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Efficient plot-based floristic assessment of tropical forests

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Abstract: The tropical flora remains chronically understudied and the lack of floristic understanding hampers ecological research and its application for large-scale conservation planning. Given scarce resources and the scale of the challenge there is a need to maximize the efficiency of both sampling strategies and sampling units, yet there is little information on the relative efficiency of different approaches to floristic assessment in tropical forests. This paper is the first attempt to address this gap. We repeatedly sampled forests in two regions of Amazonia using the two most widely used plot-based protocols of floristic sampling, and compared their performance in terms of the quantity of floristic knowledge and ecological insight gained scaled to the field effort required. Specifically, the methods are assessed first in terms of the number of person-days required to complete each sample ('effort'), secondly by the total gain in the quantity of floristic information that each unit of effort provides ('crude inventory efficiency'), and thirdly in terms of the floristic information gained as a proportion of the target species pool ('proportional inventory efficiency'). Finally, we compare the methods in terms of their efficiency in identifying different ecological patterns within the data ('ecological efficiency') while controlling for effort. There are large and consistent differences in the performance of the two methods. The disparity is maintained even after accounting for regional and site-level variation in forest species richness, tree density and the number of field assistants. We interpret our results in the context of selecting the appropriate method for particular research purposes.

Key Words: Amazonia, biodiversity, diversity, efficiency, forest, inventory, Neotropics, Peru, survey, tropical

INTRODUCTION

Floristic inventory is a necessary prerequisite for much fundamental research in tropical community ecology, such as modelling patterns of species diversity or understanding species distributions. Quantitative floristic sampling also provides necessary context for planning and interpreting long-term ecological research. For example, floristic inventory can help to decide how to stratify sampling effort for monitoring forest processes, or to interpret the ecosystem significance of results from individual species-level experimental manipulations. On a wider scale inventories are also critical for protected-area and development planning, which require geographically referenced, replicated and comparable samples to support decisions on where to focus conservation resources or development activities.

However, large parts of the tropical flora remain chronically understudied (Prance *et al.* 2000). The need for inventory work is especially great in the Neotropics, with six global biodiversity hotspots (Myers *et al.* 2000) and 35% of all higher plant species (Gentry 1982). Basic floristic inventory has proved difficult in neotropical forests for several reasons. First, the high diversity creates difficulties for identification both in the field and in the herbarium. Second, forests tend to be remote with access to field-sites both expensive and time-consuming. Third, inventory is physically challenging and risky, requiring tree-climbing to gain voucher collections. And fourth, few tropical countries can afford to devote scarce resources to science so most suffer from a shortage of botanists. In Peru for example, a country with 20 000 higher plant species – 8% of the world total – there are fewer than ten botanists expert in the Amazonian flora.

Given these conditions, recent reviews emphasize the

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need to ensure that protocols for tropical biodiversity assessment are 'efficient' – in other words that they maximize inventory result for a given level of investment in scarce field resources (Campbell *et al.* 2002, Fisher 1999, Lawton *et al.* 1998, Phillips & Miller 2002, Tuomisto 1998). Efficient plot-based inventory is not an end in itself, but in situations where funds and expertise are limiting it contributes to better ecological understanding. For example, if the purpose of a research project is to understand the pattern and factors controlling diversity across a landscape it is vital to be able to achieve a sufficient density of samples across the landscape. In general the efficiency of any ecological inventory can be maximized in two ways – either by optimizing sampling strategies and survey design, or by changing the field sample unit itself. The former is widely debated in the literature (Austin & Heyligers 1989, Gillison & Brewer 1985, Thompson & Seber 1994, Wessels *et al.* 1998), but in the tropics there has been surprisingly little effort to evaluate the performance of the field protocols themselves. The simplest inventory involves ad hoc collecting, but this is notoriously subject to various forms of sampling bias (cf. Nelson *et al.* 1990) and therefore is of limited value to ecologists. More useful, quantitative floristic protocols usually involve sampling selected plant groups at fixed localities, as this enables evaluation of site-specific ecological parameters and of their variation across landscapes, regions or continents. Yet the protocols used may still not be optimally matched to these purposes, and comparisons of different protocols are lacking.

Our aim in this paper is to explore this issue and identify key principles that determine how efficiently floristic information is accumulated in species-rich forest inventory. A broad and useful definition of statistically 'efficient' research is that which yields the greatest increase in statistical power per unit of investment in field effort. How this definition is applied depends on the context, i.e. the ultimate purpose of the research. Here we focus on two kinds of questions relevant to ecologists and conservationists working at the landscape scale and greater: (1) Where are the most diverse forests found (and why)? (2) How floristically differentiated are forests across the study region (and why)? In this context statistically efficient research maximizes the rate at which elements in the target community, such as tree species, are encountered in the field. We quantify and compare the efficiency of the two most widely used approaches to basic plant biodiversity surveys in the Neotropics using extensive new datasets from Amazonia. We show that the leading inventory research methods have markedly different floristic efficiencies, and that these differences impact on the extent to which each method can detect ecological patterns. We hope that the results will help to stimulate further comparative research, more efficient inventory, and ultimately more efficient conservation planning.

