Assessing size–class dynamics of a neotropical gallery forest with stationary models

Iris Roitman [a,*], Jerome K. Vanclay [b,1]

[a] *Universidade de Brasília, PO Box 04357, Brasília 70919970, Brazil*
[b] *Southern Cross University, Lismore, New South Wales 2480, Australia*

ABSTRACT

We used stationary matrix models to assess size–class dynamics of a protected neotropical gallery forest in Central Brazil, and tested their predictive capacity for different calibration periods. Data series comprised of all trees (with diameter ≥ 10 cm) registered in 151 (10 m × 20 m) permanent plots in the years of 1985, 1988, 1991, 1994, 1999, 2004, and 2009. Demographic and diameter growth rates fluctuated, and recruitment slightly decreased after 1991. All models produced reliable ($P > 0.05$) short-term projections ($\leq$10 years). However, models calibrated before 1991 produced unreliable >10-year projections. The model calibrated over the 1991–1994 period reliably predicted size–class structure after 5 consecutive 3-year simulations (15 years). Results show that short-term (10-year) size–class structure of protected neotropical rainforests can be reliably predicted using stationary matrix models; and that predictions are slightly sensitive to the calibration period. Although stand dynamics were variable and affected by environmental stochasticity, size–class structural dynamics remained close to constant after 1991, since all projections from stationary models calibrated after that year were similar to the observed data ($P > 0.05$). This indicates that, under the recent levels of natural disturbances, the forest has maintained stability in the size–class dynamics.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Size–class matrix models can reveal important information on how forests behave under certain conditions (Keyfitz and Caswell, 2005) and have extensive application in forestry (see Liang and Picard, 2013). When calibrated on undisturbed forests, they help evaluate sustainability of particular harvesting regimes (Gourlet-Fleury et al., 2005). Stationary models (fixed-parameter models) assume transition probabilities are constant over time. This assumption is evidently false, because size–class parameters do change over time and are, in fact, density-dependent (Buongiorno and Michie, 1980). This explains the widespread application of density-dependent models (variable-parameter models) for forestry applications (Hao et al., 2005; Lin and Buongiorno, 1997; Orois and Soalleiro, 2002; Solomon et al., 1986; Zhao et al., 2005). Although the stationary assumption compromises long-term

predictions, stationary size–class models are useful tools for forest management and conservation.

Keyfitz (1972) distinguished the terms forecast and projection. The former predicts what will happen in the future, whereas the latter describes what would happen under certain conditions. Forecasts can be unrealistic, but projections provide valuable information about present conditions of the forest, and the populations experiencing them. A powerful way to study the present conditions is to examine their projected consequences, if model parameters (mortality, growth and recruitment) remain constant. Demographic projections are particularly revealing because they integrate the impact of environmental conditions on vital rates throughout the life cycle. Knowing size–class parameters under given circumstances conveys a great deal of biological information about those circumstances (Keyfitz and Caswell, 2005).

Stationary models for size–structure projections are widely used for tropical forest management (Bruner and Moser, 1973; Buongiorno and Michie, 1980; Picard et al., 2007, 2009). However, little is known about multiple or long-term forecasts from these models, and how the reliability of predictions changes with calibration period. Most published models calibrated for natural

---

* Corresponding author. Tel.: +55 61 3468 3911.
  E-mail addresses: irisroitman01@gmail.com (I. Roitman),
jerry.vanclay@scu.edu.au (J.K. Vanclay).
[1] Tel.: +61 2 6620 3700.

tropical and sub-tropical forests have relied on few measurements and, therefore, projections could not be tested *ex post* against observed data (Pulz et al., 1999; Spathelf and Durlo 2001; Teixeira et al., 2007). Besides, the few studies comparing the projected and the observed size–class distributions tested only for short-term single projections (Austregésilo et al., 2004; Vasconcelos et al., 2009).

The present study is based on seven measurements of a well-protected neotropical gallery forest over a 24-year period. The two main objectives are: to test the predictive capacity of stationary size–class models, based on different calibration periods, for single step and multiple-step projections, by validating model projections against field data; and to assess size–class structure dynamics based on the analysis of these models and their projections.

2. Methods

2.1. Study site

Gallery forests are riparian corridors of non-deciduous tropical forests that act as buffer zones protecting rivers. In the Brazilian savannah biome, called Cerrado, they connect the world's two largest neotropical forests, the Amazon and Atlantic Forest (Oliveira-Filho and Ratter, 1995). The Gama stream gallery forest covers 64 ha in the East-Central region of Brazil, near the city of Brasília ($\cong 16°$ S, $48°$ W) at an altitude of 1100 m. The forest is surrounded by campo limpo (natural dry grassland) vegetation, with an abrupt transition between these vegetation types (Fig. 1). The topography undulates gently, and the soil is well drained, dystrophic, with high aluminum saturation, and low nutrient concentration.

Köppen's (1900) classification categorizes the climate as Aw, with rainy summers and dry winters. Mean annual rainfall between 1984 and 2009 was of 1392 mm, with a mean annual temperature of 22 °C. Environmental data registered close to the study area, at the Brazilian Institute of Geography and Statistics' Ecological Reserve (RECOR-IBGE), revealed annual precipitation cycles with alternate periods of high and low annual precipitation. The period 1991–1994 departed from this trend and exhibited higher-than-average annual precipitation each year. Variations in mean annual temperatures were also observed, with a temperature increase trend after 1991 (Fig. 2).

