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Species richness and density evaluation for plants with aggregated distributions: fixed vs. variable area methods

Rita de Cássia Quitete Portela[1,*], *Alexandra dos Santos Pires*[2], *Maria Isabel Guedes Braz*[1] *and Eduardo Arcoverde de Mattos*[1]

[1] *Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Caixa Postal 68020, Ilha do Fundão, Rio de Janeiro, RJ 21941-590, Brasil*

[2] *Departamento de Ciências Ambientais, Instituto de Florestas, Universidade Federal Rural do Rio de Janeiro, Rod. BR 465, Km 07, Cidade Universitária, Seropédica, Rio de Janeiro, RJ 23890-000, Brasil*

*Correspondence address. Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Caixa Postal 68020, Ilha do Fundão, Rio de Janeiro, RJ 21941-590, Brasil. Tel: +55-2-13-93-86-317; Fax: +55-2-13-93-86-332; E-mail: ritaportela@gmail.com

Abstract

Aims

Knowledge of species richness is of prime importance to both basic and applied aspects of ecological studies. However, quantifying plant species richness in the tropics is potentially time-consuming because of high species diversity. Plant species richness estimates are also frequently biased, because many rare species are not detected. To address these problems, the use of a variable area method has been proposed as an alternative to fixed area methods, but its applicability to plants with aggregated distributions has been questioned based on simulation studies. We use empirical data to compare the efficiency and accuracy of a variable area method and a fixed area method for estimating species richness, density and basal area for plants with aggregated distributions, using palms as a model taxon.

Methods

Adult palms were sampled in twenty 10 × 30 m transects in an Atlantic Forest in Rio de Janeiro state, Brazil. All individuals were considered in the fixed area method, while in the variable area method only the first six adults in each transect were sampled; in this case, transect length was defined according to the distance of the sixth adult from the beginning of the transect. When fewer than six individuals were observed in a given transect, transect length was extended up to 50 m to search for additional individuals. The efficiency of both methods was compared based on species rarefaction curves, using the Chao 1 statistic (for abundance data). For each species we calculated mean density per transect and basal area, according to each sampling method. Sampling effort in terms of the number of individual plants and the area necessary to characterize maximum species richness in each sampling method, as well as mean time taken to sample a single transect, were compared as measures of efficiency.

Important findings

An accurate estimate of species richness was achieved using both methods, but in the variable area method, a quarter of the number of individuals and half the area was sufficient to characterize maximum species richness. Density and basal area did not differ between methods for any of the species studied. In the fixed area method sampling effort was 90 min per transect, whereas in the variable area method it was 30 min per transect. The variable area method, with its faster assessment of palm species richness, should facilitate greater spatial representativeness by making it easier to sample a larger number of plots at different spatial scales. We thus find sufficient evidence to recommend the variable area method for rapid and robust evaluations of species richness for palms with aggregate distributions, as well as for other plants with similar spatial patterns, in tropical forests.

Keywords: basal area, biodiversity, inventory, palms, taxon sampling

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INTRODUCTION

Estimating species richness is of prime importance to both basic and applied aspects of ecological studies. Although biological inventories have been done worldwide for decades, we still do not know how many species exist (Pimm *et al.* 2014). Quantifying plant richness in the tropics is potentially time-consuming because of high species diversity and the difficulties inherent in estimating and comparing species richness based on sampling data collected in the field (Abrahamson *et al.* 2011; Colwell *et al.* 2012). In addition, there is yet no appropriate methodological framework for gauging species numbers (Slik *et al.* 2015).