Protocols

We used a 16-y history of sampling across a pair of forested Amazon landscapes to determine the relative efficiency of the two inventory protocols, each of which can yield site-specific data on the diversity, composition and structure of forests. Quantitative floristic results from both methods are widely reported and analysed in the tropical ecological literature. The first standard method involves a one-time census of all stems ≥10 cm diameter in an area of 1 ha or occasionally larger – the '1-ha method'. One-hectare inventories are used routinely and extensively by botanists, and quantitative floristic data are regularly used to infer major ecological pattern and process at local, regional and continental scales (Campbell 1994, Gentry 1988*a*, *b*; Pitman *et al.* 1999, Terborgh & Andresen 1998, ter Steege *et al.* 2000, Vásquez & Phillips 2000). These samples are sometimes converted into long-term plots to monitor forest processes but this requires significant extra investment (Alder & Synnott 1992) and, as we show later, in practice only occurs sporadically. The second method involves sampling all stems ≥ 2.5 cm diameter in 10 × 0.01-ha transects each of 2 × 50 m – the '0.1-ha method' (as developed by Gentry 1982, 1988*a*). The 0.1-ha method samples a larger part of the flora, because of the lower size cut-off, and has been applied mostly in the Neotropics (Clinebell *et al.* 1995, Gentry 1995, Gillespie *et al.* 2000, Phillips & Raven 1997), although ecological analyses have successfully used such data to model forest structure, diversity and composition at pantropical and global scales (Enquist & Niklas 2001, Gentry 1991, 1993). The total number of 0.1-ha inventories is > 650 (Phillips & Miller 2002, G. Aymard *pers. comm.*, P. Berry *pers. comm.*, B. Boyle *pers. comm.*, C. Cerón *pers. comm.*, T. Killeen *pers. comm.*). This compares with > 400 discrete 1-ha floristic samples made in neotropical old-growth forest (ter Steege *pers. comm.*) and > 700 1-ha samples throughout the tropics (O. Phillips, Y. Malhi, S. Lewis & T. Baker, unpubl. data). Both methods are applied slightly differently from one research team to another. For example many 1-ha and 0.1-ha samples deliberately exclude all lianas, and, unlike Gentry, many practitioners of the 0.1-ha method sample within a ≈ 2-ha grid. The main application for > 90% of 0.1-ha samples and > 50% of 1-ha inventories is eco-floristic assessment, and this is the purpose for which we are comparing the methods in this paper. We emphasize that we aim to compare the methods that ecologists actually use most frequently for this purpose: we do not aim to evaluate *all* methods that they could use.

Study sites

We conducted floristic inventories in two regions of primary forest in lowland Amazonian Peru (Loreto and Madre de Dios departments), recording over 2000 species of woody plants in 16 × 1-ha samples and 128 × 0.1-ha samples, distributed to capture the main ecological variation among mature forests as revealed by a Landsat TM image (canopy spectral variation) and confirmed by ground-truthing the image with members of local forest communities (edaphic and topographic variation). Samples were randomly sited with respect to local forest developmental phases (Appendix 1). In all cases, the central questions motivating the initial inventory of these samples were to understand how environmental factors may control the distribution of species and species diversity, although samples have since been used for a variety of purposes. Each study region consists of the primary lowland rain forests within 50 km of the regional capitals of Iquitos (Loreto) and Puerto Maldonado (Madre de Dios). Each region is characterized by substantial edaphic and floristic compositional variation (Tuomisto *et al.* 1995, Vásquez 1997), but almost uniform altitude and climate. The Loreto study region lies at a slightly lower altitude than the Madre de Dios study region (100–150 m vs. 200–260 m asl). Madre de Dios has a seasonal tropical climate (annual rainfall ~ 2200 mm, with 3–4 mo per year receiving less than 100 mm, and a mean annual temperature of ~ 25 °C; Duellman & Koechlin 1991, Phillips *et al.* unpubl. data), while Loreto is equatorial (annual rainfall averages ~ 2800 mm, with no distinct dry season, and a mean annual temperature of ~ 26 °C; Vásquez & Phillips 2000).

METHODS

Fieldwork

The 1-ha protocol involves firstly surveying a 1-ha area, and then measuring and identifying all trees ≥ 10 cm diameter at 1.30 m height (= diameter at breast height, dbh). Where necessary, diameters are measured above buttresses and other stem irregularities. In our plots we also censused lianas and stranglers ≥ 10 cm diameter, but these typically contributed only 1–5% of total stems. Every measured plant is identified or recorded as a unique 'morphospecies' and a voucher collection made if the taxon is encountered for the first time or if its identity is uncertain. Where the intention is to establish these as long-term plots, as opposed to one-off inventories, all trees must also be tagged and mapped, and special care may be needed with ensuring accurate diameter measurements. These modifications are time-consuming, so in our analyses we excluded the extra time involved in converting our 1-ha floristic inventories into long-term sample plots.

Our 0.1-ha samples represent the sum of ten 2 × 50-m subplots. Plants with a stem dbh of 2.5 cm or more and rooted within the transect area are included in the sample, with the same protocols for measurement and collection as for the 1-ha method. The 2 × 50-m subplots can either *each* be oriented at random (the Gentry protocol, nine samples initiated by the late Alwyn Gentry in which we participated) or within a 100 × 180-m systematic sampling grid (the modified 0.1-ha protocol, 119 samples) in which *all* subplots are oriented in the same direction chosen at random. Of this latter group of 119 samples, we completed 96 as part of an integrated biodiversity assessment protocol that also involved forestry and sociological assessments of timber and non-timber forest resources, so in our analyses we excluded the extra time involved in integrating the different techniques. The full protocols for establishing, collecting and analysing 0.1-ha forest samples are described in detail elsewhere (Gentry 1982, 1988*a*; Phillips & Miller 2002).

Both 1-ha and 0.1-ha inventories were made within the same forest types in each region, as determined on the basis of spectral and edaphic properties. At all sites our teams had broadly equivalent expertise, with one field botanist already expert in the long-term study of the regional flora and one tree-climber, which allows direct comparison of the two methodologies both within and between-regions. Additional botanists, tree-measurers and a note-taker were also often present, and the number of such assistant fieldworkers varied substantially. For every 1-ha and 0.1-ha sample we made a voucher collection for every species not recognized. The probability of an Amazonian tree being fertile at any one point in time is less than 4% (Vásquez & Phillips 2000), so repeated collections of sterile plants were often needed to reliably distinguish morphospecies. A full set of duplicates is deposited in Peruvian herbaria (AMAZ, USM) and in the USA (MO), with partial collections held at Peru at IIAP (Iquitos), CUZ (Cusco) and MOL (Lima) and duplicates sent to family specialists worldwide.

