, N., A. BAR-HEN, AND A. FRANC. 2002. Modeling forest dynamics with a combined matrix/individual-based model. *For. Sci.* 48(4):643–652.
- PICARD, N., A. BAR-HEN, AND S. GOURLET-FLEURY. 2007. Estimator of upgrowth transition parameters for size-classified matrix from small samples. *Ecol. Model.* 204(1–2):59–69.
- PICARD, N., A. BAR-HEN, AND Y. GUÉDON. 2003a. Modelling forest dynamics with a second-order matrix model. *For. Ecol. Manage.* 180(1–3):389–400.
- PICARD, N., P. CHAGNEAU, F. MORTIER, AND A. BAR-HEN. 2009. Finding confidence limits on population growth rates: Bootstrap and analytic methods. *Math. Biosci.* 219(1):23–31.
- PICARD, N., AND A. FRANC. 2001. Aggregation of an individual-based space-dependent model of forest dynamics into distribution-based and space-independent models. *Ecol. Model.* 145:69–84.
- PICARD, N., S. GOURLET-FLEURY, AND P. SIST. 2003b. Using process-dependent groups of species to model the dynamics of a tropical rain-forest. P. 237–248 in *Modelling forest systems*, Amaro, A., D. Reed, and P. Soares (eds.). CAB International Publishing, Wallingford, MA.
- PICARD, N., F. MORTIER, AND P. CHAGNEAU. 2008a. Influence of estimators of the vital rates in the stock recovery rate when using matrix models for tropical rainforests. *Ecol. Model.* 214(2–4):349–360.
- PICARD, N., F. MORTIER, V. ROSSI, AND S. GOURLET-FLEURY. 2010b. Clustering species using a model of population dynamics and aggregation theory. *Ecol. Model.* 221(2):152–160.
- PICARD, N., D. OUÉDRAOGO, AND A. BAR-HEN. 2010c. Choosing classes for size projection matrix models. *Ecol. Model.* 221(19):2270–2279.
- PICARD, N., Y. YALIBANDA, S. NAMKOSSERENA, AND F. BAYA. 2008b. Estimating the stock recovery rate using matrix models. *For. Ecol. Manage.* 255(10):3597–3605.
- PLATT, W.J., G.W. EVANS, AND S.L. RATHBUN. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *Am. Nat.* 131(4):491–525.
- PONCE, J.E. 2006. *Sostenibilidad del manejo de los bosques secos tropicales de Bolivia aplicando múltiples objetivos*. Proyecto FOMABO, Documento Científico No. 1, Cochabamba, Bolivia. 34 p.
- PORTÉ, A., AND H.H. BARTELINK. 2002. Modelling mixed forest growth: A review of models for forest management. *Ecol. Model.* 150(1–2):141–188.
- PRESS, W.H., S.A. TEUKOLSKY, W.T. VETTERLING, AND B.P. FLANNERY. 1992. *Numerical recipes in C: The art of scientific computing*. Cambridge University Press, Cambridge, UK. 994 p.
- PRICE, O., AND D.M.J.S. BOWMAN. 1994. Fire-stick forestry: A Matrix model in support of skilful fire management of *Callitris intratropica* R.T. Baker by North Australian aborigenes. *J. Biogeogr.* 21(6):573–580.
- PUKKALA, T., AND T. KOLSTRÖM. 1988. Simulation of the development of Norway spruce stands using a transition matrix. *For. Ecol. Manage.* 25(3–4):255–267.
- PULZ, F.A. 1998. *Estudo da dinâmica ea modelagem da estrutura diamétrica de uma floresta semidecídua Montana na região de Lavras-MG*. MSc thesis, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil. 156 p.
- PULZ, F., J. SCOLFORO, A. OLIVEIRA, J. MELLO, AND A. OLIVEIRA FILHO. 1999. Acuracidade da predição da distribuição diamétrica da uma floresta inequiana com a matriz de transição. *Cerne* 5(1):1–14.
- QU, Z., AND H. HU. 2006. Estimation of transition probabilities in forest matrix transition models. *Chin. J. of Appl. Ecol.* 17(12): 2307–2310 (in Chinese).
- QU, Z., S. QU, AND C. TANG. 2007. Dynamic simulation and management of forest resources based on Matrix model. *J. Northe. For. Univ.* 35(6) (in Chinese).