A total of 52 families and 105 tree species were found in 1985, considering trees with diameter at breast height (dbh) $\geq$ 10 cm. Species richness gradually increased to 112 species in 2009. Species abundance distribution was typical of tropical forests: in 1985 and 2009, a large portion of tree species had five stems or less per hectare (72.38% and 76.32%, respectively), and the 10 most abundant species comprised almost half of the total number of stems (47.71% and 48.50%, respectively). The five most dominant species in 1985, in terms of relative abundance and basal area, were
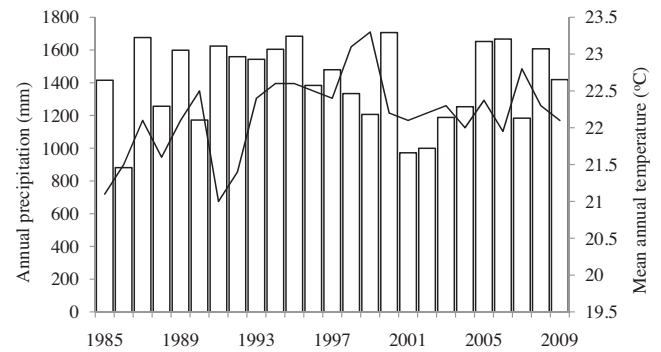

Fig. 2. Annual precipitation (mm) and mean annual temperature (°C) between 1985 and 2009 registered close to the study area, at the Brazilian Institute of Geography and Statistics' Ecological Reserve (RECOR-IBGE).

Lamanonia ternata Vell., *Copaifera langsdorffii* Desf., *Aspidosperma olivaceum* Müll. Arg., *Licania apetala* (E. Mey.) Fritsch, and *Metrodorea stipularis* Mart. (Felfili, 1995a). Most dominant species have kept a strong occupation since 1985. Tree density and basal area decreased, respectively, from 649.7 ind. ha^{-1} and 30.6 m^2 ha^{-1} in 1985 to 617.9 ind. ha^{-1} and 28.6 m^2 ha^{-1} in 2009. The forest is highly dynamic and has presented fluctuations in stand mortality and recruitment during the study period (Felfili, 1995a,b; Roitman, 2011) (Table 1).

2.2. Sampling

The sample consists of 151 permanent plots of 10 m × 20 m (3.02 ha) contiguously distributed in 10 transects, perpendicular to the water course and 100 m apart (Fig. 1). Data consisted of all stems with girth $\geq$ 31 cm ($\cong$10 cm diameter) at breast height, measured in 1985, 1988, 1991, 1994, 1999, 2004, and 2009. Matrix models included data on all sampled tree species.

2.3. Model construction and analysis

2.3.1. Size–class interval

When choosing size–class intervals we must regard an essential unrealistic assumption of size–class models: all trees in the same class behave exactly the same. Narrow intervals are more precise but may lead to empty states (classes with no trees) or intermediate absorbing states (classes in which all trees are retained), both of which compromise multi-step projections. The balance between size–class and census intervals defines model resolution. For a given calibration period, greater resolution may be gained with smaller size–class intervals. On the other hand, shorter size–class intervals result in a greater number of parameters of the model. Therefore, there should be a compromise in which classes
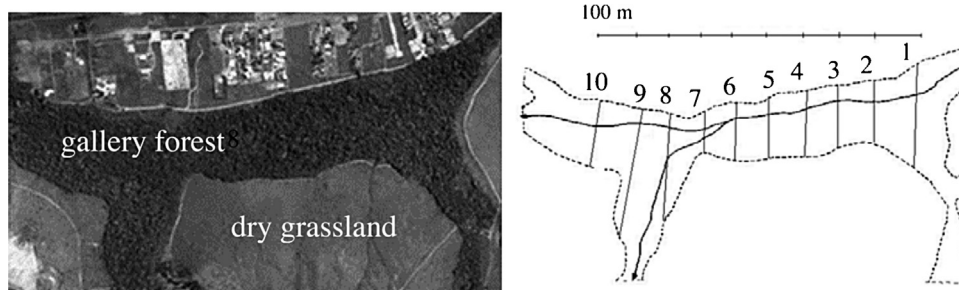

Fig. 1. Gama stream gallery forest in Fazenda Água Limpa, Brasília – DF, and the sample composed of 10 transects perpendicular to the water course.

Table 1
Species richness, tree density, basal area, mean annual diameter increment, and linear mortality and recruitment rates registered in 3.02 ha of the Gama gallery forest between 1985 and 2009. Where sp: number of species, BA: basal area, m: mortality rate, r: recruitment rate, Inc.: mean annual diameter increment rate, St. dev.: standard deviation.

Year	sp (sp ha^{-1})	Density (ind. ha^{-1})	BA (m^2 ha^{-1})	Period	m (% yr^{-1})	r (% yr^{-1})	inc. (cm yr^{-1})	Inc. St.dev
1985	35.1	649.7	30.6					
1988	35.4	645.4	30.3	1985–1988	3.36	3.14	0.258	0.297
1991	35.4	651.7	30.1	1988–1991	2.91	3.23	0.206	0.293
1994	36.1	637.4	30.3	1991–1994	3.29	2.56	0.263	0.357
1999	36.1	593.4	29.1	1994–1999	3.71	2.33	0.21	0.279
2004	37.1	617.2	30.0	1999–2004	1.55	2.35	0.235	0.278
2009	37.1	617.9	28.6	2004–2009	2.31	2.33	0.136	0.251

are narrow enough for good resolution and wide enough not to proliferate the parameters. In the present study, we used eleven 5-cm size–classes, to ensure that each size–class (except the largest with dbh >60 cm) had at least one stem transitioning to the next class, thus, avoiding absorbing states below the maximum size.

