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Is size structure a good measure of future trends of plant populations? An empirical approach using five woody species from the Cerrado (Brazilian savanna)

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RESUMO

(A estrutura de tamanho é uma boa medida de tendências futuras em populações de plantas? Uma abordagem empírica com cinco espécies lenhosas de Cerrado). As estruturas de tamanho de populações têm sido frequentemente usadas para inferir sobre a capacidade de regeneração de uma população, assumindo que as estruturas de tamanho com formato "J-invertido" representam populações estáveis. Nós apresentamos uma abordagem empírica desta questão com cinco espécies lenhosas de Cerrado. Usando dados de contagem de todas as plantas destas cinco espécies por um período de doze anos, nós analisamos a distribuição de tamanho dos indivíduos de duas maneiras: a) por meio de histogramas de frequência em classes de tamanho, e seu ajuste a uma curva exponencial negativa; b) calculando o coeficiente de Gini. Para verificar a existência de uma relação entre a estrutura de tamanho e as tendências futuras em número, consideramos a estrutura de tamanho no ano do primeiro censo. Foram analisadas as mudanças em número ao longo do tempo, por meio das taxas de crescimento populacionais e por análises de viabilidade de populações que fornece as taxas médias de crescimento das populações, sua variância e a probabilidade de extinção da população em um dado intervalo de tempo. Tanto as distribuições de frequência como o coeficiente de Gini não foram bons indicadores de tendências numéricas futuras das populações. Recomendamos que medidas de estrutura de tamanho não devem ser usadas como base para decisões de manejo sem que análises demográficas mais apropriadas sejam realizadas.

Palavras-chave: análise de viabilidade populacional, coeficiente de Gini, dinâmica populacional, formato "J-invertido"

ABSTRACT

(Is size structure a good measure of future trends in plant populations? An empirical approach using five woody species from the Cerrado (Brazilian savanna)). Size distributions in woody plant populations have been used to assess their regeneration status, assuming that size structures with "reverse-J" shapes represent stable populations. We present an empirical approach of this issue using five woody species from the Cerrado. Considering count data for all plants of these five species over a 12-year period, we analyzed size distribution by: a) plotting frequency distributions and their adjustment to the negative exponential curve and b) calculating the Gini coefficient. To look for a relationship between size structure and future trends, we considered the size structures from the first census year. We analyzed changes in number over time and performed a simple population viability analysis, which gives the mean population growth rate, its variance and the probability of extinction in a given time period. Frequency distributions and the Gini coefficient were not able to predict future trends in population numbers. We recommend that managers should not use measures of size structure as a basis for management decisions without applying more appropriate demographic studies.

Key words: Gini coefficient; population dynamics; reverse-J shape; population viability analysis

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Introduction

The structure of a plant population is the result of the actions of biotic and abiotic factors upon the growth and mortality rates of individuals and of past recruitment events (Hutchings 1997). The size structure of a population is determined by factors influencing size variations among individuals, such as differences in seed size, time of germination of each seed in relation to its neighbors, growth rate of each plant (which depends on ecological and genetic factors), distance of each plant to its closest neighbor (competition), and the behavior pattern of herbivores (Hutchings 1997).

The size structure of plant populations has been frequently used to assess regeneration status and to predict future population changes by assuming that populations with many small stems in relation to larger ones are self-replacing or increasing, whereas populations with relatively few small stems are believed to be declining in abundance (Knight 1975; Lorimer 1980; Sarukhán 1980; Felfili and Silva-Júnior 1988; Silva-Júnior and Silva 1988; Hart *et al.* 1989; Read *et al.* 1995; Hay 2002; Buyavejchewin *et al.* 2003; Baker *et al.* 2005). Johnson *et al.* (1994) and Condit *et al.* (1998) have already pointed out how complicated it is to make inferences about the future trends of populations using point data from the size structure, since declining populations can show size structures with a classic "reverse-J" shape and increasing or stable populations can show size structures that do not adjust to the negative exponential curve due to differences in growth rates among size classes. Wright *et al.* (2003) showed that shade-tolerance and other demographic traits such as fecundity, seed mortality, seedling mortality, recruitment, sapling growth and sapling mortality rates are related to population size structure, but there is no empirical evidence that population size structures are related to changes in population size. However, due to the difficulty of gathering appropriated demographic data (which is very time consuming), this kind of inference is still being made.