- RAGO, P.J., AND R.M. DORAZIO. 1984. Statistical inference in life-table experiments: The finite rate of increase. *Can. J. Fish. Aquat. Sci.* 41(9):1361–1374.
- RALSTON, R., J. BUONGIORNO, B. SCHULTE, AND J. FRIED. 2003a. Non-linear matrix modelling of forest growth with permanent plot data: The case of uneven aged Douglas-fir stands. *Int. Trans. Oper. Res.* 10(5):461–482.
- RALSTON, R., J. BUONGIORNO, B. SCHULTE, AND J. FRIED. 2003b. *WestPro: A computer program for simulating uneven-aged Douglas-fir stand growth and yield in the Pacific Northwest*. USDA For. Serv., Pacific Northwest Research Station, Portland, OR. 36 p.
- RAMULA, S., AND K. LEHTILÄ. 2005. Importance of correlations among matrix entries in stochastic models in relation to number of transition matrices. *Oikos* 111(1):9–18.
- RAMULA, S., M. REES, AND Y.M. BUCKLEY. 2009. Integral projection models perform better for small demographic data sets than matrix population models: A case study of two perennial herbs. *J. Appl. Ecol.* 46(5):1048–1053.
- ROBERTS, M.R., AND A.J. HRUSKA. 1986. Predicting diameter distributions: A test of the stationary Markov model. *Can. J. For. Res.* 16(1):130–135.
- ROGERS-BENNETT, L., AND D.W. ROGERS. 2006. A semi-empirical growth estimation method for matrix models of endangered species. *Ecol. Model.* 195(3–4):237–246.
- ROLLIN, F., J. BUONGIORNO, M. ZHOU, AND J.L. PEYRON. 2005. Management of mixed-species, uneven-aged forests in the French Jura: From stochastic growth and price models to decision tables. *For. Sci.* 51(1):64–75.
- SABLE, S.E., AND K.A. ROSE. 2008. A comparison of individual-based and matrix projection models for simulating yellow perch population dynamics in Oneida Lake, New York, USA. *Ecol. Model.* 215(1–3):105–121.
- SALGUERO-GÓMEZ, R., AND B.B. CASPER. 2010. Keeping plant shrinkage in the demographic loop. *J. Ecol.* 98(2):312–323.
- SALGUERO-GÓMEZ, R., AND H. DE KROON. 2010. Matrix projection models meet variation in the real world. *J. Ecol.* 98(2):250–254.
- SALGUERO-GÓMEZ, R., AND J.B. PLOTKIN. 2010. Matrix dimensions bias demographic inferences: Implications for comparative plant demography. *Am. Nat.* 176(6):710–722.
- SANQUETTA, C.R. 1999. ARAUSIS: Sistema de simulação para manejo sustentável de florestas de Araucária. *Floresta* 29(1–2):115–121.
- SANQUETTA, C.R., J.E. ARCE, F. DOS SANTOS GOMES, AND E. COUTINHO DA CRUZ. 1999. Evaluación y simulación precoces del crecimiento de rodales de *Pinus taeda* L. con matrices de transición. *Rev. Cien. For. Quebracho* 7:31–42.
- SANQUETTA, C.R., D.A. BRENA, AND H. ANGELO. 1996. Matriz de transição para simulação da dinâmica de florestas naturais sob diferentes intensidades de corte. *Ciën. Flor.* 6(1):65–78.
- SANQUETTA, C.R., U.S. DA CUNHA, L.F. WATZLAWICK, AND M.L.B. CAMPOS. 2001. Projeção da distribuição diamétrica de

- fragmentos de florestas semidecíduas com matriz de transição. *Rev. Ciên. Exatas Nat.* 3(1):75–85.
- SANQUETTA, C.R., H. ANGELO, D.A. BRENA, AND J.B. MENDES. 1995. Predição da distribuição diamétrica, mortalidade e recrutamento da floresta natural com matriz Markoviana de potência. *Floresta* 24(1–2):23–36.
- SCHMIDT, I.B., L. MANDLE, T. TICKTIN, AND O.G. GAOUE. 2011. What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J. Appl. Ecol.* 48(4):815–826.
- SCHULTE, B., J. BUONGIORNO, C.-R. LIN, AND K. SKOG. 1998. SouthPro: A computer program for managing uneven-aged loblolly pine stands. USDA For. Serv., Forest Products Laboratory, Madison, WI. 47 p.