In the tropics, studies focusing on plant diversity have generally been carried out using fixed area methods (Abrahamson *et al.* 2011; Baraloto *et al.* 2012; Fisch and Gomes 2015; Magnusson *et al.* 2005; Phillips *et al.* 2003). These methods are usually based on large plots that are time-consuming to survey, which prohibits the sampling of a large number of replicate plots (Abrahamson *et al.* 2011; Kissa and Sheil 2012). Consequently, plots are not well distributed, and species that are aggregated or occur at low abundances are likely to be missed or under-represented (Abrahamson *et al.* 2011; Fisch and Gomes 2015). Designs that favour the sampling of a small area per plot are faster to conduct and can facilitate higher replication spread throughout a large region, increasing the representativeness of the sampling design (Abrahamson *et al.* 2011). In general, stem density varies among replicates, resulting in different amounts of sampling effort and data per plot (Kissa and Sheil 2012, Sheil *et al.* 2003). Using fixed area methods, the amount of data collected is therefore much greater than is actually required to characterize species diversity and forest composition (Sheil *et al.* 2003). In the current situation of rapid landscape changes, as a result of anthropogenic impacts (Laurance and Wright 2009; Laurance *et al.* 2012) coupled with a lack of knowledge about biodiversity in the tropics (Slik *et al.* 2015), methods that provide rapid and accurate estimates of species richness are urgently needed.

Variable area methods (Batcheler and Craib 1985; Engeman and Sugihara 1998; Parker 1979; Sheil *et al.* 2003) are expected to improve sampling efficiency over fixed area methods in many ways (Sheil *et al.* 2003; Nath *et al.* 2010). They can provide a rapid and robust assessment of species diversity and composition using short search distances. These methods also avoid collecting an excessive amount of information, since assessments are not dependent on stem density and the amount of effort is similar among plots. They are also relatively easy to apply and understand and produce robust estimates of species diversity and composition. Furthermore, such methods can be very useful for evaluating species diversity in difficult terrain, e.g. along altitudinal gradients. Finally, for plants with aggregated distributions, the use of variable area methods could be expected to improve species richness estimates, because they favour sampling a higher number of replicates over sampling a large number of conspecifics within the same plot. However, despite the expected advantages of these methods, few studies have tested their efficiency and accuracy. In the only study based on empirical data, Nath *et al.* (2010) found that variable area methods carried out in three different habitats of an agroforestry system were significantly more efficient per unit of field effort per replicate than fixed area square plots. However, two simulation studies considering spatial patterns suggested that variable area methods would perform well for species that are randomly distributed but would be biased for plants with aggregated distributions (Engeman and Sugihara 1998; Nath *et al.* 2010).

In this study, we compare variable and fixed area methods with respect to efficiency using sampling effort (effort was defined as time required to sample each transect) and accuracy using species rarefaction curves. We used palms—a plant group characterized by aggregated distributions—as a model taxon. The family Arecaceae comprises 183 genera and about 2400 species distributed throughout the tropics (Baker *et al.* 2011). In Brazil, there are 38 genera and 282 species of Arecaceae, of which about 122 species are endemic (Leitman *et al.* 2012). The largest diversity centres of the group in Brazil are the Amazon (135 spp.) and Cerrado (92 spp.), followed by the Atlantic Forest (62 spp.; Leitman, *et al.* 2012). In spite of their abundance, representativeness and importance in tropical forests (Eiserhardt *et al.* 2010; Fisch and Gomes 2015; Oliveira *et al.* 2014) palms are generally under-represented in inventories and ecological studies. Careful matching of inventory purpose to sampling methods has always been important for ecologists and is especially so now in the context of rapid environmental change in the tropics.

MATERIALS AND METHODS

Study area

The study was carried out in the Guapiaçú Ecological Reserve (REGUA, 22°25′02″S, 42°44′18″W), Rio de Janeiro state, Brazil. This private reserve is located within the Macacu Environmental Protection Area (APA Macacu) and overlaps with the Três Picos State Park. It comprises 7200 ha of a 58 000-ha contiguous area of forest and covers the elevation range 20–2000 m above sea level (ASL). The climate of the region is warm tropical with a daily temperature range of 14–37.1°C (Azevedo 2012). Average annual precipitation is 2600 mm, most of which falls over the austral summer, from November to April, while winters are dry (Azevedo 2012). The reserve is surrounded by areas of cultivation and pasture (Azevedo 2012). The vegetation up to 800 m ASL is dominated by Sapotaceae and Myrtaceae and numerous large woody vines and liana species. The montane forest is dominated by a dense understory, along with Myrtaceae, Sapotaceae and Lauraceae species supporting prominent epiphytic vegetation (Azevedo 2012).