At every inventory plot we also collected soil samples (0–15 cm below the organic material layer). Within each plot soil was collected with an augur at at least 10 random locations distributed across the whole extent of the plot, and then bulked so that each 1-ha or 0.1-ha sample is represented by one soil sample. Tropical soils are notoriously variable at small scales (Jetten *et al.* 1993) so bulking the subsamples helps to ensure the sample is representative of prevailing conditions for each floristic sample. For each plot the composite samples were air-dried, cleaned by removing macroscopic organic material, and subsampled. Drainage conditions were assessed visually, and chemical composition and physical structure of soil were analysed at the Agricultural Research Center in Finland. Soil analyses were carried out primarily following methods described by van Reeuwijk (1995). Soil pH was measured in a 1 M KCl suspension. Exchangeable Ca, Mg, K and Na were extracted with 1 M ammonium acetate (pH 7.0). Exchangeable Al was extracted with 1 M KCl. Effective cation exchange capacity (ECEC) was calculated as the sum of cations, expressed in cmol(+) kg^{-1}. Base saturation (%) was calculated as the percentage of Ca, K, Mg and Na of ECEC. Plant-available P was determined by the Bray 1 method (0.03 M NH_4F–0.025 M HCl extraction). Clay (< 2 μm), silt (2–63 μm) and sand (0.63–2 mm) content was determined after a pre-treatment with citrate – dithionite – bicarbonate. Loss of weight on ignition (LOI) was determined by heating the dried soils at 420 °C for 6 h.

Comparison of methods – crude inventory efficiency

Most neotropical floristic samples are incomplete: usually some species cannot be identified because it proves impossible to confidently refer sterile collections to a known species concept. Moreover, species names change so the species list from any neotropical forest sample is in a continuous state of flux. We therefore limit our comparisons to the effort required to achieve each individual field-complete sample, with field-complete defined as the point at which (1) the diameter of every tree has been measured, (2) every species in the sample has either been fully identified or has been collected and assigned to a morphospecies for that plot, (3) multiple duplicates of each collection have been preserved in alcohol, (4) field-notes and collection notebooks have been suitably annotated, (5) a GPS reading has been made and (6) a representative soil sample has been collected.

We calculated *effort* per sample in terms of the number of person-days needed to complete each sample's fieldwork. We then used these values to estimate the efficiency with which floristic knowledge was gained from each sample, with crude inventory efficiency (*CIE*) computed as the number of species recorded divided by the person-days in the field.

$$CIE = \frac{\text{Nspecies encountered}}{\text{effort}}$$

We calculated two variants of *CIE*: CIE_{s+t}, with all shrub and tree species in the numerator, and CIE_t, with only tree species in the numerator.

To analyse the results, we used a non-parametric procedure (Kruskall–Wallis) to explore differences in the forests sampled in each region, and sought the best-fit regression models to describe *effort* in terms of the species number and plant density of the forests. Likewise, sample efficiency was compared between regions and methods (using the Kruskall–Wallis test). We used step-wise regression analysis to explore the contributions of different attributes of the inventory method and the forest itself to explaining both the effort required to complete each inventory, and the efficiency with which each inventory was performed. Each variable's impact was tested in turn by evaluating its contribution after accounting for the effect of all other variables.

Comparison of methods – proportional inventory efficiency and tree inventory efficiency

The non-scandent floras sampled by 1-ha and 0.1-ha methods differ: the flora potentially ≥ 10 cm dbh is a subset of the larger flora of species that are potentially ≥ 2.5 cm dbh. Therefore, other things being equal, the 0.1-ha method should capture more species and achieve higher crude inventory efficiency scores. We conducted further analyses to account for this, by reporting efficiency of species capture as a proportion of the size of the method's overall target flora (i.e. 'species capable of attaining a self-supporting stem ≥ 10 cm diameter' for the 1-ha method, 'species capable of attaining a self-supporting stem ≥ 2.5 cm dbh' for the 0.1-ha method), and by estimating efficiency with respect to the core shared flora of species potentially attaining ≥ 10 cm diameter. In other words, (Q1) how efficiently does each method sample a proportion of its actual target flora? and (Q2) how efficiently does each method work when sampling only the shared flora?

To address the first question we compute a proportional inventory efficiency (*PIE*) for each sample as its crude inventory efficiency for all species divided by the number of species in the target flora.

$$PIE = \frac{(\text{Nspecies encountered})/\text{effort}}{\text{Nspecies in target flora}}$$

This is problematic since the total number of tree and shrub species occurring in a locality is only known for a few sites in the Neotropics, which include our Iquitos region but not our Madre de Dios region (Table 1). The relative size of tree and shrub floras reflects forest conditions and may also vary with methodological factors. For example, widely dispersed species may have larger diameters than narrowly dispersed species (Pitman *et al.* 2001, Ruokolainen & Vormisto 2000), so the varying area used to define the 'sites' may affect the relative proportion of each habit. While the exact definitions used to delineate trees from shrubs and/or treelets may vary from collector to collector, most compilations share an explicit or implicit definition of trees as self-supporting plants capable of reaching at least 10 cm dbh (and therefore capable of being recorded in 1-ha plots). Inspection of Table 1 suggests that reported differences between localities do reflect real underlying differences in the preponderance of different plant growth forms in different conditions, with smaller species relatively frequent in richer-soil forests (Costa Rica, Panama and Ecuadorian Amazonia) and infrequent in the poor-soil forests of central and eastern Amazonia, which is consistent with results from ecological samples (Gentry & Emmons 1987). Recognizing the methodological and phenomenological variation, we still wanted to draw general conclusions about the efficiency of each method, so our approach is to use the extreme

Table 1. Habit comparisons in neotropical moist and wet forest lowland florulas for sites > 1 km^2.

