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Rapid Simultaneous Estimation of Aboveground Biomass and Tree Diversity Across Neotropical Forests: A Comparison of Field Inventory Methods

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ABSTRACT

A standardized rapid inventory method providing information on both tree species diversity and aboveground carbon stocks in tropical forests will be an important tool for evaluating efforts to conserve biodiversity and to estimate the carbon emissions that result from deforestation and degradation (REDD). Herein, we contrast five common plot methods differing in shape, size, and effort requirements to estimate tree diversity and aboveground tree biomass (AGB). We simulated the methods across six Neotropical forest sites that represent a broad gradient in forest structure, tree species richness, and floristic composition, and we assessed the relative performance of methods by evaluating the bias and precision of their estimates of AGB and tree diversity. For a given sample of forest area, a 'several small' (< 1 ha) sampling strategy led to a smaller coefficient of variation (CV) in the estimate of AGB than a 'few large' one. The effort (person-days) required to achieve an accurate AGB estimate (< 10% CV), however, was greater for the smallest plots (0.1 ha) than for a compromise approach using 0.5 ha modified Gentry plots, which proved to be the most efficient method to estimate AGB across all forest types. Gentry plots were also the most efficient at providing accurate estimates of tree diversity (< 10% CV of Hill number). We recommend the use of the 0.5 ha modified Gentry plot method in future rapid inventories, and we discuss a set of criteria that should inform any choice of inventory method.

Key words: biodiversity assessment; carbon stocks; monitoring; permanent plot; survey; tropical rain forest.

TROPICAL FORESTS HAVE LONG BEEN RECOGNIZED TO HARBOR A SIGNIFICANT PROPORTION OF GLOBAL BIODIVERSITY (Gaston 2000, Myers *et al.* 2000), with at least a third of all higher plant species occurring in the Neotropics and 12 percent in Amazonian forests alone (Gentry 1982). Recently, the conservation value of tropical forests has been expanded to include their important contribution to carbon storage and potential mitigation of global climate change (Gullison *et al.* 2007). Tropical forests are estimated to account for an estimated 229 Pg of aboveground biomass carbon (Baccini *et al.* 2012), or nearly half of that estimated to be stored in vegetation worldwide (Houghton 2005), with remote sensing and ground based estimates of carbon in the Amazon basin alone varying from 86 to 96 Pg (with about 20% uncertainty) (Malhi *et al.* 2006, Saatchi *et al.* 2007).

Rising rates of deforestation and degradation in tropical forests have underlined the need for information on the spatial distribution of ecosystem properties, including biodiversity and carbon stocks, to assist managers when setting aside zones for protection (Venter *et al.* 2009, Saatchi *et al.* 2011). Despite substantial efforts by researchers over the past 30 yr, the structure and composition of large areas of tropical forests remains poorly (or un-) studied (Foster *et al.* 1998, Feeley & Silman 2011), thereby complicating management decisions in many tropical countries. Much of the effort necessary to inventory sites of the highest priority is expended on travel, such that time in the field becomes extremely valuable. A standardized rapid inventory method that provides information on *both* biodiversity and carbon stocks will thus represent an important tool to enhance our

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ability to maximize biodiversity conservation and to help quantify potential carbon emissions that result from deforestation and degradation (REDD). A standardized rapid inventory method will also be critical in the immediate future to provide calibration points for remote sensing methods, estimating forest carbon stocks (Asner *et al.* 2010, Saatchi *et al.* 2011) and floristic composition (Asner & Martin 2011). Herein, we test a variety of plot methods to establish the most accurate and efficient way to reach this goal.

The most widespread forest inventory method used for both tree diversity and aboveground tree biomass (AGB) estimates is the 1 ha plot (*e.g.,* Phillips *et al.* 2009, Stropp *et al.* 2009), as initially recommended by the Food and Agriculture Organization (FAO 1981). Recent studies, however, have challenged whether these plots are the most appropriate size and shape to measure floristic composition because they may miss rare species or overrepresent spatially aggregated species (Phillips *et al.* 2003b). Critiques have also been leveled against the AGB estimates from 1 ha plots because the plots may be too small to accurately characterize carbon stocks for static measures (Wagner *et al.* 2010), or to monitor their temporal dynamics (Chambers *et al.* 2009). Several alternatives to 1 ha plots have been suggested, differing primarily in their sizes, shapes, and the minimum size of trees inventoried (Table 1). Among these, is the Gentry plot method (Boyle 1996, Phillips *et al.* 2003a,b), a modified version of which has been used to estimate AGB across contrasting Amazonian forests (Baraloto *et al.* 2011).

Sampling methods can be evaluated based on two concepts that together define the accuracy of their estimators: *sampling bias*, which refers to deviations of estimates from the true value; and *sampling precision*, which refers to the breadth of variation in the estimate (Walther & Moore 2005).

1. Sampling bias for estimates of AGB may occur, for example, because allometries for tree biomass were not calibrated in the site where they are applied (Clark *et al.* 2001). The choice of plot method should not introduce bias into estimates of AGB as each plot represents a sample from the biomass distribution of the considered area. The mean of the samples is an unbiased estimator of the mean AGB value of the area. It supposes that the plots are placed randomly with equal probability. In contrast, sampling bias represents an important issue in estimating species richness, because methods contrast markedly in the proportion of species present in a site that are sampled (Brose *et al.* 2003, Walther & Moore 2005, Beck & Schwanghart 2010).
2. Sampling precision represents the reduction in variance of AGB and species occurrences between plots. This variability is influenced both by spatial variation in AGB and species distributions; as well as by plot characteristics (size, shape; Laurance *et al.* 1998).

The most efficient protocol for assessing tree species diversity and AGB simultaneously will reach a compromise between the accuracy of both estimators (in terms of bias and precision) vs. the amount of resources (time and/or money) necessary to implement the protocol (Phillips *et al.* 2003b, Abrahamson *et al.* 2011). Efficient plot-based sampling is especially important for rapid inventories to assess protected areas (Foster *et al.* 1998, Higgins & Rukolainen 2004) and for the calibration of remote sensing analyses across large areas (Asner *et al.* 2010, Saatchi *et al.* 2011). However, to date, no empirical comparison is available from which to draw inferences for choosing an appropriate protocol across the many different forest types that exist in the tropics.