The aim of this study was to investigate, from an empirical data set, whether measures of size structure are related to future trends in the number of plant populations, given by the population growth rates and by the probability of extinction within a certain future time based on population viability analysis (PVA - Morris & Doak 2002).

Materials and methods

Study site

This study was conducted in a Cerrado (Brazilian savanna) fragment called Valério at the Estação Ecológica e Experimental de Itirapina (22° 15' S; 47° 49' W, 760 m a.s.l.), in the municipality of Itirapina, São Paulo State, Southeastern Brazil. The climate in this region is Köppen's Cwa, with an average annual rainfall of 1425 mm, concentrated from October to May (Delgado 1994) and average temperatures between 16.2 and 20.1 °C in the dry season and between 19.5 and 22.3 °C in the wet season (Giannotti 1988). The soil is Haplic Arenosol according to the FAO classification system (Oliveira & Prado 1994): a deep, very sandy soil (over 80% sand), with low nutrient content, high aluminum content, and free drainage.

The vegetation physiognomy is a dense Cerrado (following the classification of Ribeiro & Walter 1998), with a predominance of arboreal elements, a canopy cover varying between 50% and 70%, and plants with an average height of 5-8 m. The Valério fragment has an area of about 60 ha, and is isolated by a 30 m-wide firebreak from plantations of *Pinus elliottii* Engelm. and *Eucalyptus saligna* Sm. The fragment has been protected from human action (fire, cattle and plant collection) since 1984. In other studies done in this fragment, a total density of 7,156.3 trees.ha^{-1} and a basal area of 8.43 m^2.ha^{-1} were recorded, with a total of 47 woody species with a trunk diameter at soil level (DSL) ≥ 3 cm (Aoki *et al.*, personal communication). Salomão *et al.* (personal communication) found that the site has a high floristic similarity (more than 50%, Sørensen similarity coefficient) with other Cerrado fragments in the municipality of Itirapina.

Study Species

Dalbergia miscolobium Benth. (Fabaceae), *Miconia albicans* (Sw.) Steud. (Melastomataceae), *Xylopia aromatica* (Lam.) Mart. (Annonaceae), *Roupala montana* Aubl. (Proteaceae) and *Vochysia tucanorum* Mart. (Vochysiaceae) are woody species frequently found in floristic and phytosociological studies of the Cerrado (*lato sensu*) in the region of Itirapina, in the state of São Paulo (Mantovani 1987), and at other Cerrado areas in Brazil (Lorenzi 1992, Martins *et al.* 1996, Durigan *et al.* 2004). Hereafter the species will be referred by their generic names. *Dalbergia* and *Vochysia* are considered trees, while *Roupala, Xylopia* and *Miconia* are considered treelets.

Data Collection

In a 0.16 ha permanent plot, all the plants of the studied species were annually counted and measured (but not tagged) from 1995 to 2007, except *Roupala* that was censused from 1996 to 2007. The trunk diameter at the soil height was measured with a caliper (precision = 0.1 mm), or, in the case of irregular (not cylindrical) trunks, the perimeter of the trunk at soil height was measured with a ruler strip. These data were collected during the field courses of the Graduate Program of Ecology of the Universidade Estadual de Campinas (UNICAMP) (Santos *et al.* 2007), and the techniques of measuring the plants were standardized between years. In 1998 and 2000 these courses were not offered and data were not collected.