Two calibration periods (1988–1991 and 1991–1994) had no mortality in the last class, resulting in absorbing states (trees accumulate indefinitely). Long-term simulations should apply the mortality rate from an adjacent size class. A better alternative is probably to estimate the mortality functions using logistic regression rather than by tabulating data for each class (Vanclay, 1991). The unrealistic long-term behavior of the model is basically an issue of parameter estimation. An inherent constraint of tree growth matrix models that include both mortality and growth relates to the fact that trees are long-lived organisms which tend to grow continuously for most part of their life-span. Therefore, optimal intervals (size–class and calibration intervals) for estimating growth parameters are different from the ones estimating mortality.

2.3.2. Transition matrices

The large number of measurements allowed the construction of six matrix models calibrated over different time intervals (1985–1988, 1988–1991, 1991–1994, 1994–1999, 1999–2004, and 1985–1991), reserving at least one interval for validation against observed data. For each calibration interval, a 12×12 transition matrix (**G**) was built, the first 11 states represent transition probabilities between size–classes, and the last state represents class mortality (Table 2).

The transition matrix consisted of the ratio of trees from a given class that, during the given calibration period, remained in that class (elements in the main diagonal), died (mortality ratio) (elements in the last row), moved up to one or more classes (upgrowth) (elements below the main diagonal, except for the last row) or moved down to a different class due to stem loss or shrinkage (elements above the main diagonal).

Reduction in tree diameter is common in continuous inventories in tropical regions (Condit et al., 1993; Milton et al., 1994; Holder, 2008; Pastur et al., 2007; Roitman et al., 2008), and is often accounted for in stand growth models (Higuchi et al., 2008; Mews et al., 2014). Diameter reduction can be caused by bark loss, insect attacks, canopy reduction, loss of large stems, etc. It can also be associated to physiological stress of suppressed trees (competition) (Pastur et al., 2007), water availability (e.g., low bark and sapwood water content) (Baker et al., 2002; Holder 2008), and sometimes precedes tree death (Swaine et al., 1987; Finegan and Camacho, 1999).

Transition to a previous class due to diameter reduction was observed only once (from class two to class one), during the 1999–2004 period, whereas progression to more than one class was more common and happened in all calibration periods (Table 2).

$$\mathbf{G} = \begin{bmatrix} p_{11} & p_{12} & & & & & & & & & \\ p_{21} & p_{22} & & & & & & & & & \\ p_{31} & p_{32} & p_{33} & & & & & & & & \\ & p_{42} & p_{43} & \cdot & & & & & & & \\ & & P_{53} & \cdot & \cdot & & & & & & \\ & & & \cdot & \cdot & \cdot & & & & & \\ & & & & \cdot & \cdot & & & & & \\ & & & & & \cdot & & & & & \\ p_{11,1} & p_{11,2} & p_{11,3} & \cdots & & & & & & p_{ai} & p_{11,11} & \\ p_{m1} & p_{m2} & p_{m3} & \cdots & & & & & & p_{mi} & p_{mm} \end{bmatrix} \quad (1)$$

(column headers: 12.5 17.5 22.5 27.5 32.5 37.5 42.5 47.5 52.5 57.5 ≥60 m)

where **G** = 12×12 transition matrix for a given calibration period, p_{11} = ratio of trees from class one that remained in class one, p_{21} = ratio of trees that transitioned from class one to class two, p_{ai} = ratio of trees from class i that moved a–i classes, p_{12} = ratio of trees that retrieved from class two to class one, p_{mi} = ratio of trees from class i that died, p_{mm} = 1.

2.3.3. Models' general form

Recruitment was assumed constant (Mendonza and Setyarso, 1986), and displayed as the number of recruits per size–class during calibration period. Single-step projections were made by adding the recruitment vector (**r**) to the product of transition matrix (**G**) and initial size–class distribution vector (**y**$_0$), as follows. Treating recruitment as a separate vector reduces variability within the matrix, and this general form is widely used in forest modelling (e.g., Buongiorno and Michie, 1980; Lin and Buongiorno, 1997; Osho, 1995; Porté and Bartelink, 2002; Pulz et al., 1999; Spathelf and Durlo, 2001).

$$\mathbf{y}_1 = \mathbf{G}\mathbf{y}_0 + \mathbf{r} \quad (2)$$

where $\mathbf{y}_1$ = 12-stage vector after a single-step projection, in which the first eleven states display size–class distribution, and the last one shows number of dead trees during a single projection period; **G** = transition matrix, $\mathbf{y}_0$ = initial 12-stage vector, representing initial size–class distribution (last matrix element = 0); and **r** = recruitment vector, representing the number trees recruited to each size–class.

Recruitment is often included as non-zero values in the top row of the population models, as presented in Caswell (2001). These values are not transition probabilities, but rather express size–class fecundity (Vanclay, 1994). A powerful advantage of such models, given their mathematical properties, is that they allow us to directly assess population stability based on dominant eigenvalues, stable-stage distributions (dominant eigenvectors) and damping ratios (Caswell, 2001). Dominant eigenvectors may indicate optimal stand structure, but not optimal stand density. Therefore, the central problem in forest management, determining optimum growing stock levels, cannot be solved with eigenvalues (Vanclay, 1994). Moreover, it is very difficult to estimate relative contribution of each class to recruitment especially for mixed-

Table 2
Transition matrices (**G**) built over six different calibration periods (1985–1988, 1988–1991, 1991–1994, 1994–1999, 1999–2004, 1985–1991. Transition probabilities values were rounded to three decimal places.