Area (km^2)	Country	Locality	Tree species	Shrub and treelet species	Tree species, % of all erect woody species	Source
100	Brazil	Reserva Ducke	1175	143	89.2%	da Ribeiro *et al.* 1999
15	Costa Rica	La Selva	*c.*310[1]	*c.* 260[1]	*c.* 55%[1]	Hammel 1990
> 50 000	Ecuador	Ecuadorian Amazonia < 500 m asl	1356[2]	1132[2]	54.5%[2]	Jørgensen & León-Yánez 1999
c. 1	French Guiana	Nouragues, low forests of inselbergs	48% of florula	11% of florula	81.4%	Poncy *et al.* 1998
6200	French Guiana	Sinamary River region terra firme forest	322	119	73.0%	Bordenavé *et al.* 1998
15	Panama	Barro Colorado Island	*c.* 235[1]	*c.* 175[1]	*c.* 57%[1]	Foster & Hubbell 1990
c. 7500	Peru	Iquitos	1280	428	74.9%	Vásquez 1997
c. 80 000	Peru	All Madre de Dios	1004	Unknown	Unknown	Pitman *et al.* 2001

[1] Approximate figures: read off a graph.
[2] Some overlap: a few species may be categorized in more than one habit.

tree:shrub ratios to delineate the approximate boundaries within which most landscapes should fall, and then test whether the differences in efficiency between methods are qualitatively consistent across this range. We therefore compute *PIE* values for three scenarios – a shrub-rich Ecuadorian scenario where trees are 54.5% of the combined tree, shrub and treelet flora of *c.* 2488 species; a shrub-poor Central Amazonian scenario where trees are 89.2% of a combined flora of 1318 species; and an intermediate North Peru scenario where trees are 74.9% of a combined flora of 1708 species.

To address the second question, we define tree inventory efficiency (*TIE*) as the sample CIE_t divided by the number of species in the target flora that are trees.

$$TIE = \frac{(\text{Ntree species encountered})/\text{effort}}{\text{Ntree species in target flora}}$$

We classify species in our 0.1-ha and 1-ha samples as 'trees' if they attain $\geq$ 10 cm dbh as self-supporting plants in Gentry (1988*a*), Vásquez (1997), Vásquez & Phillips (2000), and in our unpublished 0.1-ha and 1-ha plot data from lowland Loreto and Madre de Dios totalling more than 50 ha. For the 1-ha methodology *TIE* must by definition always be equal to *PIE*. But for the 0.1-ha methodology we find empirically that *TIE* > *PIE* when computed assuming a shrub-rich 'Ecuadorian' target flora and *TIE* < *PIE* when computed assuming a shrub-poor 'Central Amazonian' target flora. In practice our *TIE* scores are conservative estimates of the efficiency with which 0.1-ha plots can detect tree species because we have no way of separately accounting for the labour required to inventory tree species and that needed to inventory shrubs in 0.1-ha samples.

Comparison of methods – ecological efficiency

We also compared the methods in terms of the efficiency with which we were able to use them to distinguish statistically significant ecological patterns in the forest samples (ecological efficiency). The potential choice of ecological questions and statistical approaches is extremely broad so we limit ourselves to two basic questions that interest ecologists and conservationists ((Q1) how does alpha-diversity vary across the landscape? (Q2) how does species composition vary across the landscape?) and address these with simple analyses. Our intention here is to compare ecological efficiency of each method empirically to only a first approximation. This is an exploratory analysis – we do not pretend that these are the only important questions and recognize that both need to be addressed in greater depth to provide definitive evaluations across all scales, levels of spatial resolution and forest conditions.

We used the associated dataset of soil chemical and physical properties to test whether and how alpha-diversity in tropical forests may be influenced by edaphic factors. This is a contentious issue, with different authors reporting conflicting results (Clinebell *et al.* 1995, Givnish 1999, Huston 1980, ter Steege & Hammond 2001). We hypothesized that alpha-diversity should be partly controlled by soil factors, with (1) diversity greatest at sites with low soil fertility (because on richer soils the best competitors will be able to monopolize a greater share of resources – cf. Huston 1994), and (2) diversity lowest in forests with poor drainage (because fewer species are expected to be able to survive periods of soil anaerobiosis – cf. for example Tuomisto & Poulsen 2000). We used Fisher's Alpha as our metric of forest diversity because it is robust to the effects of varying sample size (Condit *et al.* 1996), and we focus our analysis on the Madre de Dios forests where we have invested most effort in 0.1-ha and 1-ha inventories. To explore the potential edaphic controls on diversity, we used ordination by a principal components analysis (PCA) to describe the major gradients in normalized and standardized soil variables, and then tested the effects of these gradients on forest diversity using multiple regression. Ordination axes are statistically independent, so PCA ensures that multiple regressions do not have the collinearity problems that

Table 2. Comparison of forest diversity and density by region. Mean and standard deviation of species per plot, Fisher's Alpha per plot, and density are reported by region and sample protocol. Kruskall–Wallis results (z-values) test the null hypothesis that forests in each region have the same value.