Data Analysis

We chose two ways of assessing the size distribution of plants within the populations: density histograms of DSL classes and the degree of size hierarchy of each population measured by the Gini coefficient (Weiner & Solbrig 1984). Density histograms are the method most commonly used to characterize the size structure of plant populations, but as the size structure is obtained by the placement of individual plants into classes, the shape of the size structure depends on the choice of the class interval. Feeley *et al.* (2007) found that the skewness coefficient was the static size structure measure that better predicted future variation in the number of the studied populations, but the evaluation of size inequalities, given by the Gini coefficient and the Lorez curve, seems to be more relevant to ecological and evolutionary questions than the skewness coefficient (Weiner & Thomas 1986). Therefore, we also used the Gini coefficient, which is independent of placement of individual plants into size classes, to measure the degree of hierarchy of size within the population. Size hierarchy is defined as a frequency distribution of individual plant sizes in which relatively few individuals contribute most of the population's biomass and most individuals are relatively small (Weiner & Solbrig 1984). The Gini coefficient has a value of zero when all the plants of the population have the same size, and one when virtually one individual concentrates all the biomass of the population (Weiner & Solbrig 1984). The DSL structure obtained for each species on the first census year was used as a basis to evaluate if there is a relationship between the size structure and the subsequent changes of population number and probabilities of local extinction on this small spatial scale.

The interval of DSL classes for the density histograms was chosen by taking into account the size amplitude and plant abundance. We chose DSL class limits with the maximum of one decimal, considering the precision of the method used to measure the plants. We used five DSL classes with an interval of 1.5 cm for *Miconia*; four classes with an interval of 3 cm for *Roupala;* seven size classes with an interval of 3 cm for *Vochysia* and six DSL classes with an interval of 3 cm for *Xylopia*. The *Dalbergia* population was divided into six DSL classes, with an interval of 4 cm, but this species turned out to be a different case because it had an extremely great variation of the number of smaller plants (coefficient of variation = 105.46%, data not shown) due to massive recruitment episodes in 1997, 2002, 2003 and 2007. However, these recruitment events were probably balanced by high mortality rates on the recruit size class, since in the years following the recruitment events we have not observed a high number of plants in the first or second DSL classes, indicating that the new plants that entered the population in the massive recruitment events were dead on the consecutive census. Including this great variation of the number of smaller plants in the PVA could mask the real trend of the population number, so we decided to perform all the analysis excluding the DSL < 4 cm class for *Dalbergia*.

To test for the adjustment of the observed curve of the density histogram of size distribution to the negative exponential model we analyzed the regression between the number of plants in each size class and the mid point of each class. The Gini coefficients were calculated using WINGINI (Santos 1996), and we performed a bootstrap test with 500 iterations to test for the significance of the differences of the Gini values obtained for each species.

The changes in number of the studied populations over time were analyzed by the mean population growth rates, its variance and by the total population growth rate considering the numbers of plants on the first and last census. The total population growth rate, that represents the global variation in number over the studied period, was calculated as:

$\Lambda t = \sqrt[t]{\frac{N_f}{N_1}}$, where N_f is the number of plants on the final census, N_1 is the number of plants on the first census and t is the number of years between the first and the last census.

To calculate the extinction risk of the studied populations, we performed a simple PVA (Population Viability Analysis) based on the number of plants over the census period (Morris & Doak 2002). Even though demographic PVA's, which use demographic data to build projection matrix models, can yield more informative predictions for most species, better predictions can occur only when there is enough data to estimate the many parameters these models require. With less information, the simple count-based approach can give much more reliable results, even for species with highly structured populations (Morris & Doak 2002). The count-based PVA first calculates the mean (μ) and the variance (s^2) of the natural logarithm of λ (the growth rate of the population) using simple transformations and a linear regression. The log-lambda growth rates are normally distributed and hence are better suited for statistical estimation than do the skewed lambda values themselves (Morris & Doak 2002). If μ is lower than zero, the population is predicted, on average, to decline over time; conversely, if μ is greater than zero, the population is predicted to grow, on average, although a positive μ does not necessarily indicate safety from random extinction.