2.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	$\geq$60	m
G$_{1985-1988}$											
0.783											
0.066	0.776										
0.001	0.133	0.780									
		0.149	0.857								
			0.100	0.830							
				0.126	0.800						
					0.150	0.886					
						0.091	0.561				
							0.268	0.667			
								0.167	0.688		
									0.188	0.857	
0.150	0.091	0.071	0.043	0.044	0.05	0.023	0.171	0.167	0.125	0.143	1.000
G$_{1988-1991}$											
0.818											
0.071	0.823										
0.001	0.088	0.811									
	0.003	0.120	0.838								
			0.095	0.827							
				0.113	0.827						
					0.111	0.765					
						0.098	0.815				
							0.185	0.778			
								0.185	0.600		
									0.200	1.000	
0.11	0.086	0.069	0.068	0.060	0.062	0.137		0.037	0.200		1.000
G$_{1991-1994}$											
0.796											
0.076	0.792										
0.001	0.100	0.805									
	0.003	0.117	0.791								
			0.132	0.817							
				0.115	0.805						
			0.005	0.008	0.122	0.688					
						0.250	0.704				
							0.185	0.808			
								0.115	0.643		
								0.038	0.357	1.000	
0.127	0.105	0.078	0.073	0.061	0.073	0.063	0.111	0.038			1.000
G$_{1994-1999}$											
0.627											
0.115	0.756										
0.003	0.109	0.736									
	0.009	0.140	0.649								
			0.146	0.610							
			0.005	0.235	0.741						
				0.007	0.123	0.711					
						0.178	0.839				
						0.022	0.065	0.615			
								0.231	0.667		
								0.038	0.083	0.967	
0.256	0.126	0.124	0.200	0.147	0.136	0.089	0.065	0.115	0.250	0.033	1.000
G$_{1999-2004}$											
0.721	0.009										
0.202	0.750										
0.007	0.144	0.719									
		0.203	0.647								
		0.005	0.259	0.646							
				0.292	0.753						
				0.009	0.204	0.651					
						0.279	0.647				
							0.235	0.632			
						0.023		0.263	0.667		
									0.133	0.935	
0.071	0.098	0.074	0.094	0.053	0.043	0.047	0.118	0.105	0.200	0.065	1.000
G$_{1985-1991}$											
0.641											
0.124	0.641										
0.004	0.187	0.628									
0.001	0.012	0.238	0.700								

Table 2 (*Continued*)

2.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	≥60	m
		0.007	0.176	0.681							
			0.222		0.650						
				0.250		0.636					
					0.205		0.439				
						0.390		0.417			
							0.333		0.375		
								0.375		0.857	
0.229	0.160	0.128	0.124	0.096	0.100	0.159	0.171	0.250	0.205	0.143	1.000

Table 3
Number of trees recruited to the first two size–classes in all calibration periods based on plot inventories.

Class	Calibration period					
	1985–1988	1988–1991	1991–1994	1994–1999	1999–2004	1985–1991
1st	185	188	149	222	208	339
2nd		1	2	2	3	3

species models. Although we can estimate size–class fructification, it is impractical to determine parents of new recruits, especially when vegetative reproduction is common and newborns may take decades to reach minimum threshold diameter of tropical forest inventories.

Size–class distributions after n-step projections ($\mathbf{y}_n$) were calculated as follows:

$$\mathbf{y}_n = \mathbf{G}^n \mathbf{y}_0 + \mathbf{r} \tag{3}$$

where $\mathbf{y}_n$ = 12-stage vector projected for n-step projections, $\mathbf{y}_0$ = size–class vector at time 0, in which the last element is the number of dead trees, $\mathbf{G}$ = transition matrix, and $\mathbf{r}$ = constant recruitment vector.

2.3.4. Validation and analysis

Models were validated against the observed data on every simulated occasion that coincided with field measurements. Predictive validation compared projected against observed data with non-parametric Kolmogorov–Smirnov test ($P > 0.05$), based on (Austregésilo et al., 2004; Sokal and Rohlf, 1995). The test is based on the maximum absolute difference (D_{max}) between the two cumulative frequency distributions. All the calculations were done using Microsoft Excel 2010 software.

Under the assumption that annual probability ratios are constant within a calibration period, mortality and up-growth ratios were also expressed on a yearly basis in order to compare ratios between models based on calibration periods of different lengths (three, five and six-year periods).

$$p_{yr} = 1 - (1 - p_t)^{1/t} \tag{4}$$

where Δt = calibration period (yr); p_{yr} = annual probability ratio; p_t = probability ratio obtained over the calibration period.