TABLE 1. *Inventory methods commonly used for surveying of aboveground biomass and/or plant diversity in Neotropical forests.*

Method	Area covered (ha)	Area inventoried (ha)	dbh min (cm)	Permanent	Effort (person-days)*	Existing plots in Neotropics	Reference
Gentry Plot†	2	0.1	2.5	No	7	> 800	Boyle (1996); Phillips *et al.* (2003a,b)
Whittaker Plot†	0.1	0.1	2.5	No	7	At least 100	Campbell *et al.* (2002)
Modified Gentry Plot†	2	0.5	Variable	Yes	8	160	Baraloto *et al.* (2011)
0.5 ha Plot†	0.5	0.5	2.5	Yes	15	Unknown	
1 ha Plot†	1	1	10	Yes	25	> 750	FAO (1981)
Circular plot	0.28	0.28	10	Yes	5	> 130	Asner *et al.* (2010)
Brazil Forest Service NFI plot	4	0.4	Variable	Yes	5–10	Thousands to be implemented	D. Piotto, pers. comm.
Large CTFS Plot	Up to 52	Up to 50	1	Yes	> 500	9	Condit (1995)
Ad hoc botany	Variable	NA	NA	No	Variable	NA	Hopkins (2007)

*See text for details of calculations.

†Indicates method analyzed in this study.

Herein, we use a simulation approach to estimate AGB and tree biodiversity within large permanent plots from six Neotropical forests representing a broad gradient in tree species richness (88–821 species among trees $\geq$ 10 cm in diameter at 1.3 m height [dbh] per 50 ha plot) and forest structure (AGB of 283–494 Mg ha^{-1}) (Table 2). In particular, we address three objectives. First, we test a range of plot sizes and shapes to determine the most accurate (least bias and greatest precision) and most efficient (accuracy per unit effort) method to estimate AGB and tree biodiversity. Second, we evaluate whether there exists a general trade-off among methods in the accuracy of information they provide for tree diversity vs. aboveground biomass estimates. Third, we analyze the extent to which different inventory methods may be appropriate among forests differing in structure and floristic composition.

METHODS

ESTIMATING BIODIVERSITY AND CARBON STOCKS.—Our dataset comprised Neotropical forest sites including (1) permanent plots of at least 10 ha to permit within-plot sampling of all methods and (2) reliable data for tree spatial locations and dbh for carbon estimates and species identifications for biodiversity estimates. For each site, we chose the most reliable recent inventory census for that plot (Table 2).

At each site, we considered five possible plot methods among those most commonly used in tropical forests (Table 1). Three of these methods employ contiguous rectangles of different shapes, and two (Gentry plots) are composites of belt transects across a 2 ha area. These Gentry plots group either ten 2 × 50 m belt transects (modified Gentry plot; Phillips *et al.* 2003a,b) or an extension of these for AGB estimates to 10 × 50 m transects for larger trees $\geq$ 20 cm dbh (revised 0.5 ha modified Gentry plot; Baraloto *et al.* 2011, inspired by Phillips *et al.* 2001). Comparing the composite Gentry plots with rectangular subplots of 0.5 or (respectively, 0.1) hectare of the same area, thus allows us to evaluate the influence of plot shape (contiguous vs. spread) on the accuracy of the forest descriptors. Although the methods considered herein are by no means exhaustive, they represent the large majority of published regional studies on AGB and tree diversity in the Neotropics (Table 1). We did not consider circular plots that have been employed in temperate forests, such as the USDA Forest Service's Forest Inventory and Analysis program (Lichstein *et al.* 2010). Circular plots are widely regarded as difficult to demarcate in the dense understory of tropical forests (Alder & Synnott 1992), although a few research groups continue to use them for calibration of remote sensing estimates of AGB (*e.g.,* Asner *et al.* 2010).

We evaluated the individual tree AGB using the formula of Chave (2005) for moist tropical forests without tree height data, as the heights were not available for all plots.

$$\mathrm{PAGB}_i = \mathrm{wsg}_i \times e^{(-1.499+2.14\times\log(\mathrm{DBH}_i)+0.207\times(\log \mathrm{DBH}_I)^2-0.028\times(\log \mathrm{DBH}_i)^2)}$$

with DBH$_i$ of tree *i* in cm and wood specific gravity (wsg$_i$) of tree *i* without dimension. Our simulations were conducted following Stegen *et al.* (2009) as site-level means, with values for Paracou and Nouragues calculated by referencing a local wood density database with species composition (Sarmiento *et al.* 2011). We note that the Chave (2005) allometry without height may overestimate AGB in forests where tree height is lower for a given tree dbh than the forests from which datasets were collected (Feldpausch *et al.* 2011), but this should not affect the results, we present herein, even though it may exaggerate spatial variability in stands with skewed dbh structures.

For biodiversity, we compared 1 ha plots and the 0.1 ha plots of different shapes (single rectangle vs. Gentry multiple transect), as these are the two most popular methods currently used to estimate biodiversity (Campbell *et al.* 2002, Phillips *et al.* 2003a,b, Stropp *et al.* 2009). The 0.5 ha modified Gentry plot was designed to extend sampled surface area only for AGB estimates and thus uses floristic information only from its 0.1 ha

TABLE 2. *Description of the permanent plot sites used in this study. Precise floristic composition and data for stems < 10 cm dbh were only available for the first three sites.*

Site	Area (ha)	Dimensions (m × m)	Year of census	Aboveground tree biomass (Mg ha^{-1})	Species richness ($\geq$ 2.5 cm dbh)	Species richness ($\geq$ 10 cm dbh)	Community wsg*	Stem Density ($\geq$ 2.5 cm dbh)(ha^{-1})
BCI (Panama)	50	1000 × 500	2005	322	276	228	0.545	2388
Luquillo (Puerto Rico)	16	500 × 320	2000	360	139	88	0.604	2084
Yasuní (Ecuador)	25	500 × 500	2003	283	1038	821	0.588	3233
Nouragues GP (French Guiana)	10	1000 × 100	2008	443	–	†	0.782	–
Nouragues PP (French Guiana)	12	300 × 400	2008	494	–	†	0.782	–
Paracou (French Guiana; six plots)	37.5	250 × 250	2009	432	–	†	0.782	–

*wsg values from CTFS plots were applied as site-level means from Stegen *et al.* (2009).

†Taxonomic inventories of the complete study area are not yet completed.

Gentry plot core. We evaluated estimates of biodiversity, including total species number S in each sample (Walther & Moore 2005) as well as Hill numbers, which represent the number of equally abundant species yielding the same diversity as the sample (Jost 2006).

SIMULATING DIFFERENT PLOT METHODS.—We simulated the five plot methods in each large permanent plot. For each plot method, we partitioned the large permanent plot into simulated subplots of different sizes and shapes, to cover the largest possible area of the permanent plot with no subplot overlap. We sampled from the resulting subplot units with replacement to obtain a statistical population for each plot method. Depending on the size of the permanent plot (Table 2) and the plot method simulated (Table 1), we were able to place at least ten simulated plots in each permanent plot. For each plot method in each permanent plot, we generated randomly 1000 populations for a series of 1–20 plots (depending on plot method). We calculated estimates of AGB and biodiversity (S and Hill number) for each population.