Field sampling/methods comparison

We constructed inventories of palm species between September and December 2011. The variable area method we used was based on and modified from a more complex, yet versatile, method proposed by Sheil *et al.* (2003). Twenty 10 × 30 m transects were established in the study area, spaced at least 100 m from each other. For the fixed area method, all adult palms found in each transect were sampled. Adults are individual with evidence of past or present reproduction. For the variable area method, only the first six adults were considered, and transect length was defined as the distance of the sixth adult from the beginning of the transect. When fewer than six individuals were observed in a transect, transect length was increased by up to 50 m to search for additional individuals. The number of individuals required for each transect (six) was chosen in order to keep the method practical and efficient (Engeman and Sugihara 1998; Nath *et al.* 2010). Multi-stemmed individuals were counted only once. In both methods we counted the number of individuals per species in a given area (density) and measured individuals' basal diameter to calculate the basal area. Palm species were identified based on Henderson (2009, 2011).

Data analysis

We compared the accuracy of the two methods based on species rarefaction curves, using Chao 1 (for abundance data) in EstimateS 8.20 (Colwell 2009). The curves were constructed using the abundance of each species within each sample (Gotelli and Colwell 2001). The rarefaction curve was produced from 1000 random resamples drawn without replacement from the pool of number of individuals and number of transects. Rarefaction curves were then constructed based on both individuals and transects.

For the variable area method, we calculated mean density and basal area of each species per transect following Sheil *et al.* (2003). We used linear regression to assess how well the two methods corresponded. The density and basal area of each species estimated via the variable area method were used as explanatory variables, and those estimated by the fixed area method were the response variables. The basal area regression was done using log-transformed values. Paired *t*-tests were used to compare the mean values for each species across the methods.

We used the Fligner–Killeen test to test whether the variance of density and basal area for each species differed significantly between the methods. This is a non-parametric test based on the ranks of the absolute values of the centred samples (Crawley 2013). We also compared the efficiency of the two methods with respect to sampling effort. Effort was defined as time required to sample each transect. Finally, to confirm the spatial distribution (aggregation, or degree of clumping) of all species, based on the two sampling methods, we calculated the Morisita index of dispersion, I_δ (Morisita 1962), for each species using Ecological Methodology version 5.2 (Kenney and Krebs 2000).

RESULTS

Using the fixed area method, we recorded a density of 783.3 individuals ha^{-1}, comprising 12 palm species and subspecies in six genera, whereas using the variable area method, we found 11 palm species and subspecies in 5 genera and recorded a density of 921.5 individuals ha^{-1}. The total area sampled was 0.6 ha using the fixed area method and 0.28 ha using the variable method. All taxa were sampled in both methods, except for a single *Attalea dubia* individual that was sampled only in the fixed area method (Table 1).

Considering the accuracy of the variable area method in estimate species diversity, an asymptote of species richness was reached for both methods using the Chao 1 estimator, and the curves did not differ significantly (Fig. 1). Besides that, the data collected using the fixed area method were well explained by the data collected using the variable area method, for both density (y = 0.712x + 11.386, R^2 = 0.938, P < 0.05) and basal area (y = 1.016x – 0.035, R^2 = 0.867,

Table 1: Species, density (individuals per hectare) and basal area (cm^2 m^{-2}) of palms estimated by two sampling methods (fixed and variable area) in the Guapiaçú Ecological Reserve (REGUA), Rio de Janeiro state, Brazil