3. Results

All models (except for $\mathbf{G}_{1985-1991}$) were tested for single-step projections. All single-step projections proved to be statistically similar ($P > 0.05$) to the observed data (Table 4). Two models were projected for two consecutive periods ($\mathbf{G}_{1985-1988}$ and $\mathbf{G}_{1994-1999}$) and offered reliable predictions (for a 6-yr and a 10-yr period, respectively). Model $\mathbf{G}_{1991-1994}$, produced a reliable simulation after five consecutive time-steps, totaling 15-years. Models $\mathbf{G}_{1985-1988}$, $\mathbf{G}_{1988-1991}$ and $\mathbf{G}_{1985-1991}$ failed to predict the forest's structure after seven-step, six-step and three-step projections, respectively. Annual up-growth ratios increased from classes one to three (Fig. 3C and D) in all calibration periods, except for 1999–2004, in
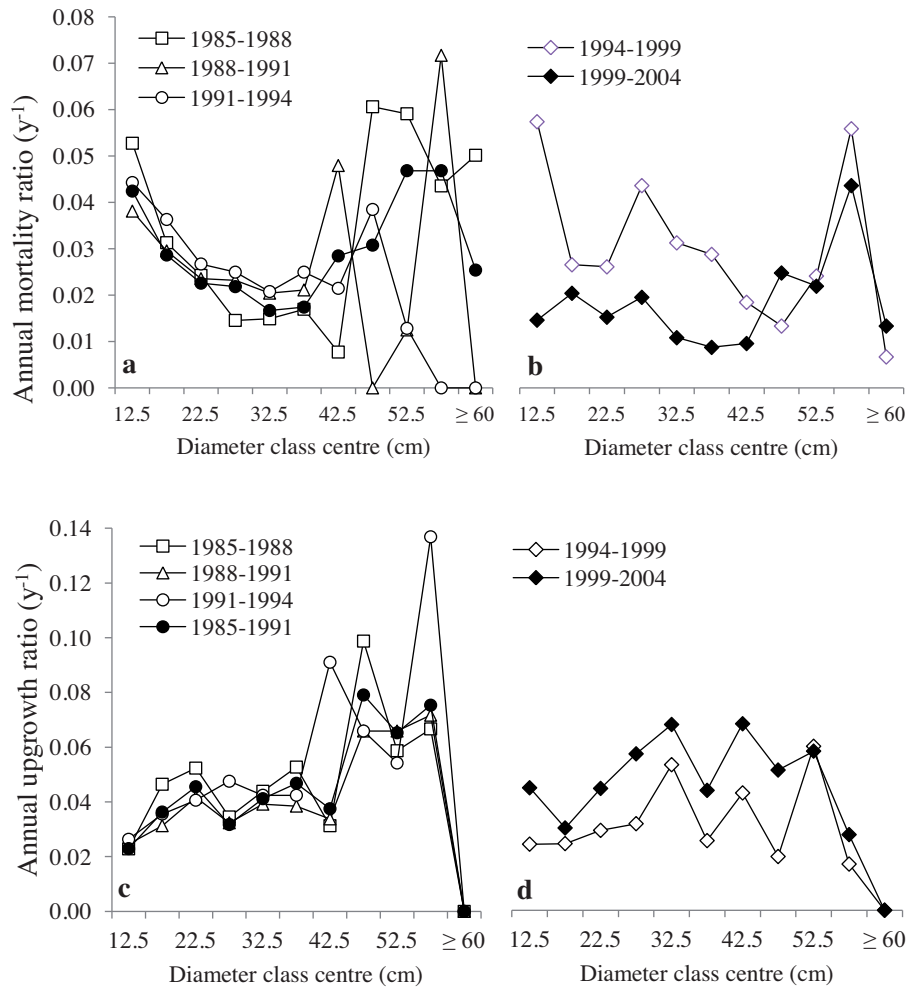
Table 4
Observed and projected size–class distributions, and Kolmogorov–Smirnov test results. D_{max}: maximum absolute difference between observed and expected cumulative distributions; Dα: threshold for Kolmogorov–Smirnov; ns: projected and observed data are statistically similar ($P > 0.05$). Projected values marked in bold represent the class in which D_{max} was observed.

Model projections	Observed distributions (Y_{year})				Projected distributions									
	Y_{1991}	Y_{1994}	Y_{2004}	Y_{2009}	$Y_{1985-1988}$ 1988–1991	$Y_{1985-1988}$ 1988–1994	$Y_{1988-1991}$ 1991–1994	$Y_{1994-1999}$ 1999–2004	$Y_{1985-1988}$ 1988–2009	$Y_{1988-1991}$ 1991–2009	$Y_{1991-1994}$ 1994–2009	$Y_{1994-1999}$ 1999–2009	$Y_{1999-2004}$ 2004–2009	$Y_{1985-1991}$ 1991–2009
Class center (cm) 12.5														
12.5	789	777	719	766	761	781	**833**	**666**	833	**959**	745	640	**722**	**903**
17.5	351	340	406	411	**329**	**305**	346	346	257	359	303	340	447	315
22.5	256	242	209	211	264	250	240	199	**194**	194	**193**	186	211	194
27.5	220	205	158	151	231	237	216	144	234	186	150	124	142	204
32.5	131	136	118	98	133	133	129	94	138	118	130	**78**	117	127
37.5	82	81	103	81	82	82	83	96	84	82	80	94	111	82
42.5	48	45	48	53	57	63	46	43	84	41	39	43	53	54
47.5	27	31	34	31	20	16	27	36	16	24	34	38	35	20
52.5	26	26	20	18	25	22	25	15	13	22	30	12	21	15
57.5	14	12	16	16	15	14	13	15	9	11	10	15	17	10
≥60	24	30	31	30	21	21	27	32	18	39	54	33	31	28
D_{max}					0.0162	0.0156	0.0172	0.0088	0.0613	0.0608	0.0413	0.0240	0.0324	0.0519
Dα					0.0434 [ns]	0.04378 [ns]	0.0434 [ns]	0.0457 [ns]	0.0444	0.0435	0.0451 [ns]	0.0463 [ns]	0.0442 [ns]	0.0439