STATISTICAL METHODS.—We evaluated the relative performance of the five methods using measures of bias and precision. Our analysis is not completely symmetrical because measures of bias are not relevant for comparing plot methods in their estimates of AGB. The true value of AGB in a regional site is the mean of a distribution of sampling points in that region; and randomly placed plots, no matter the method used, will provide unbiased estimates of this mean, even if they may be imprecise. In contrast, the true value of diversity for a regional site is a parameter for which sampling methods may be biased (Walther & Moore 2005). We measured bias in estimates of diversity using a transformed value of scaled mean error referred to as the percent of actual richness (Baltanas 1992) estimated from the entire larger permanent plot.

We also measured precision for both AGB and diversity using the coefficient of variation (CV) as a normalized measure of dispersion. We considered an accurate estimate for biomass and Hill numbers to be achieved when the CV was < 10 percent of the mean (Wagner *et al.* 2010).

We compared among plot methods in several ways. Estimates of AGB are reported relative to surface area rather than number of plots, and so we retained this presentation to permit subsequent interpretations based on the shape and number of simulated plots. For example, an area of 2 ha can be achieved with two simulated plots of 1 ha, or four simulated plots of 0.5 ha, or 20 simulated plots of 0.1 ha. For biodiversity, we also made calculations based on the total number of individuals sampled (Gotelli & Colwell 2010, Magurran & Queiroz 2010).

To compare the efficiency among different methods, we built CV models using one predictor, the *Effort*. *Effort* is defined as the number of person-days required to implement each plot, estimated based on the lead author's experience with different research teams in five countries across the Amazon (Table 1). We considered an average level of competence for a field research team relative to spatial orientation for mapping and measuring trees and botanical knowledge for tree sampling and identification, following criteria implemented by Phillips *et al.* (2003b), including tree dbh measures and mapping, assignment to morphospecies, field preparation of herbarium vouchers, and organization of field notebooks. Those authors report an average of 4.6 person-days for a 0.1-ha Gentry plot and 28.3 d for a 1-ha plot in Peruvian forests, which are faster times than we have observed across the region (7 and 35 person-days, respectively), and with a more skewed ratio (Gentry plots are completed more than six times faster than 1-ha plots in their study vs. five times faster in ours; Table 1).

We defined the CV Effort model following Wagner *et al.* (2010):

$$\mathrm{CV} = \alpha \times \mathit{Effort}^{\beta} \times \varepsilon$$

ε being the error term of the model. It can be transformed to

$$\log(\mathrm{CV}) = \log(\alpha) + \beta \times \log(\mathit{Effort}) + \log(\varepsilon)$$

with $\varepsilon \sim N(0; \sigma^2)$ to achieve linearity When predicting *Effort* required to reach a target CV, note that because the exponential of the error distribution centered on 0 is not exactly centered on 1, the back-transformation of the log scale was appropriately corrected.

RESULTS

ABOVEGROUND BIOMASS (AGB) ESTIMATES.—The relative performance of methods for estimating AGB was largely consistent among the six forests. In general, multiple smaller plots (< 1 ha) performed much better than fewer larger plots (1 ha); that is, for a given surface area sampled, the use of multiple smaller plots resulted in a smaller CV in the estimate of AGB (Fig. 1). The 0.5 ha modified Gentry plots provided an exception to this rule, outperforming or equalling the performance of 0.1 ha plot methods in five of the six sites (all, but BCI). For the plots sampling 0.1 ha, the rectangular format (part of the Whittaker plot, Campbell *et al.* 2002) outperformed the original Gentry plot (0.1 ha) in three sites (BCI, Luquillo, Nouragues PP). In contrast, the 0.5 ha Gentry plot outperformed the square 0.5 ha plot in all sites except BCI.

When translated into the actual effort required to achieve an accurate estimate of site AGB (< 10% CV), the disadvantage of installing multiple smaller plots becomes apparent, with consistently greater effort required to realize accurate AGB estimates using 0.1 ha plots of any shape (Fig. 2). The 1 ha plots, despite their relatively high cost to implement (Table 1), were more efficient to inventory than the smallest plots, although 1 ha plots were still inferior to the 0.5 ha modified Gentry plots. The 0.5 ha modified Gentry plots consistently emerge as the best compromise when compared to all other methods, with the lowest overall effort necessary to accurately estimate AGB.

Although the relative performance of methods for AGB was consistent among sites, the effort necessary to achieve accurate

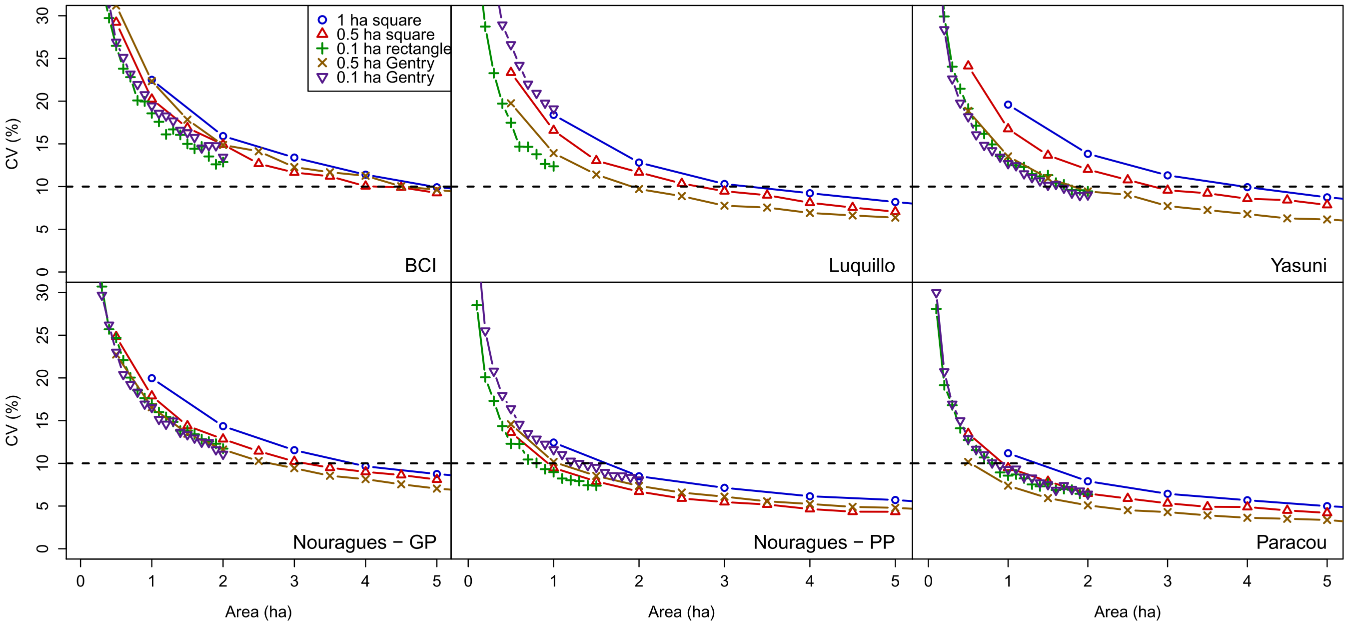

FIGURE 1. The relative precision of five plot methods (see Table 1 for full descriptions) for estimating aboveground tree biomass across six Neotropical forests. Each point represents 1000 simulations of each plot method in each forest site. Reference lines indicate an accepted minimum accurate performance at a coefficient of variation (CV) of 10 percent. (Color version of all figures available in Supporting Information).