	Loreto	Madre de Dios	z
0.1-ha samples			
Species	177 ± 54.8	92 ± 21.9	6.01***
Fisher's Alpha	178 ± 92.4	58 ± 20.1	5.49***
Plants	351 ± 77.3	238 ± 54.3	6.02***
1-ha samples			
Species	303 ± 13.1	162 ± 38.5	3.25**
Fisher's Alpha	224 ± 39.6	78 ± 23.4	3.25**
Plants	665 ± 95.6	583 ± 57.0	2.39*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

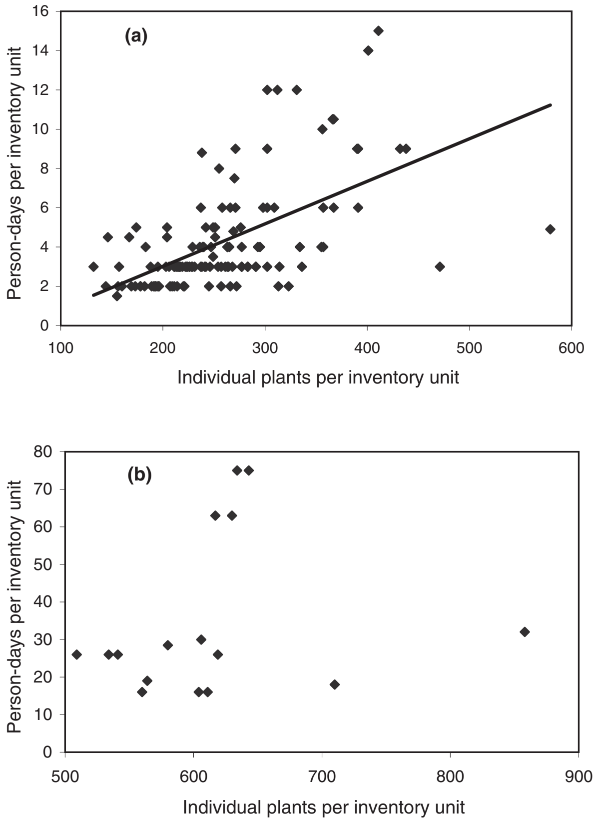

Figure 1. *Effort* required to complete inventory as a function of plant density. Solid line represents the best-fit linear model. (a) All Peruvian 0.1-hectare inventories: Person-days = −1.320 + 0.0217 plants; R^2 = 33.4%, F = 30.3, $P < 0.001$. (b) All Peruvian 1.0-hectare inventories: no significant relationship.

would arise from testing contributions of all 16 soil variables simultaneously. To facilitate comparison of 1-ha samples with 0.1-ha samples with respect to the same target population (tree species) we use Fisher's Alpha values based on trees alone.

Finally, we explored the degree of habitat association at the level of individual identified tree species using Indicator Species Analysis (Dufrene & Legendre 1997), that takes account of both relative abundance and relative frequencies of each species across the landscape to parameterize a null model of random expectations for each species. To keep the analysis as simple but universal as possible we constructed a dichotomous habitat classification for all moderately and well-drained samples. Samples were categorized as 'base-poor' ($[\mathrm{Ca}^{2+}] < 100$ ppm) or 'base-rich' ($[\mathrm{Ca}^{2+}] > 100$ ppm), which broadly equate to Pleistocene and Holocene river terraces (Rasanen *et al.* 1992), allowing us to assess association in just two habitat categories while using most of our data. Significance of habitat association was estimated by a Monte Carlo procedure that reassigns species densities and frequencies to habitats 1000 times. The probability of Type I error is based on the proportion of times that the highest indicator value across habitats (*IVmax*) from the randomized data set equals or exceeds the *IVmax* from the actual data set. The null hypothesis is that *IVmax* is no larger than would be expected by chance, so that the species has no indicator value. This approach does not account for possible spatial autocorrelation in the data (i.e. any distance decay in floristic similarity maintained by environment-independent processes such as dispersal limitation), but, as we show later, spatial autocorrelation probably does not affect our conclusions.

RESULTS

There are substantial regional differences in the forests, whether sampled by the 0.1-ha or 1-ha method (Table 2). First, Madre de Dios forests are much less diverse than the Loreto forests, and both protocols indicate a similar magnitude of difference (e.g. mean Fisher's Alpha values in Loreto are three times those in Madre de Dios regardless of protocol). Our samples from Loreto include a site (Allpahuayo) with the highest Fisher's Alpha value (242) published from a 1-ha sample anywhere in the world (Vásquez & Phillips 2000) and the greatest number of woody species (275) yet inventoried with the 0.1-ha method (Clinebell *et al.* 1995, Gentry & Ortíz 1993). Second, the density of stems $\geq$ 10 cm dbh, and especially of stems $\geq$ 2.5 cm dbh, is significantly greater in the aseasonal Loreto forests than in the seasonal Madre de Dios forests.

The *effort* required to complete a field sample depends on the number of individual plants sampled, at least for 0.1-ha samples (Figure 1), and especially on the number of species sampled regardless of the protocol (Figure 2), confirming that the diversity of the forest has a major impact on the inventory process. Not surprisingly, given the much higher species density and significantly higher stem density, inventories in Loreto forests required more effort to complete than inventories in Madre de Dios forests (Table 3).