Fig. 3. Annual mortality and upgrowth ratios of the six matrices constructed in the present study. Calibration periods prior to 1994 are represented in a and c, whereas calibration periods after 1994 are represented in b and d.

which growth rates increased from classes two to four. For trees with diameter <30 cm (≅80% of the sample) annual mortality ratios decreased with size–class in calibration periods prior to 1994 (Fig. 3A). Size-dependent mortality suggests competition driven mortality among smaller trees. For larger trees, which are less affected by competition, mortality is often triggered by stochastic disturbances (fire, wind, extreme droughts, insect outbreaks, etc.). Mortality pattern in larger size–classes (diameter ≥40 cm) was erratic (Fig. 3A), as expected for stochastic mortality. Nonetheless, high variation can be partly explained by the reduced number of trees with larger size–classes (since mortality estimates are sensitive to the total number of trees on each class).

The 1994–1999 period was marked by higher mortality, especially in classes one and three, followed by classes four and five (Fig. 3B). High mortality during this period may have contributed the lower mortality and higher up-growth observed between 1999 and 2004 (Fig. 3B and D).

4. Discussion

This study demonstrated that stationary size–class transition models based on short calibration periods can generate reliable short-term (≤ 10 year) projections (Table 4), in spite of temporal fluctuations in the forest's vital rates, known as environmental stochasticity (Keyfitz and Caswell, 2005) (Table 4). A 10-year projection is a short period when considering the tropical forest's

natural cycles, but it is long enough to provide valuable information on the implications of present practices, and thus, of forest management and conservation measures.

Longer calibration periods may incorporate such fluctuations in forest dynamics and, therefore, should deliver more reliable long-term projections. This assumption was not tested in the present study because available data allowed testing only of short-calibration periods. Conversely, as calibration period increases, there is a trade-off between the benefits from incorporating temporal fluctuations and model resolution. The amount of time needed to include considerable fluctuations, particularly in highly dynamics forests, may be longer than the half-life of the forest. In Gama gallery forest, for instance, half-life of the forest, calibrated over the 1985–2009 period was ≅24 years (Roitman, 2011).

Mortality and recruitment tend to be underestimated in the first class(es) as calibration period increases because it does not account for recruited trees that die within the period. This trend has a major significance when comparing estimates produced over different census-interval lengths (Lewis et al., 2004; Sheil and May, 1996). However, these errors in recruitment and mortality should compensate since both will be underestimated, and there should be little effect over model projections. Due to the small difference between calibration interval lengths, there was no apparent reduction in mortality estimates as calibration period increased (Fig. 3A and B).

Table 5
Projected distributions (Y_{2009}) from 1994 to 2009 with models $\mathbf{G}_{1985-1988}$ and $\mathbf{G}_{1988-1991}$, and respective Kolmogorov–Smirnov ($P > 0.05$) test results. Y_{2009}: observed distribution in 2009, D_{max}: maximum absolute difference between observed and expected cumulative distributions; Dα: threshold for Kolmogorov–Smirnov. Projected values marked in bold represent the class in which D_{max} exceeded Dα critical value.

Diameter class centre (cm)	Y_{2009}	Y_{2009} ($\mathbf{G}_{1985-1988}$)	Y_{2009} ($\mathbf{G}_{1988-1991}$)
12.5	766	832	**938**
17.5	411	266	348
22.5	211	**197**	192
27.5	151	219	181
32.5	98	130	118
37.5	81	82	82
42.5	53	74	41
47.5	31	14	25
52.5	18	15	24
57.5	16	11	12
≥60	30	23	42
D_{max}		0.049	0.051
Dα		0.045	0.044

General trends in mortality and up-growth ratios indicate that the trees belonging to the smallest size classes grow slower, have greater chances of dying and lesser chances of moving up to subsequent classes (Fig. 3A–D). Size–class dependent mortality observed prior to 1994 suggests competition driven mortality during that period (Fig. 3A and B). Temperature increase and lower precipitation after 1994 may have contributed to the observed increase in mortality for the 1994–1999 period. Increased mortality rates are often associated to high temperature and drought events, such as the ones caused by El Ninõ (Clark, 2004; Laurance et al., 2009).

The 1991–1994 period was marked with higher-than-average annual precipitation and annual temperature increase (Fig. 1). This period offered a reliable insight into forest dynamics for following 15-year period (1994–2009) (Table 4), whereas the two other 3-yr based models, $\mathbf{G}_{1985-1988}$ and $\mathbf{G}_{1988-1991}$, offered reliable projections for 10 years or less. Mortality ratio trends were quite similar in these three periods. However, recruitment in 1985–1988 and 1988–1991 was higher than 1991–1994 and the subsequent periods (Tables 1 and 3). For this reason, projections to 2009 produced by models calibrated prior to 1991 ($\mathbf{G}_{1985-1988}$, $\mathbf{G}_{1988-1991}$ and $\mathbf{G}_{1985-1991}$) overestimated the number of trees in the first class (Tables 4 and 5).