- SCHULTE, B.J., AND J. BUONGIORNO. 2004. A growth and yield model for naturally-regenerated mixed shortleaf pine forests in the southern United States of America. *Int. For. Rev.* 6(1): 19–29.
- SEBERT-CUVILLIER, E., M. SIMONET, V. SIMON-GOYHENECHÉ, F. PACCAUT, O. GOUBET, AND G. DECOCQ. 2010. PRUNUS: A spatially explicit demographic model to study plant invasions in stochastic, heterogeneous environments. *Biol. Invas.* 12(5): 1183–1206.
- SERREZE, M.C., M. DYURGEROV, V. ROMANOVSKY, W.C. OECHEL, J.T. ZHANG, R.G. BARRY, J.E. WALSH, F.S. CHAPIN III, AND T. OSTERKAMP. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climate Change* 46:159–207.
- SHEIL, D., D.F.R.P. BURSLEM, AND D. ALDER. 1995. The interpretation and misinterpretation of mortality rate measures. *J. Ecol.* 83(2):331–333.
- SHEIL, D., AND R.M. MAY. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J. Ecol.* 84(1): 91–100.
- SHIMATANI, K., S. KAWARASAKI, AND T. MANABE. 2008. Describing size-related mortality and size distribution by nonparametric estimation and model selection using the Akaike Bayesian information criterion. *Ecol. Res.* 23(2):289–297.
- SHIMATANI, I.K., Y. KUBOTA, K. ARAKI, S.-I. AIKAWA, AND T. MANABE. 2007. Matrix models using fine size classes and their application to the population dynamics of tree species: Bayesian non-parametric estimation. *Plant Species Biol.* 22(3):175–190.
- SILVERTOWN, J., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* 81(3):465–476.
- SIST, P., N. PICARD, AND S. GOURLET-FLEURY. 2003. Sustainable cutting cycle and yields in a lowland mixed dipterocarp forest of Borneo. *Ann. For. Sci.* 60(8):803–814.
- SOARES, C.P.B., R. DE ABREU DEMOLINARI, H. GARCIA LEITE, AND A. LOPES DE SOUZA. 2009. Predição do crescimento em povoamentos clonais de eucalipto não desbastados utilizando matrizes de transição não estacionárias. *Árvore* 33(5):831–840.
- SOCHEER, L.G. 2004. *Dinâmica e biomassa aérea de um trecho de Floresta Ombrófila Mista aluvial no município de Araucária, Paraná*. MSc thesis, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. 102 p.
- SOLOMON, D.S., R.A. HOSMER, AND H.T. HAYSLETT. 1986. A two-stage matrix model for predicting growth of forest stands in the Northeast. *Can. J. For. Res.* 16:521–528.
- SPATHELF, P., AND M.A. DURLO. 2001. Transition matrix for modeling the dynamics of a subtropical seminatural forest in southern Brazil. *For. Ecol. Manage.* 151(1–3):139–149.
- STAGE, A.R. 1973. *Prognosis model for stand development*. USDA For. Serv., Res. Paper. 32 p.
- STAVINS, R.N. 2001. *Experience with market-based environmental policy instruments. Resources for the future*. Discussion Paper 01-58, Washington, DC. 88 p.
- STEPKA, T.F. 2008. *Modelagem da dinâmica e prognose da estrutura diamétrica de uma Floresta Ombrófila Mista por meio de matriz de transição e razão de movimentação*. MSc thesis, Universidade Estadual do Centro-Oeste, Irati, Paraná, Brazil.
- STEPKA, T.F., A. NOGUEIRA DIAS, A. FIGUEIREDO FILHO, S. DO AMARAL MACHADO, AND A.R. SAWCZUK. 2010. Prognose da estrutura diamétrica de uma Floresta Ombrófila Mista com os métodos razão de movimentos e matriz de transição. *Pes. Flor. Bras.* 30(64):327–335.
- SÚAREZ, A., AND E. SOMARRIBA. 2002. Aprovechamiento sostenible de madera de *Cordia alliodora* de regeneración natural en cacaotales y bananales de indígenas de Talamanca, Costa Rica. *Agrofor. Am.* (35–36):50–54.
- SUZUKI, T., AND T. UMEMURA. 1974. Forest transition as a stochastic process. P. 358–379 in *Growth models for tree and stand simulation*, Fries, J. (ed.). Royal College of Forestry, Stockholm, Sweden.