Species	Density		Basal area	
	Fixed area	Variable area	Fixed area	Variable area
Astrocaryum aculeatissimum	18.3 ± 27.5 (1.5)	26.5 ± 75.3 (2.8)	0.18 ± 0.29 (1.58)	0.26 ± 0.71 (2.73)
Attalea dubia	1.7 ± 7.4 (4.47)	0 ± 0 (0)	0.25 ± 1.11 (4.47)	0 ± 0 (0)
Bactris caryotifolia	10 ± 26.7 (2.6)	6.3 ± 20.4 (3.1)	0.01 ± 0.02 (2.53)	0.01 ± 0.02 (3.13)
Bactris vulgaris	46.7 ± 120.6 (2.5)	45.1 ± 150.6 (3.3)	0.03 ± 0.08 (2.37)	0.04 ± 0.10 (2.70)
Euterpe edulis	61.7 ± 83.2 (1.3)	59.6 ± 99.2 (1.7)	1.1 ± 1.74 (1.59)[a]	0.68 ± 1.52 (2.21)[a]
Geonoma elegans	8.3 ± 18.33 (2.2)	27.4 ± 67.8 (2.5)	0.01 ± 0.03 (3.13)	0.04 ± 0.10 (2.51)
Geonoma pohliana subsp. *fiscellaria*	161.7 ± 349.3 (2.2)	136.1 ± 280.7 (2.1)	0.37 ± 0.78 (2.11)	0.34 ± 0.64 (1.90)
Geonoma pohliana subsp.*kuhlmannii*	61.7 ± 195.3 (3.2)	100.1 ± 308.5 (3.0)	0.04 ± 0.12 (3.38)	0.07 ± 0.23 (3.32)
Geonoma pohliana subsp. *pohliana*	8.3 ± 18.3 (2.2)	18.5 ± 74.5 (4.0)	0.03 ± 0.06 (2.36)	0.05 ± 0.19 (3.72)
Geonoma pohliana subsp.*trinervis*	13.3 ± 38.0 (2.85)	12.9 ± 40.0 (3.1)	0.03 ± 0.07 (2.57)	0.01 ± 0.04 (3.01)
Geonoma schottiana	323.3 ± 285.1 (0.8)	455.1 ± 638.2 (1.4)	0.57 ± 0.83 (1.48)	0.60 ± 0.93 (1.56)
Lytocaryum weddellianum	68.3 ± 141.2 (2.1)	34.09 ± 129.4 (3.8)	0.08 ± 0.16 (2.06)	0.04 ± 0.15 (3.48)
Total	783.3 ± 479.6 (0.6)	921.5 ± 850.8 (0.92)	2.67 ± 2.16 (0.80)	2.14 ± 1.76 (0.82)

Values are mean, standard deviation and coefficient of variation in parenthesis.
[a]Significant difference between the methods (Fligner–Killeen: median chi-squared).