After gap formations or canopy openings caused by small disturbances, tree growth and regeneration is expected to increase. However, it may take many years for a seedling to reach the minimum size to be included in the sample. Assuming a mean annual increment of 0.25 cm year^{-1}, a juvenile with 1 cm diameter would take 36 years to reach 10-cm minimum threshold for this study. Therefore, unless calibration period is long enough to cover time-lag in recruitment response, a constant (instant) recruitment model may be more realistic than a model that assumes recruitment is negatively affected by stand density. In fact, Gama gallery forest had small reductions in both density and recruitment over the study period (Table 1). Therefore, recruitment rates should indicate the forest's response to remote disturbances, whereas size–class transition probabilities reflect the immediate response of the forest against recent environmental changes.

Tropical forests are highly dynamic non-linear systems. Many ecological processes that occur within these forests are driven by stochastic and unpredictable events. Fluctuations in vital rates dynamics are common (Condit et al., 1995; Lewis et al., 2004; Phillips et al., 2004), and reflect the forest's response to the changes in the environment. Periods in which transition probabilities remain relatively constant may indicate the systems stability against environmental changes. The fact that all tested single

projections were reliable indicates that the observed demographic and growth fluctuations did not alter transition probabilities in the forest's diameter distribution for the following period. This means that environmental changes, such as natural disturbances and climatic changes, that triggered observed demographic and growth fluctuations, were relatively small and had no short-term visible effect over size–class transition probabilities.

The greatest discrepancy between total mortality and recruitment occurred in the period 1994–1999, during which a total mortality of 357 trees was offset by a mere 224 recruits. Normal trends returned in the two following periods, towards greater balance between recruitment and mortality. Nevertheless, the model $\mathbf{G}_{1994-1999}$ reliably predicted the size–class structure of the forest for two consecutive periods (10 years), suggesting that the apparently abnormal mortality did not affect the utility of transition probabilities for the following decade. Moreover, the fact that the 1994–2009 projection (with model $\mathbf{G}_{1991-1994}$) was statistically similar to the observed distribution in 2009 indicates that, despite demographic changes, probability transitions registered in the 1991–1994 period have remained close to constant for the 15-year projection period.

5. Conclusions

This study presents two major contributions for tropical forest modelling. It demonstrates that: (i) stationary matrix models can reliably predict short-term (10-year) size–class structural dynamics of neotropical rainforests; and (ii) predictions are slightly sensitive to the calibration period and interval. The latter result has rarely been shown, as most studies are restricted to the choice of class width rather than the choice of time interval.

Size–class stationary models revealed important insights into the forest's dynamics. General trends showed that smaller trees grow slower and have more chances of dying. Although stand dynamics were variable within the last 18 years of the study period, size–class structural dynamics remained relatively constant, as all projections from models calibrated after 1991 were similar to observed field data. This indicates that, under the recent levels of natural disturbances, the forest has maintained stability in size–class dynamics.

Acknowledgements

References

Austregésilo, S.L., Ferreira, R.L.C., da Silva, J.A.A., Souza, A.L., Meunier, I.M.J., Santos, E.S., 2004. Comparação de métodos de prognose da estrutura diamétrica de uma floresta estacional semidecidual secundária. Revista Árv. 28 (2), 227–232.

Baker, T.R., Affum-Baffoe, K., Burslem, D.F.R.P., Swaine, M.D., 2002. Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of dry season diameter change. For. Ecol. Manage. 171, 261–274.

Bruner, H.D., Moser, J.W.J., 1973. A Markov chain approach to the prediction of diameter distributions in uneven-aged forest stands. Can. J. For. Res. 3, 409–417.

Buongiorno, J., Michie, B.C., 1980. A matrix model for uneven-aged forest management. For. Sci. 26, 609–662.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, second ed. Sinauer Associates, Sunderland.

Clark, D.A., 2004. Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. Philos. Trans. R. Soc. B 359, 477–491.

Condit, R., Hubbell, S.P., Foster, R.B., 1993. Mortality and growth of a commercial hardwood 'el cativo' *Prioria copaifera* in Panama. For. Ecol. Manage. 62, 107–122.

Condit, R., Hubbell, S.R., Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol. Monogr. 65, 419–439.

Felfili, J.M., 1995a. Growth, recruitment and mortality in Gama gallery forest in central Brazil over a six-year period (1985–1991). J. Trop. Ecol. 11, 67–83.

Felfili, J.M., 1995b. Diversity: structure and dynamics of a gallery forest in central Brazil. Vegetatio 117, 1–15.

Finegan, B., Camacho, M., 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988–1996. For. Ecol. Manage. 121, 177–189.

Gourlet-Fleury, S., Cornu, G., Jésel, S., Dessard, H., Jourget, J., Blanc, L., Picard, N., 2005. Using models to predict recovery and assess tree species vulnerability in logged tropical forests. A case study from French Guiana. For. Ecol. Manage. 209, 691–785.

Hao, Q., Meng, F., Zhou, Y., Wang, J., 2005. A transition matrix growth model for uneven-aged mixed-species forests in the Changbai Mountains, Northeastern China. New For. 29, 221–231.

Higuchi, P., Oliveira-Filho, A.T., Silva, A.C., Machado, E.L.M., Santos, R.M., Pifano, D.S., 2008. Dinâmica da comunidade arbórea em um fragmento de floresta estacional semidecidual montana em Lavras, Minas Gerais, em diferentes classes de solos. Rev. Arv. 32 (3), 417–426.

Holder, C.D., 2008. Diameter growth and decline in a tropical montane cloud forest of the Sierra de las Minas, Guatemala. J. Trop. For. Sci. 20 (4), 292–299.

Keyfitz, N., Caswell, H., 2005. Applied mathematical demography – Statistics for Biology and Health, fourth ed. Springer, New York.