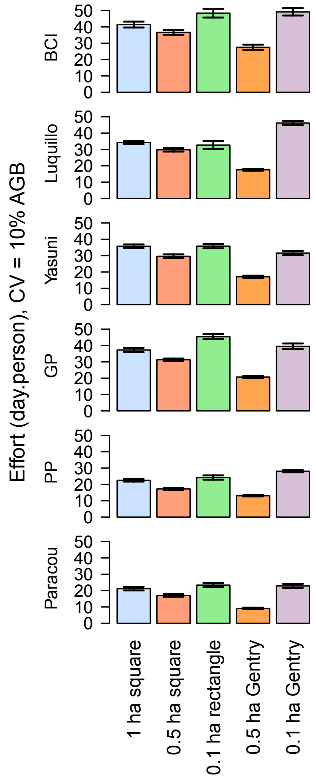

FIGURE 2. The sampling effort (in person-days) required to achieve accurate estimates of aboveground tree biomass (maximum of 10% coefficient of variation) across six Neotropical forests using five different plot methods. Shown are the mean values (with 5 and 95% confidence intervals) of 1000 simulations of each plot method in each forest site.

measurements of AGB (< 10% of CV) varied widely across different Neotropical forests. At Paracou, for example, an accurate estimate of AGB can be obtained with a single 0.5 ha modified Gentry plot (8 person-days), whereas at BCI a minimum of 32 person-days, and four 0.5 ha Gentry plots, would be necessary (Fig. 2).

TREE DIVERSITY ESTIMATES.—Reliable floristic data was available from three of the six sites (BCI, Luquillo and Yasuní), for which species-individual accumulation curves for different plot methods are presented in Figure 3. The smaller plots clearly sample a larger proportion of the overall flora in each of the three sites than do the 1 ha plots. At BCI, however, the composition of trees $\geq$ 10 cm dbh has more balanced relative abundances, such that the Hill number is actually larger than that of the community of trees $\geq$ 2.5 cm dbh (Fig. 3). As a consequence, 1-ha plots may actually overestimate the total diversity of this site, and smaller plots may underestimate diversity by sampling dominant species, depending on the target community of interest. Between the two 0.1 ha smaller plot methods differing in shape (rectangle vs. Gentry), little difference in sampling performance was apparent in any of the three sites (Fig. 3).

The three plot methods differed substantially in the precision of estimates for tree diversity. Across the three forests, the Gentry plots were the most precise, and the 1 ha plots were the least precise (Fig. 4). To assess the relative performance of plot methods at estimating tree diversity, we considered a precision of 10 percent CV to be acceptable. The smaller plot methods outperformed the 1 ha plots in the effort required to obtain estimates of tree diversity with this precision (Fig. 5). Across all

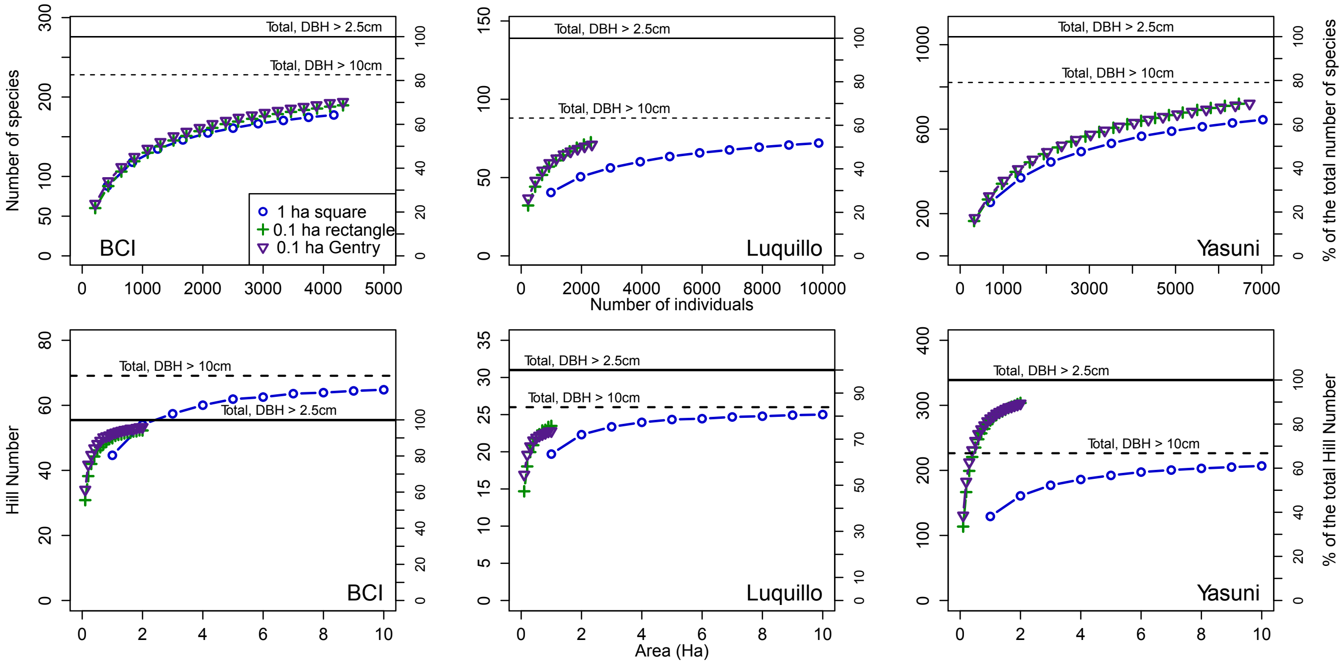

FIGURE 3. Tree diversity estimates from simulated samples of three plot methods across three Neotropical forests. Each point represents 1000 simulations of one of three plot methods in each forest site. Reference lines indicate the total number of species or the Hill number equivalent recorded in each forest at the two minimum size criteria for different plot methods (see Table 1). The percent of actual richness (PAR) is indicated on the second *y*-axis for reference. Note that the 1-ha plot method estimates tree diversity for stems $\geq$ 10 cm dbh, whereas the other two methods estimate diversity of stems $\geq$ 2.5 cm dbh.