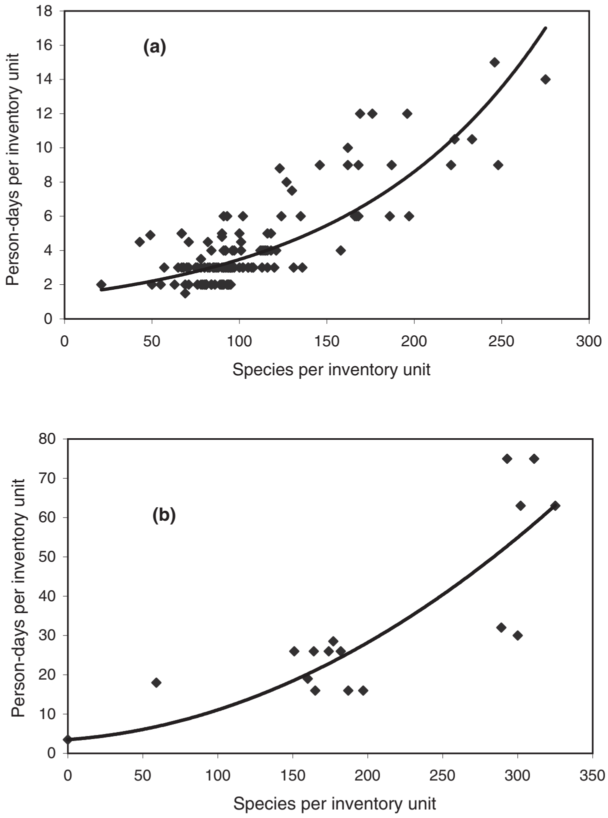

Figure 2. *Effort* required to complete inventory as a function of species richness. Solid line represents the best-fit polynomial model. (a) All Peruvian 0.1-hectare inventories: Person-days = 1.00 + 0.015 species + 0.000126 $(\text{species})^2$; $R^2 = 69.4$ %, F = 140, $P < 0.001$. (b) All Peruvian 1.0-hectare inventories: Person-days = 3.5 + 0.0278 species + 0.0005 $(\text{species})^2$; $R^2 = 69.9$ %, F = 16.7, $P < 0.001$. The fit for (b) is forced through the estimated time investment needed for a hypothetical plot with 0 species – i.e. the effort required to locate and layout a sample, take a GPS reading, make a soil sample and commute to and from the site.

Inventory efficiency

1-ha samples on average record more species than 0.1-ha samples in both Loreto (z = 3.70, $P < 0.001$), and in Madre de Dios (z = 4.17, $P < 0.001$). However, individual 1-ha samples also require much more *effort* than individual 0.1-ha samples in both Loreto (z = 3.70, $P < 0.001$) and in Madre de Dios (z = 5.21, $P < 0.001$). As a result, our 0.1-ha inventories were substantially more efficient in terms of floristic data gained per effort invested. The crude inventory efficiency (CIE_{s+t}) of 0.1-ha samples is three to four times that of 1-ha samples (CIE_t) in Loreto (20.3 ± 6.0 vs. 6.2 ± 2.7 species per person-day, mean ± S.D., z = 3.67, $P < 0.001$) and in Madre de Dios (30.5 ± 9.4 vs. 7.8 ± 2.9 species per person-day, z = 5.16, $P < 0.001$).

When adjusted for the different number of species in the target flora the magnitude of the efficiency difference between the protocols is reduced. However, these proportional inventory efficiency results (Table 4) show that the 0.1-ha protocol is still about twice as efficient as the 1-ha protocol in shrub-rich forests and about three times as efficient in shrub-poor forests. When only tree species are considered in the sample and the target flora, then the 0.1-ha protocol is more than three times as efficient (tree inventory efficiency) as the 1-ha protocol whichever assumption is made about the richness of shrub species in the flora (Table 4).

Table 3. Comparison of sample *effort* by region. Mean and standard deviation of the mean (person-days per sample) are reported for each sample protocol in each region, with results from Kruskall–Wallis tests of the null hypothesis that there is no difference in sample *effort* between regions.

	Loreto	Madre de Dios	z
0.1-ha samples	9.0 ± 2.9	3.3 ± 1 3	7.09***
1-ha samples	56.3 ± 20.4	21.8 ± 5.2	3.25**

** $P < 0.01$, *** $P < 0.001$.

Although these results suggest that the inventory method itself was an important factor in determining effort and efficiency, they do not prove it conclusively. The apparent difference between methods could be driven by covarying differences in species richness, plant density or the number of field assistants. We therefore developed regression equations for inventory effort and efficiency that model the potential contribution of all factors. After accounting for the effects of species richness, plant density and the number of assistants available to help in the field, the inventory method itself still contributed significantly ($P < 0.01$) to models of sample *effort*, CIE_{s+t}, *PIE* and *TIE*, regardless of the target flora richness and habit distribution.

Soils, diversity and ecological efficiency

Soils varied substantially among the 106 plots in Madre de Dios with soil samples, but soil variables are highly inter-correlated within sites. A PCA (Table 5) showed that nearly half the variation in the soils dataset could be accounted for by a single axis ('factor 1') that describes a gradient from sites with high clay, cation content and CEC to those with high sand and low cation content and CEC. Much smaller amounts of variation are described principally by variation in Al^{3+} and pH (axis 2), silt (axis 3) and drainage and total P (axis 4).

First, we had hypothesized that alpha-diversity would be partly controlled by edaphic factors, but it was impossible to detect any soil-mediated effect on diversity for our 10 × 1-ha plots: no soil variable or PCA factor correlates with 1-ha tree alpha-diversity. In the 96 × 0.1-ha plots Fisher's Alpha was significantly correlated with a number of soil factors, including pH ($r_s = -0.29$, $P < 0.01$), drainage ($r_s = 0.23$, $P < 0.03$) and ECEC ($r_s = -0.21$, $P < 0.05$), results consistent with our two initial hypotheses.

Table 4. Protocols compared in terms of inventory efficiencies, under different assumptions about the relative importance of shrubs and trees in the target flora. See text for details. All values are expressed × 10^2; comparisons are with Kruskall–Wallis non-parametric tests.