- TAHVONEN, O. 2009. Optimal choice between even- and uneven-aged forestry. *Nat. Resour. Model.* 22(2):289–321.
- TAHVONEN, O., T. PUKKALA, O. LAIHO, E. LÄHDE, AND S. NIINIMÄKI. 2010. Optimal management of uneven-aged Norway spruce stands. *For. Ecol. Manage.* 260(1):106–115.
- TEIXEIRA, L.M., J.Q. CHAMBERS, A.R. SILVA, A.J.N. LIMA, V.M.C. CARNEIRO, J. DOS SANTOS, AND N. HIGUCHI. 2007. Projeção da dinâmica da floresta natural de Terra-firme, região de Manaus-AM, com o uso da cadeia de transição probabilística de Markov. *Acta Amazon* 37(3):377–384.
- TEIXEIRA, L.M., A.J.N. LIMA, A.R. SILVA, F.R. PINTO, V.M.C. CARNEIRO, J. DOS SANTOS, AND N. HIGUCHI. 2005. Projeção da dinâmica da floresta natural de Terra Firme, região de Manaus, AM, Brasil, com o uso da cadeia de Markov. In *50 congresso florestal nacional—A floresta e as gentes*, Silva, R., and F. Páscoa (eds.). Sociedade Portuguesa de Ciências Florestais, Viseu, Portugal.
- TERESCZUCH, S.M., P.M. MACDONAGH, A.J. DE OLIVEIRA, L.E. RIVERO, AND N.M. LUJÁN BULFE. 2007. Predicción de la estructura diamétrica de especies comerciales de un bosque subtropical por medio de matrices de transición. *Floresta* 37(1): 71–82.
- TUCKER, B.C., AND M. ANAND. 2003. The use of matrix models to detect natural and pollution-induced forest gradients. *Community Ecol.* 4(1):89–100.
- TULJAPURKAR, S. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theor. Popul. Biol.* 21(1):114–140.
- TULJAPURKAR, S. 1989. An uncertain life: Demography in random environments. *Theor. Popul. Biol.* 35(3):227–294.
- TULJAPURKAR, S., U.K. STEINER, AND S.H. ORZACK. 2009. Dynamic heterogeneity in life histories. *Ecol. Lett.* 12(1):93–106.
- TULJAPURKAR, S.D. 1990. *Population dynamics in variable environments*. Springer, New York. 154 p.
- TULJAPURKAR, S.D., AND S.H. ORZACK. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. *Theor. Popul. Biol.* 18(3):314–342.
- TURNER, M.G., W.L. BAKER, C.J. PETERSON, AND R.K. PEET. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems* 1(6):511–523.
- URIBE, G. 1993. *On the relationship between continuous and discrete models for size-structured population dynamics*. PhD thesis, University of Arizona, Tucson, AZ.
- USHER, M.B. 1966. A matrix approach to the management of

- renewable resources, with special reference to selection forests. *J. Appl. Ecol.* 3:355–367.
- USHER, M.B. 1969. A matrix model for forest management. *Biometrics* 25(2):309–315.
- USHER, M.B. 1979. Markovian approaches to ecological succession. *J. Anim. Ecol.* 48(2):413–426.
- USHER, M.B. 1981. Modelling ecological succession with particular reference to Markovian models. *Vegetatio* 46: 47:11–18.
- VAN GROENENDAEL, J., H. DE KROON, AND H. CASWELL. 1988. Projection matrices in population biology. *Trends Ecol. Evol.* 3(10):264–269.
- VAN HULST, R. 1980. Vegetation dynamics or ecosystem dynamics: Dynamic sufficiency in succession theory. *Vegetation* 43(1–2): 147–151.
- VAN MANTGEM, P.J., AND N.L. STEPHENSON. 2005. The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. *J. Ecol.* 93(4):737–747.
- VAN NES, E.H., AND M.M. SCHEFFER. 2005. A strategy to improve the contribution of complex simulation models to ecological theory. *Ecol. Model.* 185(2–4):153–164.
- VANCLAY, J.K. 1994. *Modelling forest growth and yield: Applications to mixed tropical forests*. CAB International, Wallingford, UK. 312 p.
- VANDERMEER, J. 1978. Choosing category size in a stage projection matrix. *Oecologia* 32:79–84.