To evaluate the probability of local extinction on this small spatial scale considered within a certain time period, a quasi-extinction threshold should be chosen (Morris & Doak 2002). This threshold may be considered the level below which the population is "effectively" extinct or critically endangered. It is frequently chosen to be above the number at which positive density dependence, demographic stochasticity, or strong inbreeding is thought to occur. There is no agreement on literature with regards to the minimum size of a viable population: for example, Matthies *et al.* (2004) found that the minimum number of individuals necessary to make a population likely to persist over time varies strongly even among closely related short-lived species; Nantel *et al.* (2002) found that the extinction threshold for *Panax quinquefolius* L. and *Allium tricoccum* Aiton varied from 30 to 90 plants. Other authors have used lower thresholds to calculate the probabilities of extinction of plant populations, such as 20 (Morris & Doak 2002), one (e.g. Garcia 2003, Quintana-Ascencio *et al.* 2003) or zero individuals (complete extinction – Gotelli & Ellison 2002). Considering the small size of the study area, we decided to perform the PVA with four different quasi-extinction thresholds: 20, ten, five and one individual. Given the quasi-extinction threshold and the current population size of each species (2007 census), the probability density of the quasi-extinction threshold in a small segment of time is given by the so-called inverse Gaussian distribution (Morris & Doak 2002). To calculate the probability that the threshold is reached in any time between the present and a future time of interest (on this case we used 500 years) we summed up the probabilities for each small interval of time; the result is the Cumulative Distribution Function (CDF) for the time of quasi-extinction. The PVA analyses were done using a tool (named Tool G) on an Excel worksheet designed by D. Doak *et al.*, available at http://bio.research.ucsc.edu/people/doaklab/natconserv/index.html.

If any of the main assumptions of the PVA (density independence, absence of temporal autocorrelation, no catastrophes or bonanzas and no observation error) was violated, we used only the mean and variance of the population growth rates and the total population growth rate to evaluate the changes in number over time of the studied populations.

Results

The total number of plants on the first census differed among species, as well as the number of plants of each species over time (Fig. 1). In spite of this great variation in density, on the first census the DSL distribution of the five studied species adjusted to the negative exponential curve at the 95% significance level (Fig. 2). The negative exponential size distribution is usually known as the "reverse-J" shape, with proportionally many small plants relative to the larger ones. The degree of hierarchy, measured by the Gini coefficient, differed among the studied populations ($p<0.01$ for all comparisons): the species with the highest degree of hierarchy (i.e., many small stems relative to the larger ones) was *Roupala,* and the species with the lowest degree of hierarchy was *Dalbergia* (Tab. 1). Based on these results, if a population with a high proportion of small plants relative to the larger ones (with a "reverse-J" shape or a high Gini value) is thought to be stable and self-regenerating, the five species we studied should be relatively stable in number over time and present a low extinction risk.

Table 1. Gini coefficient obtained for the studied species on the first census year, at Itirapina, SP.

Species	Gini
Dalbergia miscolobium	0.2383
Miconia albicans	0.5624
Roupala montana	0.6553
Vochysia tucanorum	0.5082
Xylopia aromatica	0.6163

Considering the variation in the number of plants over time, all the study species, except *Roupala,* had values of average λ lower than one. However, the values were not significantly lower than one given the wide confidence intervals obtained (Tab. 2), which were caused by a great variation in population growth rates among years. Large variations in population growth rates are as dangerous for populations as low population growth rates because they could make population numbers decay and reach the minimum viable number more quickly than the populations could recover. The total population growth rates λ_t varied from 0.91 (*Vochysia*) to 0.97 (*Xylopia*) (Tab. 2), representing decreases of 65% to 22% of the initial number of plants in twelve years, respectively.

For *Xylopia* and *Roupala* one of the main assumptions of the PVA to calculate the probability of extinction in a certain time horizon was violated: the density independence. For both species, there was positive density dependence, i.e., there were higher population growth rates on the years with bigger number of plants, and vice-versa. If these results were neglected and we performed the PVA to calculate the probability of extinction, the results would be too optimistic in the cases of decline in density. Therefore, for *Xylopia* and *Roupala* we present only the total and average population growth rates, as well as its variance.