		Assumption about target flora		
		High ratio of shrubs:trees = 'Ecuadorian scenario'	Intermediate ratio of shrubs:trees = 'North Peru scenario'	Low ratio of shrubs:trees = 'Central Amazonian scenario'
Proportional inventory efficiencies (*PIE*), where *PIE* = species sampled per person day in field, as a proportion of the total target flora (i.e. trees for 1-ha method; trees and shrubs for 0.1-ha method).				
Loreto	(mean ± SD)			
	0.1-ha	0.82 ± 0.24	1.19 ± 0.35	1.54 ± 0.46
	1-ha	0.46 ± 0.18	0.48 ± 0.19	0.53 ± 0.21
Madre de Dios	(mean ± SD)			
	0.1-ha	1.23 ± 0.38	1.79 ± 0.55	2.31 ± 0.71
	1-ha	0.58 ± 0.20	0.61 ± 0.21	0.66 ± 0.23
Protocol comparison, z	Loreto	2.63 **	3.58 ***	3.58 ***
	Madre de Dios	4.60 ***	5.04 ***	5.13 ***
Tree inventory efficiencies (*TIE*), where *TIE* = tree species sampled per person day in field, as a proportion of the total tree flora.				
Loreto	(mean ± SD)			
	0.1-ha	1.22 ± 0.28	1.29 ± 0.41	1.41 ± 0.44
	1-ha	0.46 ± 0.18	0.48 ± 0.19	0.53 ± 0.21
Madre de Dios	(mean ± SD)			
	0.1-ha	1.99 ± 0.62	2.11 ± 0.65	2.29 ± 0.71
	1-ha	0.58 ± 0.20	0.61 ± 0.21	0.66 ± 0.23
Protocol comparison, z	Loreto	3.58 ***	3.58 ***	3.58 ***
	Madre de Dios	5.15 ***	5.15 ***	5.15 ***

** $P < 0.01$, *** $P < 0.001$.

Equivalent results are arrived at when considering only tree species that attain at least 10 cm dbh (Fisher's Alpha vs. pH ($r_s = -0.27$, $P < 0.01$), drainage ($r_s = 0.24$, $P < 0.02$) and ECEC ($r_s = -0.20$, $P < 0.05$)).

Within the Madre de Dios study area climatic variation is negligible so this variation in diversity cannot be due to any climatic effect. The correlations are very weak, however, suggesting that soil variation has only a small impact on diversity in these forests. In Madre de Dios the mean *effort* required to complete a 1-ha sample (21.8 person-days) is $\sim$ 6.6 × the mean *effort* needed for a 0.1-ha sample (3.3 person-days), so our 10 × 1-ha samples required an equivalent effort to that required to complete 66 × 0.1-ha samples. Thus, in order to directly compare the statistical efficiency of the techniques in discriminating possible edaphic controls of alpha-diversity of tree species, we repeatedly subsampled 66 × 0.1-ha plots 100 times (i.e. n = 100 independent, randomized selections of 66 plots) and examined the dependence of tree alpha-diversity on soil PCA factors. For each subsample, the multiple or simple linear-regression model with maximal F-value was chosen, and the process repeated for smaller subsamples of 0.1-ha plots until it was no longer possible to obtain a regression model with an F-value with $P < 0.05$. This critical point was always reached by 32 samples or fewer, even when samples happened to include only well-drained forests, and the moving average of the median scores crosses the $P = 0.05$ point at 16 randomly selected samples (Figure 3). In this particular context then, the ecological efficiency of 0.1-ha plots is superior to that of 1-ha plots by a factor of approximately 66/16 (i.e. 4.1). This is a conservative estimate since (1) the

Table 5. Site soil PCA scores.

	PCA factor			
Soil variable	1	2	3	4
ECEC	0.341	−0.097	0.032	−0.035
Mg	0.335	0.091	−0.074	0.083
Particles < 0.063 mm	0.316	−0.164	0.199	0.148
Ca	0.314	0.212	−0.097	0.106
Sand	−0.293	0.159	−0.382	−0.121
K	0.284	−0.120	−0.146	0.159
Na	0.261	0.016	−0.010	−0.300
Al/ECEC	−0.260	−0.348	0.118	−0.149
Drainage	−0.255	0.020	−0.082	0.463
LOI	0.235	−0.224	−0.200	−0.089
Clay	0.219	−0.366	−0.102	0.299
pH	0.183	0.375	0.019	0.262
DM	−0.166	0.274	0.247	0.109
P	0.152	0.205	−0.202	−0.609
Silt	0.094	0.121	0.767	−0.143
Al	−0.086	−0.538	0.111	−0.142
Cumulative variance	48.6%	66.9%	75.2%	81.9%

Table 6. Habitat indicator tree species (following Dufrene & Legendre 1997) revealed by 0.1-ha and 1-ha inventory protocols standardized for field effort and target flora. The matrix shows the number of self-supporting species ≥ 10 cm dbh that are significant habitat indicators.

	1-ha method: indicator of acid soil	1-ha method: indicator of base-rich soil	1-ha method: not a habitat indicator	Sum	Proportion of all 709 tree species attaining ≥ 10 cm in our samples
0.1-ha method: indicator of acid soil	12	0	45	57	8.0%
0.1-ha method: indicator of base-rich soil	0	13	47	60	8.5%
0.1-ha method: not a habitat indicator	13	11	568	592	83.5%
Sum	25	24	660	709	
Proportion of all 709 tree species attaining ≥ 10 cm in our samples	3.5%	3.5%	93.1%		

failure to find a significant model with our sample of 10 × 1.0-ha plots means that we cannot accurately predict how much greater effort is required with that protocol before the edaphic effect could be detected; (2) pooled soil samples from 0.1-ha represent an extent of 1.8-ha, almost twice that of the 1-ha plots, while Amazon species are known to respond to soil variation over scales of only a few metres (Vormisto *et al.* 2000).