- VASCONCELOS, S.S., N. HIGUCHI, AND M.V.N. OLIVEIRA. 2009. Projeção da distribuição diamétrica de uma floresta explorada seletivamente na Amazônia Ocidental. *Acta Amazon* 39(1): 71–80.
- VERZELEN, N., N. PICARD, AND S. GOURLET-FLEURY. 2006. Approximating spatial interactions in a model of forest dynamics as a means of understanding spatial patterns. *Ecol. Complex* 3(3):209–218.
- VIRGILIETTI, P., AND J. BUONGIORNO. 1997. Modeling forest growth with management data: A matrix approach for the Italian Alps. *Silva Fenn.* 31(1):27–42.
- VOLIN, V.C., AND J. BUONGIORNO. 1996. Effects of alternative management regimes on forest stand structure, species composition, and income: A model for the Italian Dolomites. *For. Ecol. Manage.* 87(1–3):107–125.
- WADSWORTH, R.K. 1977. *A study of diameter distributions of an uneven aged tropical forest by means of a transition matrix model*. PhD thesis, University of Washington, Seattle, WA. 153 p.
- WANG, F., G. SHAO, L. DAI, AND S. HUI. 2005. Application of matrix model in forest alternative cutting management. *Chin. J. Ecol.* 24(6):681–684 (in Chinese).
- WEI, X., X. LEI, L. HONG, J. SUN, AND P. WANG. 2011. Matrix growth model and harvest scenario simulation for multiple uses of larch-spruce-fir forests. *Sci. Silv. Sin.* 47(6):77–87.
- YANG, F.E., AND S. KANT. 2008. Forest-level analyses of uneven-aged hardwood forests. *Can. J. For. Res.* 38(2):376–393.
- ZETLAOUI, M., N. PICARD, AND A. BAR-HEN. 2006. Asymptotic distribution of stage-grouped population models. *Math. Biosci.* 200(1):76–89.
- ZETLAOUI, M., N. PICARD, AND A. BAR-HEN. 2007. Robustness of the estimators of transition rates for stage-classified matrix models. *Comput. Stat. Data Anal.* 51(10):5090–5102.
- ZETLAOUI, M., N. PICARD, AND A. BAR-HEN. 2008. Asymptotic distribution of density-dependent stage-grouped population dynamics models. *Acta Biotheor.* 56(1–2):137–155.
- ZHAO, D., B. BORDERS, AND M. WILSON. 2005. A density-dependent matrix model for bottomland hardwood stands in the Lower Mississippi Alluvial Valley. *Ecol. Model.* 184(2–4): 381–395.
- ZHOU, M., AND J. BUONGIORNO. 2004. Nonlinearity and noise interaction in a model of forest growth. *Ecol. Model.* 180(2–3):291–304.
- ZHOU, M., AND J. BUONGIORNO. 2006. Forest landscape management in a stochastic environment, with an application to mixed loblolly pine-hardwood forests. *For. Ecol. Manage.* 223:170–182.
- ZHOU, M., AND J. BUONGIORNO. 2011. Effects of stochastic interest rates in decision making under risk: A Markov decision process model for forest management. *For. Pol. Econ.* 13(5):402–410.
- ZHOU, M., J. BUONGIORNO, AND J. LIANG. 2008a. Economic and ecological effects of diameter caps: A Markov decision model for Douglas-fir/western hemlock forests. *For. Sci.* 54(4):397–407.
- ZHOU, M., J. LIANG, AND J. BUONGIORNO. 2008b. Adaptive versus fixed policies for economic or ecological objectives in forest management. *For. Ecol. Manage.* 254(2):178–187.
- ZUIDEMA, P.A. 2000. *Demography of exploited tree species in the Bolivian Amazon*. PhD thesis, Universiteit Utrecht, Utrecht, The Netherlands.
- ZUIDEMA, P.A. 2006. What dimension to use for matrix models of trees? Recommendations based on a validation of age estimate by tree ring analysis. P. 107–124 in *Demography of threatened tree species in Vietnam*, Chien, P.D. (ed.). Utrecht University, Utrecht, The Netherlands.
- ZUIDEMA, P.A., E. JONGEJANS, P.D. CHIEN, H.J. DURING, AND F. SCHIEVING. 2010. Integral projection models for trees: A new parameterization method and a validation of model output. *J. Ecol.* 98(2):345–355.