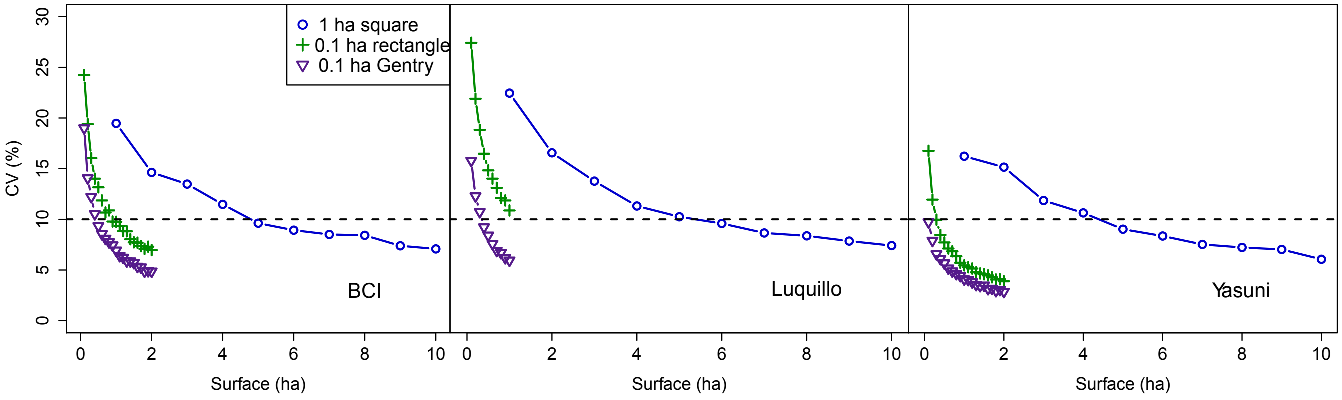

FIGURE 4. The relative precision (coefficient of variation [CV]) of three plot methods for estimating tree diversity (Hill number) across three Neotropical forests. Each point represents 1000 simulations of each plot method in each forest site. Reference lines indicate an accepted minimum precision at a CV of 10 percent. Note that the 1-ha plot method estimates tree diversity for stems $\geq$ 10 cm dbh, whereas the other two methods estimate diversity of stems $\geq$ 2.5 cm dbh.

three forests, the Gentry plots outperformed the 0.1 ha rectangular plots in estimating the Hill number, indicating an advantage of sampling a larger overall area, despite the accompanying moderate additional cost of increased time investment.

DISCUSSION

We found that one method, the modified 0.5 ha Gentry plot, outperformed all other methods for both accurate AGB and plant diversity estimates. The modified 0.5 ha Gentry plots were the most efficient method for estimating AGB across six forest types varying in structure and floristic composition (Fig. 3). Moreover, the 0.1 ha Gentry plot that forms the core of this approach is also the most efficient method for estimating tree biodiversity across three forests differing widely in species diversity (Fig. 5). We recommend this method receive serious consideration for future rapid inventories in tropical forests. Our recommendation should be weighed in light of

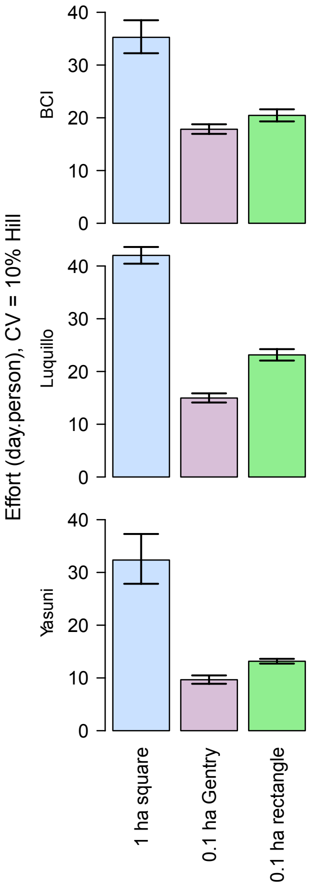

FIGURE 5. The sampling effort (in person-days) required to achieve precise estimates of the Hill number for tree diversity (maximum of 10% coefficient of variation) across three Neotropical forests using three different plot methods. Shown are the mean values (with 5 and 95% confidence intervals) of 1000 simulations of each plot method in each forest site.

the limitations of our study, in addition to other factors involved in research and monitoring studies in tropical forests that we discuss below.

Aboveground tree biomass and tree diversity admittedly do not describe all the ecosystem properties that managers might need when deciding which tropical forest areas to protect. First, biodiversity clearly encompasses more than tree species diversity. Groups, such as birds, butterflies, and beetles have been suggested to be more appropriate than trees as overall indices of site biodiversity to determine conservation priorities (Schulze *et al.* 2004, Gardner *et al.* 2008). Nevertheless, vegetation plots provide an important foundation for complementary inventories of other groups, and larger contiguous plots provide the important benefits of extensive mapped areas with associated forest structure and floristic data (Condit 1995). Smaller plot methods can also provide the basis for inventories of other taxonomic groups, with appropriate protocols in place for both contiguous and aggregate plots. For example, in French Guiana, we place the 200 m base trail of our 0.5 ha modified Gentry plots along the 4 km trails used for mammal, bird and insect surveys (de Thoisy *et al.* 2008) to permit site diversity of multiple taxonomic groups to be estimated rapidly and accurately.

A biodiversity index, such as plot-level richness, Shannon's entropy or the associated Hill number may also not be the most suitable botanical information for forest managers to prioritize sites for protection (Hopkins 2007). This is primarily because the presence of rare species with limited distribution may be more effectively recorded through *ad hoc* sampling rather than with fixed inventory plots (Foster *et al.* 1998, Gordon & Newton 2006, Hopkins 2007), although with *ad hoc* sampling, no related estimates of forest structure or quantitative comparisons among sites would be possible. A potential compromise our team has implemented with 0.5 ha modified Gentry plots in French Guiana and Peru is to add *ad hoc* sampling for the entire forest, so that a larger species occurrence list with herbarium vouchers can be produced in addition to the quantitative plot data. The intensive sampling of very large plots appears to capture rare species well (Valencia *et al.* 2004) with an added benefit that permanently marked individuals can be collected at some point with flowers or fruits.