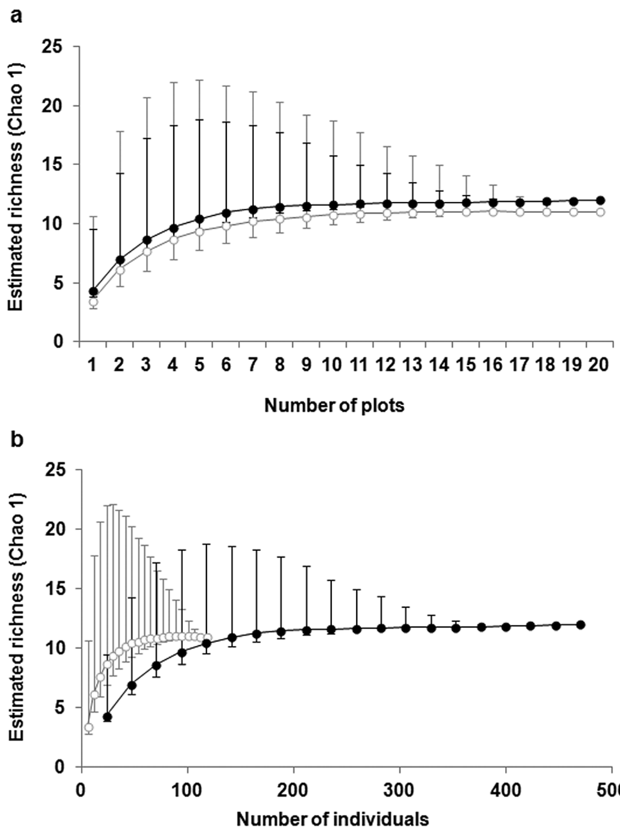

Figure 1: Transect- (**a**) and individual-based (**b**) rarefaction curves of palm species richness based on fixed (black circle) and variable (white circle) area methods in the Guapiaçú Ecological Reserve (REGUA), Rio de Janeiro state, Brazil. The graph was constructed using the Chao 1 mean, with lower and upper bounds determined as the Chao 1 95% confidence intervals. The curves were computed based on repeated resampling, using EstimateS.

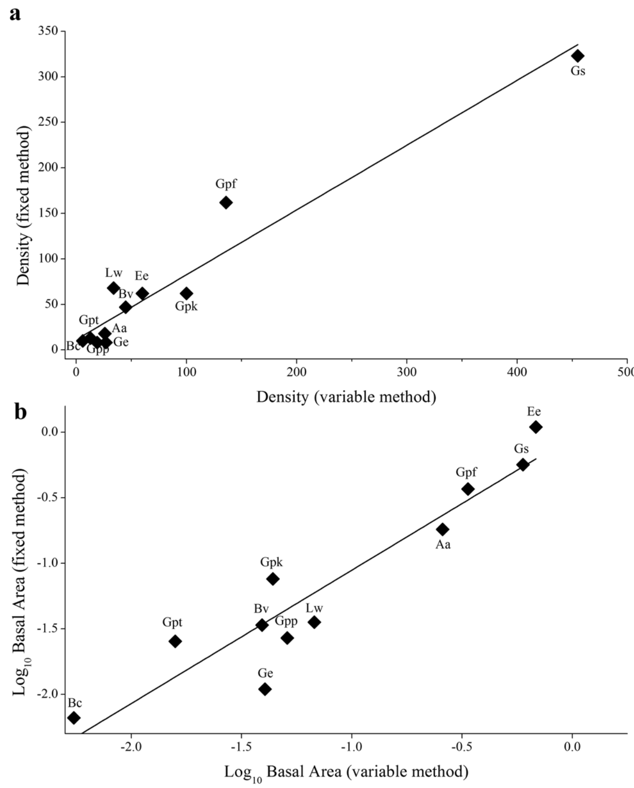

Figure 2: Linear regression of density (individuals per hectare) (**a**) and basal area ($cm^2\ m^{-2}$) (**b**) for each species, as estimated using the variable area method (explanatory variable) and fixed area method (response variable). The basal area values were log-transformed. Aa: *Astrocaryum aculeatissimum*; Bc: *Bactris caryotifolia*; Ee: *Euterpe edulis*; Ge: *Geonoma elegans*; Gpf: *Geonoma pohliana* subsp. *fiscellaria*; Gpk: *G. pohliana* subsp.*kuhlmannii*; Gpp: *Geonoma pohliana* subsp. *pohliana*; Gs: *Geonoma schottiana*; Gpt: *G. pohliana* subsp. *trinervis*; Bv: *Bactris vulgaris*; Lw: *Lytocaryum weddellianum*.

$P < 0.05$; Fig. 2). Density (paired $t = -0.956$, df = 10, $P = 0.332$) and basal area (paired $t = 0.656$, df = 10, $P = 0.527$) for each species did not differ between methods. The variance of both measures for each species also did not differ between methods, except for the basal area of *Euterpe edulis* (Fligner–Killeen: median chi-squared = 8.097, df = 1, $P = 0.004$; Table 1).

Considering efficiency, in the variable area method, a quarter of the number of individuals and half the area was sufficient to characterize maximum species richness. Additionally, sampling effort was 90 min per transect for the fixed area method and 30 min per transect for the variable area method, evidencing the efficiency of the last one in terms of time consumption.