On the PVA for *Miconia, Dalbergia* and *Vochysia*, the choice of different quasi-extinction thresholds did not change the values of probability of extinction, but, as one could expect, lower thresholds lead to longer mean time to extinction (Tab. 2). *Dalbergia, Miconia* and *Vochysia* showed negative μ values and the mean time to extinction varied between 22 and 125 years depending on the species and on the quasi-extinction threshold chosen, but for all cases the CDF lead to a $p = 1$ of reaching the quasi-extinction threshold at least once over a 500 year period (Tab. 2).

Discussion

Our results show that density histograms of size distributions are not good indicators of future trends in population number for the studied species. All the studied species showed a "reverse-J" size structure, which is usually taken as an indicator of self-replacing populations, but only *Roupala* seems to be effectively stable or increasing in population numbers. The Gini coefficient does not seem to be a better predictor of future population changes. *Roupala*, the only species that showed a "healthy" population, had the highest Gini value, showing a high degree of size inequality, which could indicate that high Gini values could be related to self-replacing populations. However, in terms of manage-

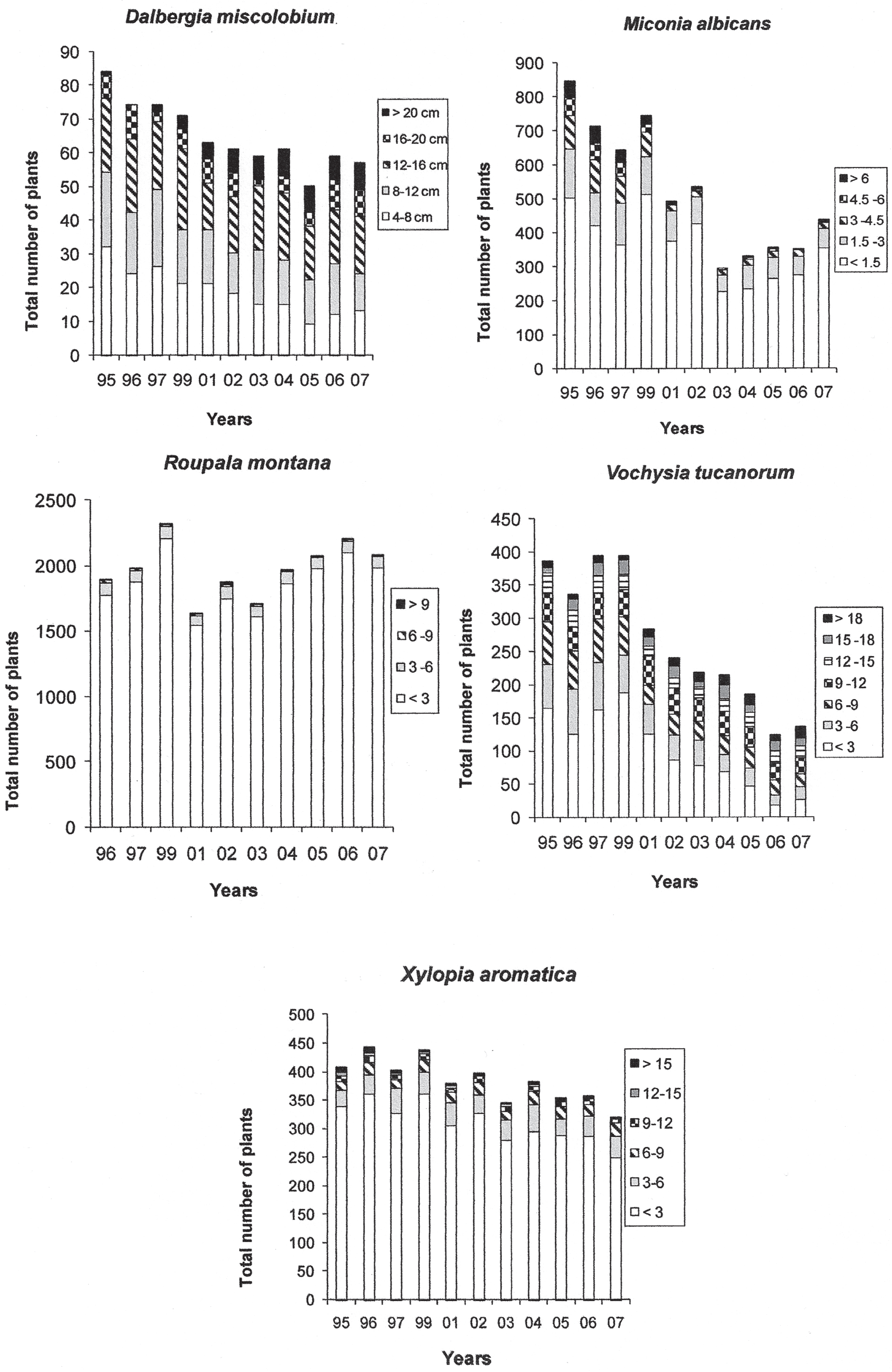

Figure 1. Variation on the number of plants in each diameter soil level (DSL) class for *Dalbergia miscolobium, Miconia albicans, Roupala montana, Vochysia tucanorum* and *Xylopia aromatica* during the study period at Itirapina, SP. Note the differences on the scale of y-axes among species.