Smaller plots with lower than 10 cm minimum tree diameter requirement have the advantage of providing information on a suite of species that are not likely to grow into the larger size classes often used in standard 1 ha plots (see Fig. 3). Smaller plots, however, often do not provide as complete a sample of tree species as do 1 ha plots (Phillips *et al.* 2003a,b) or larger plots that are crucial for long-term monitoring of species spatial and temporal dynamics and species interactions (Condit 1995). Our analysis of the BCI dataset demonstrates how this choice of minimum diameter can influence interpretations. BCI has a relative ratio of overall richness between communities with minimum diameters of 10 cm vs. 2.5 cm that is only slightly higher than that of Yasuní (83% vs. 79%; Table 1). The larger tree community, however, comprises fewer dominant species there, such that 1 ha plots would provide a larger estimate of Hill number and almost equivalent estimate of species richness, as smaller plots (Fig. 3). Current available large plot floristics data are limited to these three sites and therefore preclude speculation about why this may be the case at BCI. Nevertheless, this finding provides a caution to interpretations among different plot methods across different tropical forests in larger meta-analyses.

A second limitation to our study is that forest properties related to the ecosystem services of carbon storage and sequestration clearly encompass more than simple estimates of tree AGB. Estimates of carbon stocks in other vegetation, coarse woody debris (CWD) and soil carbon pools are required in addition to AGB estimates for trees. Soil carbon and CWD parameters can also easily be integrated into plot methods, as CWD is often estimated using interception methods along linear transects at least 250 m in length (Harmon & Sexton 1996). Such transects could be arranged across any plot type, for example, centered along the base transect of Gentry plots to integrate measures of CWD and AGB. Appropriate estimates of soil carbon pools can be assessed by modifications in any soil sampling protocol that accompanies a particular plot method (*e.g.*, Fisher *et al.* 2008).

Before making a decision on the most appropriate method for use in a given situation, our results should be integrated with other criteria. First, before adopting a specific protocol, it is wise to consider the ability of any proposed method to compare with other existing networks of plot inventories in other sites. The two most common methods in the Neotropics include 1 ha plots, which number more than 1000 (Stropp *et al.* 2009, H. ter Steege, unpubl. data) and 0.1 ha Gentry plots, of which there are currently more than 800 (Phillips *et al.* 2003a,b, Stegen *et al.* 2011, Table 1). The 1 ha plots thus remain a valuable option where resources are less limited, as they permit comparisons with plots including those managed by the RAINFOR consortium (*e.g.,* Phillips *et al.* 2009). One-hectare plots may be suboptimal for any individual purpose, such as estimates of AGB or tree diversity, as we found in this study, but they have proven to be a tested compromise to address multiple questions/purposes that can shift and expand with time.

We caution against the use of 0.1 ha Gentry plots to estimate AGB, as they can be subject to a large degree of error for a given site. Indeed, Phillips *et al.* (2006) and Stegen *et al.* (2011) report unlikely values up to 600 Mg C ha^{-1} (~ 1200 Mg AGB ha^{-1}) using 0.1 ha Gentry plots; and we must question the rates of recovery of AGB reported by Letcher and Chazdon (2009) following pasture abandonment, as they used a small number of 0.1 ha Gentry plots that may have overestimated the contribution of sparsely distributed larger trees. Instead, we suggest investing the marginal additional effort to expand these plots to the 0.5 ha modification, from which more accurate AGB estimates can be obtained, while maintaining the ability to integrate floristic data with a large network of existing plots. To our knowledge, there are currently at least 140 0.5 ha modified Gentry plots established in Peru, Bolivia, Brazil, French Guiana, and Suriname (Baraloto *et al.* 2011).

We were not able to simulate the recently developed cross-shaped aggregate plot method of the Brazilian National Forest Inventory due to its coverage area (4 ha) relative to the area of the datasets in our study (Table 2). However, we hypothesize that it would exhibit similar performance to the modified Gentry plot, with which it shares properties, including aggregation of multiple transects across a large area and relative ease of implementation (Table 1). Given the lengthy discussions from which this method was constructed, and the plans of the Brazilian Forest Service for thousands of plots to be installed between 2012 and 2015 (D. Piotto, pers. comm.), this method merits further study and consideration.

A second important criterion when choosing an inventory method is the spatial heterogeneity of forest structure at the sampling site. One drawback of composite methods, such as both the original and modified Gentry plots, is that they risk overemphasizing the impact of different habitats across the landscape. In some cases, this may be advantageous, such as when an overall estimate for a heterogeneous forest area is desired. If instead an estimate for a given forest type of limited dimensions, such as linear features, including higher tributary floodplain forests or the *Guadua*-dominated forests of the southwestern Amazon is required, then finding a homogeneous and representative 200 × 100 m area for a modified Gentry plot may prove more difficult than a 100 × 100 m plot. In Yasuní, for example, valleys and ridges separated by < 100 m within the permanent plot have markedly different floristic composition (Valencia *et al.* 2004).

One of the most important considerations for choosing an appropriate plot method is whether static (*e.g.,* AGB, basal area) or dynamic (*e.g.,* growth rates, mortality rates, biomass turnover rates) forest descriptors are a priority. Many of the rapid inventory techniques employing transects and smaller plots are not permanent, and thus do not allow easy recensusing to measure temporal dynamics in floristics, species population dynamics, or forest structure (Foster *et al.* 1998). Even though the plot size for all of the methods, we tested herein has been suggested to be less than the ideal for accurate estimates of tree mortality and carbon flux in tropical forests (~4 ha, Fisher *et al.* 2008, Wagner *et al.* 2010), we believe that marking plots and trees in small plots remains a moderate and useful investment. This is particularly true in remote areas where the majority of resources are invested in transport rather than plot establishment; in this case, permanent markings can permit subsequent measures of tree growth and survival and be linked to remote sensing analyses following changes in vegetation (Asner *et al.* 2010). Small plots will still be inadequate; however, to address interactions among tree species and the relative spatial and temporal dynamics in species' populations, community composition, and the impact of human and natural disturbances.

We agree with Foster *et al.* (1998) and Hopkins (2007) who, when citing the current escalation in deforestation and forest degradation in tropical forests, have called for rapid inventories in areas that have been under-sampled. However, we also believe that the results we present herein suggest that such rapid inventories can be accomplished at least in part using plot methods that provide quantitative data useful to estimate both AGB and tree diversity. We propose that appropriate plot methods, together with information from *ad hoc* sampling (Foster *et al.* 1998), will assist in the identification and monitoring of forest areas to meet conservation priorities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. The relative precision of five plot methods (see Table 1 for full descriptions) for estimating aboveground tree biomass across six Neotropical forests.

FIGURE S2. The sampling effort (in person-days) required to achieve accurate estimates of aboveground tree biomass (maximum of 10% coefficient of variation) across six Neotropical forests using five different plot methods.