Keyfitz, N., 1972. On future population. J. Am. Stat. Assoc. 67, 347–363.

Köppen, W., 1900. Versuch einer klassifikahtion der klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. Geogr. Z. 6, 593–611.

Laurance, S.G.W., Laurance, W.F., Nascimento, H.E.M., Andrade, A., Fearnside, P.M., Rebello, E.R.G., Condit, R., 2009. Long-term variation in Amazon forest dynamics. J. Veg. Sci. 20, 323–333.

Lewis, S.L., Phillips, O.L., Sheil, D., Vinceti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Vargas, P.N., Sonké, B., Nur Supardi, M.N., Terborgh, J.W., Martínez, R.V., 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., Picard, N., 2013. Matrix model of forest dynamics: an overview and outlook. For. Sci. 59 (3), 359–378.

Lin, C.R., Buongiorno, J., 1997. Fixed versus variable-parameter matrix models of forest growth. The case of maple-birch forests. Ecol. Model. 99 (2–3), 263–274.

Mendonza, G.A., Setyarso, A., 1986. Transition matrix forest growth model for evaluating alternative harvesting schemes in Indonesia. For. Ecol. Manage. 15 (3), 219–228.

Mews, H.A., Marimon, B.S., Maracahipes, L., Franczak, D.D., Marimon-Junior, B.H., 2014. Dynamics of the woody community of a typical cerrado in Northeastearn Mato Grosso, Brazil. Biota Neotrop. 11 (1), 73–82.

Milton, K., Laca, E.A., Demment, M.W., 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. J. Ecol. 82, 79–87.

Oliveira-Filho, A.T., Ratter, J.A., 1995. A study of the origin of Central Brazilian forests by the analysis of plant species distribution patterns. Edinb. J. Bot. 52, 141–194.

Orois, S.S., Soalleiro, R.R., 2002. Modelling the growth and management of mixed uneven-aged maritime pine-broadleaved species forest in Galicia, north-western Spain. Scand. J. For. Res. 17 (6), 538–547.

Osho, J.S.A., 1995. Optimal sustainable harvest models for a Nigerian tropical rain forest. J. Environ. Manage. 45, 101–108.

Pastur, G.M., Lencinas, M.V., Cellini, J.M., Mundo, I., 2007. Diameter growth: can live trees decrease? Forestry 80 (1), 83–88.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N.M., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C. A., Saldias, M., Torres-Lezama, A., Vinceti, B., 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philos. Trans. R. Soc. B 359, 381–407.

Picard, N., Banak, L.N., Namkosserena, S., Yalibanda, Y., 2009. The stock recovery rate in a Central African rain forest: an index of sustainability based on projection matrix models. Can. J. For. Res. 39, 2138–2152.

Picard, N., Bar-Hen, A., Gourlet-Fleury, S., 2007. Estimator of upgrowth transition rates for size-classified matrix from small samples. Ecol. Model. 204, 59–69.

Porté, A., Bartelink, H.H., 2002. Modelling mixed forest growth: a review of models for forest management. Eco. Model. 150, 141–188.

Pulz, F.A., Scolforo, J.R., Oliveira, A.D., Mello, J.M., Oliveira-Filho, A.T., 1999. Acuracidade da predição da distribuição diamétrica de uma floresta inequiânea com a matriz de transição. Cerne 5 (1), 1–14.

Roitman, I., 2011. Spatial and temporal modelling of the Gama gallery forest – DF. Doctorate Thesis. Universidade de Brasília, Brasília.

Roitman, I., Felfili, J.M., Rezende, A.V., 2008. Tree dynamics of a fire-protected cerrado sensu stricto surrounded by forest plantations over a 13-year period (1991–2004) in Bahia, Brazil. Plant Ecol. 297, 255–267.

Sheil, D., May, R.M., 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. J. Ecol. 84 (1), 91–100.

Sokal, R.S., Rohlf, F.J., 1995. Biometry, fourth ed W.H. Freeman Co., New York.

Solomon, D.C., Hosmer, R.A., Hayslett, J.R.H.T., 1986. A two-stage matrix model for predicting growth of forest stands in Northeast. Can. J. For. Res. 16, 521–528.

Spathelf, P., Durlo, M.A., 2001. Transition matrix for modeling the dynamics of a subtropical seminatural forest in southern Brazil. For. Ecol. Manage. 151, 139–149.

Swaine, M.D., Lieberman, D., Putz, F.E., 1987. The dynamics of tree populationsin tropical forest: a review. J. Trop Ecol. 3, 359–366.

Teixeira, L.M., Chambers, J.Q., Silva, A.R., Lima, A.J.N., Carneiro, V.M.C., Santos, J., Higuchi, N., 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 Amaz. 37 (3), 377–384.

Vanclay, J.K., 1991. Mortality functions for north Queensland rainforests. J. Trop. For. Sci. 4, 15–36.

Vanclay, J.K., 1994. Modelling Forest Growth and Yield. Applications to Mixed Tropical Forests. CAB International, Wallingford.

Vasconcelos, S.S., Higuchi, N., Oliveira, M.V.N., 2009. Projeção da distribuição diamétrica de uma floresta explorada seletivamente na Amazônia Ocidental. Acta Amaz. 39 (1), 71–80.

Zhao, D., Borders, B., Wilson, M., 2005. A density-dependent matrix model for bottomland hardwood stands in the Lower Mississippi Alluvial Valley. Ecol. Model. 184, 381–395.