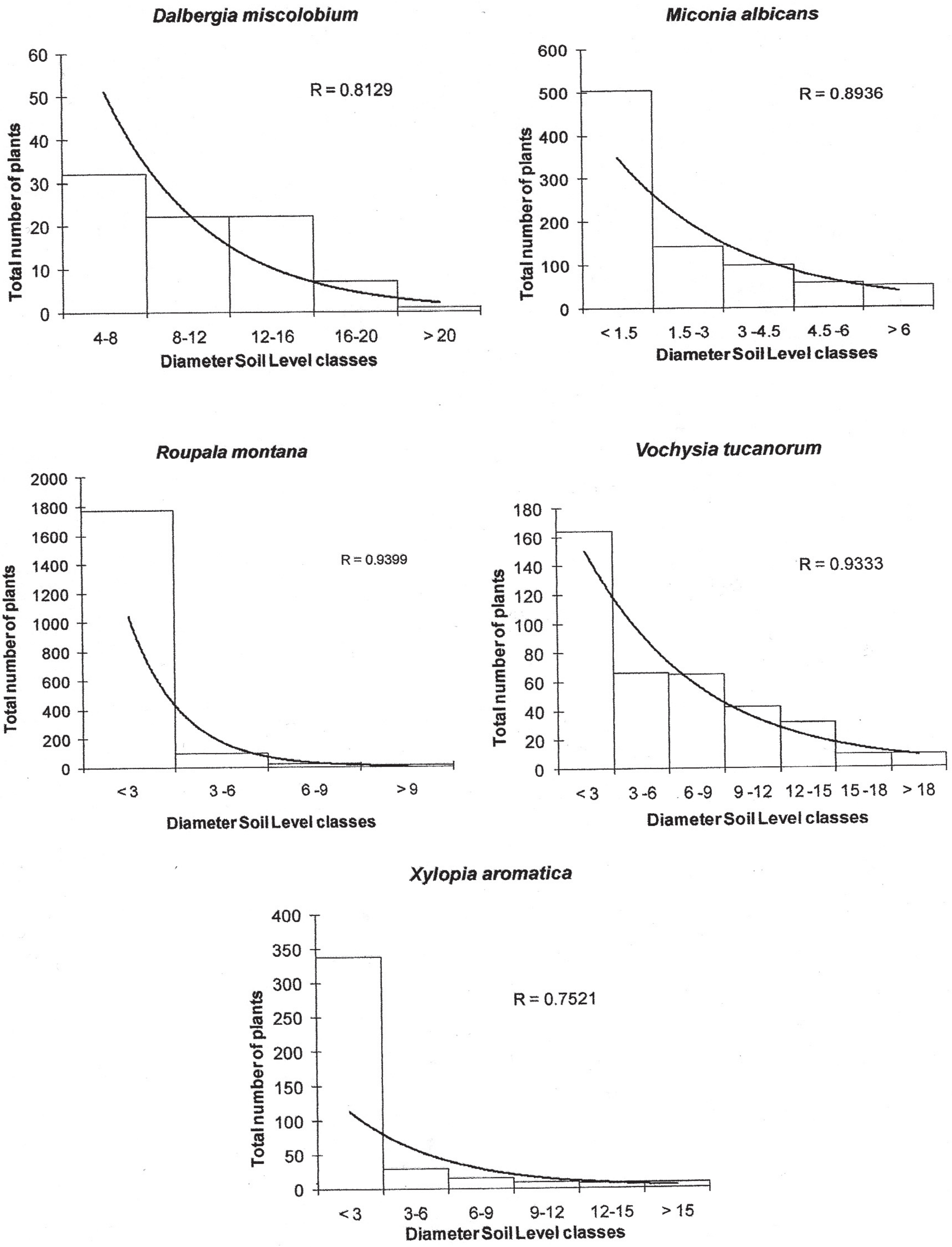

Figure 2. Density histogram of the populations on the first census year for *Dalbergia miscolobium, Miconia albicans, Roupala montana, Vochysia tucanorum* and *Xylopia aromatica* divided into diameter soil level (DSL) classes at Itirapina, SP. The adjustment of the structures to the negative exponential distribution and its respective Rvalue is also shown. For the five species, the adjustment was statistically significant at the 95% level.

Table 2. Population Viability Analysis results. Here are shown the mean (μ) and the variance (s^2) of log lambda, the average lambda for the entire census period (confidence interval in brackets), and the mean time to extinction given the quasi-extinction thresholds of 20, ten, five and one individual (probability of the populations reach the quasi-extinction threshold at least once over a 500 years time period in brackets).

	m	s^2	average l	mean time to extinction - threshold 20 (p)	mean time to extinction - threshold 10 (p)	mean time to extinction - threshold 5 (p)	mean time to extinction - threshold 1 (p)
Dalbergia miscolobium	-0.027	0.0092	0.97 (0.92-1.02)	32.4 (1)	53.8 (1)	75.3 (1)	125.11 (1)
Miconia albicans	-0.055	0.0587	0.97 (0.84-1.12)	56 (1)	68 (1)	81 (1)	110 (1)
Roupala montana	0.008	0.0164	1.01 (0.94-1.09)	-	-	-	-
Vochysia tucanorum	-0.087	0.0269	0.92 (0.84-1.01)	21.8 (1)	29.7 (1)	37.6 (1)	56 (1)
Xylopia aromatica	-0.020	0.0092	0.98 (0.93-1.03)	-	-	-	-

ment actions, it would be difficult to establish a threshold on Gini values that could indicate if populations are prone to extinction or not.

The size structures are ultimately formed by realized growth and mortality rates (Wright *et al.* 2003), and species with similar initial size structure can follow very distinct trajectories over time due to differences in vital rates. For example, if a species has a very high growth rate on the initial size classes relative to other species, it will present a lower proportion of small individuals, but this does not mean that this population is declining in number. Or, if a species has very high density dependence on the smaller size classes, a population with many small stems would not produce more reproductive adults than a population with few small stems (Feeley *et al.* 2007).

Ten years ago, Condit *et al.* (1998) showed that changes in population size observed on a 13-year period were independent of initial size distributions in a study conducted on Barro Colorado Island, Panama. In a study conducted at this same site, Wright *et al.* (2003) found that the size structure of populations was fairly robust during population fluctuations, indicating that even populations with stable "reverse-J" size structures could be declining in number. For the species we studied we found a similar result, with species showing no or little change in population structure (Fig. 1) in spite of the variation in the number observed. So, the lack of a direct relationship between size structures and future changes in population number that was found for tropical forests also applies to these woody species from Cerrado vegetation. We strongly recommend that managers should not use measures of size structure as a basis for management decisions without applying a more appropriate demographic study, considering the variation on demographic rates over time and the factors that influence this variation.

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