FIGURE S3. Tree diversity estimates from simulated samples of three plot methods across three Neotropical forests. Each point represents 1000 simulations of one of three plot methods in each forest site.

FIGURE S4. The relative precision (coefficient of variation [CV]) of three plot methods for estimating tree diversity (Hill number) across three Neotropical forests.

FIGURE S5. The sampling effort (in person-days) required to achieve precise estimates of the Hill number for tree diversity (maximum of 10% coefficient of variation) across three Neotropical forests using three different plot methods.

LITERATURE CITED

Abrahamson, I. L., C. R. Nelson, and D. L. R. Affleck. 2011. Assessing the performance of sampling designs for measuring the abundance of understory plants. Ecol. Appl. 21: 452–464.

Alder, D., and T. J. Synnott. 1992. Permanent sample plot techniques for mixed tropical forests. Oxford Forestry Institute Tropical Forestry Paper 25, 124 pp.

Asner, G. P., and R. E. Martin. 2011. Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. New Phytol. 189: 999–1012.

Asner, G. P., G. V. N. Powell, J. Mascaro, D. E. Knapp, J. K. Clark, J. Jacobson, T. Kennedy-Bowdoin, A. Balaji, G. Paez-Acosta, E. Victoria, L. Secada, M. Valqui, and R. F. Hughes. 2010. High-resolution forest carbon stocks and emissions in the Amazon. Proc. Natl Acad. Sci. USA 107: 16738–16742.

Baccini, A., S. J. Goetz, W. S. Walker, N. T. Laporte, M. Sun, D. Sulla-Menashe, J. Hackler, P. S. A. Beck, R. Dubayah, M. A. Friedl, S. Samanta, and R. A. Houghton. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat. Clim. Chang. 2: 182–185.

Baltanas, A. 1992. On the use of some methods for the estimation of species richness. Oikos 65: 484–492.

Baraloto, C., S. Rabaud, Q. Molto, L. Blanc, C. Fortunel, N. Davila, I. Mesones, M. Rios, E. Valderrama, and P. V. A. Fine. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Glob. Change Biol. 17: 2677–2688.

Beck, J. and W. Schwanghart. 2010. Comparing measures of species diversity from incomplete inventories: An update. Methods Ecol. Evol. 1: 38–44.

Boyle, B. L. 1996. Changes on altitudinal and latitudinal gradients in neotropical montane forests, p. 275. Washington University, St. Louis, Missouri.

Brose, U., N. D. Martinez and R. J. Williams. 2003. Estimating species richness: Sensitivity to sample coverage and insensitivity to spatial patterns. Ecology 84: 2364–2377.

Campbell, P., J. Comiskey, A. Alonso, F. Dallmeier, P. Nuñez Vargas, H. Beltran, S. Baldeon, W. Nauray, R. De La Colina, L. Acurio, and S. Udvardy. 2002. Modified Whittaker plots as an assessment and monitoring tool for vegetation in a lowland tropical rainforest. Environ. Monit. Assess. 76: 19–41.

Chambers, J. Q., R. I. Negrón-Juárez, G. C. Hurtt, D. M. Marra, and N. Higuchi. 2009. Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests. Ecol. Lett. 12: E22–E25.

Chave, J. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145: 87–99.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: Concepts and field methods. Ecol. Appl. 11: 356–370.

Condit, R. 1995. Research in large, long-term tropical forest plots. Trends Ecol. Evol. 10: 18–22.

Fao. 1981. Manual of forest inventory with special reference to mixed tropical forests. FAO, Rome, Italy.

Feeley, K. J. and M. R. Silman. 2011. The data void in modeling current and future distributions of tropical species. Glob. Change Biol. 17: 626–630.

Feldpausch, T. R., L. Banin, O. L. Phillips, T. R. Baker, S. L. Lewis, C. A. Quesada, K. Affum-Baffoe, E. J. M. M. Arets, N. J. Berry, M. Bird, E. S. Brondizio, P. De Camargo, J. Chave, G. Djagbletey, T. F. Domingues, M. Drescher, P. M. Fearnside, M. B. França, N. M. Fyllas, G. Lopez-Gonzalez, A. Hladik, N. Higuchi, M. O. Hunter, Y. Iida, K. A. Salim, A. R. Kassim, M. Keller, J. Kemp, D. A. King, J. C. Lovett, B. S. Marimon, B. H. Marimon-Junior, E. Lenza, A. R. Marshall, D. J. Metcalfe, E. T. A. Mitchard, E. F. Moran, B. W. Nelson, R. Nilus, E. M. Nogueira, M. Palace, S. Patiño, K. S.-H. Peh, M. T. Raventos, J. M. Reitsma, G. Saiz, F. Schrodt, B. Sonkão, H. E. Taedoumg, S. Tan, L. White, H. Woll, and J. Lloyd. 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8: 1081–1106.

Fisher, J. I., G. C. Hurtt, R. Q. Thomas, and J. Q. Chambers. 2008. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. Ecol. Lett. 11: 554–563.

Foster, R. B., N. C. Hernandez, E. K. Kakudidi, and R. J. Burnham. 1998. Rapid assessment of tropical plant communities using variable transects: an informal and practical guide. Field Museum of Chicago, Chicago, Illinois.

Gardner, T. A., J. Barlow, I. S. Araujo, T. C. Ávila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. Da Silva, and C. Da Silva Motta and C. A. Peres. 2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecol. Lett. 11: 139–150.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

Gentry, A. H. 1982. Patterns of neotropical plant species diversity. Evol. Biol. 15: 1–84.

Gordon, J. E., and A. C. Newton. 2006. Efficient floristic inventory for the assessment of tropical tree diversity: A comparative test of four alternative approaches. For. Ecol. Manage. 237: 564–573.

Gotelli, N., and R. K. Colwell. 2010. Estimating species richness. In A. E. Magurran and B. J. McGill (Eds.). Biological diversity: Frontiers in measurement and assessment, pp. 39–54. Oxford University Press, Oxford, UK.

Gullison, R. E., P. C. Frumhoff, J. G. Canadell, C. B. Field, D. C. Nepstad, K. Hayhoe, R. Avissar, L. M. Curran, P. Friedlingstein, C. D. Jones, and C. Nobre. 2007. Tropical forests and climate policy. Science 316: 985–986.

Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. LTER Network Publication 20. University of Washington, Seattle, Washington.

Higgins, M. A., and K. Ruokolainen. 2004. Rapid tropical forest inventory: a comparison of techniques based on inventory data from Western Amazonia. Conserv. Biol. 18: 799–811.

Hopkins, M. J. G. 2007. Modelling the known and unknown plant biodiversity of the Amazon Basin. J. Biogeogr. 34: 1400–1411.