According to the fixed area method, 8 of the 12 species/subspecies had an aggregated spatial distribution, although it was not possible to calculate this index for *Attalea dubia*, of which only one individual was found. Based on the variable area method, 5 of the 11 species/subspecies had an aggregated distribution, although for 5 of the remaining 6 it was not possible to calculate the Morisita index because of their very low abundance.

DISCUSSION

We found sufficient evidence to propose the use of the variable area method for rapid and robust evaluations of palm species richness, density and basal area in tropical forests. Contrary to what Engeman and Sugihara (1998) found using data simulation, the variable area method is adequate for sampling all three of these measures for species that have aggregated distributions (Eiserhardt *et al.* 2010; Oliveira *et al.* 2014 and data presented here). Engeman and Sugihara (1998) did, however, mention that simulations using artificial populations can only approximate natural processes and that the true test of the results presented in their paper would be to use field data sets, such as those presented here. The variable area method, with its faster assessment of palm species richness, should facilitate greater spatial representativeness by making it easier to sample a larger number of plots at different spatial scales. This is particularly important in systems such as the Atlantic Rain Forest, which are composed of different ecosystems and cover difficult terrain, e.g. steep altitudinal gradients.

Methodologies for assessing species richness that involve sampling large plots are costly in terms of sampling time, and plot replication is therefore generally limited (Abrahamson *et al.* 2011). Consequently, plots are not well distributed, and species that are aggregated or occur at low abundance are likely to be missed or under-represented. Phillips *et al.* (2003) compared fixed area plots of 1 ha and 0.1 ha and showed that on average sampling the smaller plots took <15% of the field time needed for the larger plots, permitting a much higher inventory density across the landscape. Designs that sample a small area are relatively fast to deploy and can facilitate considerable replication (Abrahamson *et al.* 2011). Greater inventory efficiency translates directly into greater ecological efficiency, as (other things being equal) many more samples are collected and therefore greater statistical power is attained for the same sampling effort (Phillips *et al.* 2003). The fact that the area sampled in the variable area method depends on density of individuals facilitates less intensive sampling over a larger area, because of its potential rapidity. This may therefore prove to be an efficient sampling strategy for studies in which a coarse-grained inventory of a community is required (Dobrowski and Murphy 2006).

Palms are usually poorly sampled in phytosociologial and floristic studies, because of the small diameter of individuals and the difficulty of collecting voucher specimens (Fisch and Gomes 2015). However, comparing our results with those of other studies that sampled trees (including palms) in the Atlantic Rain Forest, the findings for more abundant species were the same (Joly *et al.* 2012), even considering the results obtained using the variable area method. A small number of studies of the palm community have been carried out in the Atlantic Rain Forest (Oliveira *et al.* 2014; Pires 2006). Pires (2006) worked in a fragmented landscape of Lowland Atlantic Rain Forest using a fixed sampling area and found 10 palm species. Most of these species were the same ones that we sampled, using both methods. Oliveira *et al.* (2014) sampled palms across an altitudinal gradient in Ombrophilous Dense Forest, also using a fixed sampling area, and found 11 species, 6 of which also featured in our study. Comparing our results with the mentioned above, the 0.6 ha sampled in this study seemed to be sufficient to survey the palm community in the area. Also, the variable method surveyed accurately the same plant community. Fisch and Gomes (2015) highlighted the importance of including palms in floristic surveys as they are currently under-represented in the literature and also recommended developing more appropriate methods for sampling this family, especially because of their aggregated distribution.

Considering that palms are keystone species and structurally important in tropical forests, it is important to use methods that evaluate their diversity quickly and efficiently, especially in the context of expected climatic change. Here, we provide evidence that the variable area method is an efficient sampling method for use with plants that have aggregated distributions. We thus recommend the variable area method for rapid and robust evaluations of species richness for palms with aggregate distributions, as well as for other plants with similar spatial patterns, in tropical forests.

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