Houghton, R. A. 2005. Aboveground forest biomass and the global carbon balance. Glob. Change Biol. 11: 945–958.

Jost, L. 2006. Entropy and diversity. Oikos 113: 363–375.

Laurance, W. F., L.V. Ferreira, J. Rankin-De-Merona, and R. Hutchings. 1998. Influence of plot shape on estimates of tree diversity and community composition in Central Amazon. Biotropica 30: 662–665.

Letcher, S. G. and R. L. Chazdon. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern Costa Rica. Biotropica 41: 608–617.

Lichstein, J. W., J. Dushoff, K. Ogle, A. Chen, D. W. Purves, J. P. Caspersen and S. W. Pacala. 2010. Unlocking the forest inventory data: Relating individual tree performance to unmeasured environmental factors. Ecol. Appl. 20: 684–699.

Magurran, A. E. and H. Queiroz. 2010. Evaluating tropical biodiversity: Do we need a more refined approach? Biotropica 42: 537–539.

Malhi, Y., D. Wood, T. R. Baker, J. Wright, O. L. Phillips, T. Cochrane, P. Meir, J. Chave, S. Almeida, L. Arroyo, N. Higuchi, T. J. Killeen, S. G. Laurance, W. F. Laurance, S. L. Lewis, A. Monteagudo, D. A. Neill, P. N. Vargas, N. C. A. Pitman, C. A. Quesada, R. Salomao, J. N. M. Silva, A. T. Lezama, J. Terborgh, R. V. Martinez and B. Vinceti. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Glob. Change Biol. 12: 1107–1138.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Phillips, O. L., L. E. O. C. Aragão, S. L. Lewis, J. B. Fisher, J. Lloyd, G. Lopez Gonzalez, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. Van Der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Banki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. Alves De Oliveira, N. Cardozo Davila, C. I. Czimczik, T. R. Felpausch, M. Aparecida Freitas, E. Gloor, N. Higuchi, E. Jiménez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patinõ, M. C. Peñuela, A. Prieto, F. Ramirez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. Ter Steege, J. Stropp, R. Vasquez, P. Zelazowski, E. Alvarez Davila, S. Andelman, A. Andrade, K. J. Chao, T. Erwin, A. Di Fiore, C. Euridice Honorio, H. Keeling, T. J. Killeen, W. F. Laurance, A. Peña Cruz, N. C. A. Pitman, P. Nuñez Vargas, H. Ramirez Angulo, A. Rudas, R. Salamão, N. Silva, J. Terborgh, and A. Torres Lezama. 2009. Drought Sensitivity of the Amazon Rainforest. Science 323: 1344–1347.

Phillips, O. L., A. Lawrence, A. R. Ismodes, M. Lopez, D. Wood, S. Rose and A. J. Farfan. 2001. Uma Metodologia De Evaluacion De La Biodiversidad Y De Los Recursos Del Bosque: Um Manual Del Campo. Instituto De Investigaciones De La Amazonia Peruana, Puerto Maldonado, Peru.

Phillips, O. L., S. Rose, A. M. Mendoza and P. N. Vargas. 2006. Resilience of southwestern Amazon forests to anthropogenic edge effects. Conserv. Biol. 20: 1698–1710.

Phillips, O. L., P. N. Vargas, A. L. Monteagudo, A. P. Cruz, M. E. C. Zans, W. G. Sanchez, M. Yli-Halla, and S. Rose. 2003a. Habitat association among Amazonian tree species: A landscape-scale approach. J. Ecol. 91: 757–775.

Phillips, O. L., R. Vasquez Martinez, P. Nunez Vargas, A. Lorenzo Monteagudo, M. E. Chuspe Zans, W. Galiano Sanchez, A. Pena Cruz, M. Timana, M. Yli-Halla, and S. Rose. 2003b. Efficient plot-based floristic assessment of tropical forests. J. Trop. Ecol. 19: 629–645.

Saatchi, S. S., N. L. Harris, S. Brown, M. Lefsky, E. T. A. Mitchard, W. Salas, B. R. Zutta, W. Buermann, S. L. Lewis, S. Hagen, S. Petrova, L. White, M. Silman and A. Morel. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. Proc. Natl Acad. Sci. 108: 9899–9904.

Saatchi, S. S., R. A. Houghton, R. C. Dos Santos Alvala, J. V. Soares and Y. Yu. 2007. Distribution of aboveground live biomass in the Amazon basin. Glob. Change Biol. 13: 816–837.

Sarmiento, C., S. Patiño, C. E. T. P. Paine, J. Beauchene, A. Thibaut and C. Baraloto. 2011. Within-individual variation of trunk and branch xylem density in tropical trees. Am. J. Bot. 98: 1–10.

Schulze, C. H., M. Waltert, P. J. A. Kessler, R. Pitopang, D. Veddeler, M. Mahlenberg, S. R. Gradstein, C. Leuschner, and I. Steffan-Dewenter and T. Tscharntke. 2004. Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. Ecol. Appl. 14: 1321–1333.

Stegen, J. C., N. G. Swenson, B. J. Enquist, E. P. White, O. L. Phillips, P. M. Jørgensen, M. D. Weiser, A. Monteagudo Mendoza and P. Núñez Vargas. 2011. Variation in above-ground forest biomass across broad climatic gradients. Glob. Ecol. Biogeogr. 20: 744–754.

Stegen, J. C., N. G. Swenson, R. Valencia, B. J. Enquist and J. Thompson. 2009. Above-ground forest biomass is not consistently related to wood density in tropical forests. Glob. Ecol. Biogeogr. 18: 617–625.

Stropp, J., H. Ter Steege, Y. Malhi, atdn & rainfor. 2009. Disentangling regional and local tree diversity in the Amazon. Ecography 32: 46–54.

de Thoisy, B., S. Brosse and M. Dubois. 2008. Assessment of large-vertebrate species richness and relative abundance in Neotropical forest using line-transect censuses: What is the minimal effort required? Biodivers. Conserv. 17: 2627–2644.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J. C. Svenning, C. Hernandez, K. Romoleroux, E. Losos, E. Magard, and H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. J. Ecol. 92: 214–229.

VENTER, O., W. F. LAURANCE, T. IWAMURA, K. A. WILSON, R. A. FULLER, AND H. P. POSSINGHAM. 2009. Harnessing Carbon Payments to Protect Biodiversity. Science 326: 1368.

WAGNER, F., E. RUTISHAUSER, L. BLANC AND B. HERAULT. 2010. Effects of plot size and census interval on descriptors of forest structure and dynamics. Biotropica 42: 664–671.

WALTHER, B. A. AND J. L. MOORE. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28: 815–829.