Second, we compared the ability of each field method to detect significant species/habitat associations, using species indicator values (Dufrene & Legendre 1997). Using identical a priori habitat definitions, field effort, and target floras, we were able to define 117 indicator tree species using the 0.1-ha method but only 49 significant species/habitat associations with the 1-ha method (Table 6). The 0.1-ha method inventories fewer individual stems than the 1-ha method per sample so is expected to have a greater sampling error; however this effect is evidently more than compensated for by the much greater number of samples (factor of ~6.6) achievable for the same effort. Thus, for the purpose of detecting significant species/habitat associations, we have shown empirically that the higher density 0.1-ha sampling network provides more statistical power than the low-density 1-ha network of larger individual samples. As a result, 1-ha plots are only able to detect significant habitat associations for species with near-perfect habitat fidelity (mean ± SD IV scores of indicator species = 88.7 ± 8.9%), while the 0.1-ha samples are able to detect associations for species with much weaker habitat fidelity (36.4 ± 16.6%) ($W = 6946$, $P < 0.001$). Dispersal limitation or other spatial processes independent of habitat could affect the IV scores, inflating the apparent degree of species' habitat associations (Dufrene & Legendre 1997). However, 0.1-ha samples are somewhat less clustered than 1-ha samples (mean inter-sample distance = 39 vs. 27 km). Therefore our result of greater ecological efficiency for the 0.1-ha samples is unlikely to be driven by floristic spatial autocorrelation in these forests.

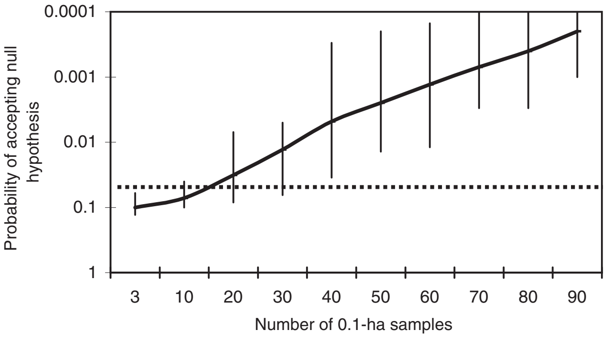

Figure 3. Relationship between sample size (number of independent 0.1-ha floristic samples in Madre de Dios) and the ability to detect a significant relationship between tree alpha-diversity and soil conditions. 0.1-ha samples were randomly subsampled 100 times to determine the range of P-values for the best-fit simple or multiple linear regression equations between tree alpha diversity and soil PCA factors 1 to 4. Solid line represents the moving-average of the median values; vertical lines indicate the upper and lower 95% confidence intervals of the mean for the given sample size; dotted line represents the point at which P (accept H_0) = 0.05.

DISCUSSION

In total we worked in the field for more than 3 person-years to establish these inventories. The effort invested in each protocol was similar (554 person-days for 0.1-ha samples, 555 person-days for 1-ha samples). This very large and evenly spread field effort helps to confer confidence in the comparative analyses presented here, as does the consistency of the direction and strength of the methodological impact on inventory and ecological efficiencies.

The results show that the 0.1-ha inventory method achieves a greater gain in floristic knowledge and understanding per unit of effort than the 1-ha inventory method. Why should this be so? First, 0.1-ha plots sample somewhat fewer individuals than do 1-ha plots, and since the gradient of species–individual curves falls with increasing sample size (Condit *et al.* 1996), the former method must record fewer repeats of the same species. However this effect is of limited importance as the 0.1-ha method samples individual plants much more quickly than 1-ha plots (about 2.7 times more rapidly in Madre de Dios, and about 3.3 times more rapidly in Loreto; based on data in Tables 2 and 3), and in any case the smaller number of individuals also has the effect of increasing sampling error. Second, and more significantly, the 1-ha method inventories larger trees and therefore requires many more climbs to identify and collect vouchers. This is time-consuming and physically demanding. By contrast, the 0.1-ha method samples stems down to 2.5 cm diameter, so that most plants collected in the 0.1-ha inventory are accessible from the ground. Finally, while the 0.1-ha method actually traverses a larger patch of forest (cf. Methods) it requires less labour to lay out the sample, because the inventories are effectively transect lines rather than rectangular plots. For all these reasons 0.1-ha plots sample tree species more rapidly than 1-ha plots.

Greater inventory efficiency translates directly into greater ecological efficiency, because other things being equal, many more samples and therefore greater statistical power are attained for the same effort in the field. We showed that on average each 0.1-ha sample takes ~15% of the field time needed for a 1-ha sample, permitting a much higher inventory density across the landscape. Better ecological insight for the same effort is always desirable, but it is especially important for tropical ecologists where expertise and funding needed for inventories are usually limiting. Our analysis of Madre de Dios inventory samples showed that soils probably have only weak and subtle impacts on tree alpha-diversity that were not detectable with the 1-ha dataset. Yet significant soil–diversity relationships were found with subsampled 0.1-ha datasets equivalent to one quarter of the field effort expended in inventorying the 1-ha plots. Similarly, 0.1-ha samples were more than twice as efficient as 1-ha samples at detecting significant habitat–species associations.

While the 0.1-ha method is clearly the more efficient of the two leading plot-based protocols used for floristic assessment in neotropical forests, we cannot conclude that it is the *single best* method for making all ecofloristic samples for four reasons. First, our comparisons have excluded the substantial but hard to quantify effort required of herbarium botanists to convert field-morphospecies concepts into full species identifications, and this effort will presumably be greater for 0.1-ha samples than 1-ha samples because of the different rate with which they encounter species. Second, the 1-ha method clearly suits many purposes reasonably well – as we discuss further below it is an important multi-purpose protocol. Third, there are no data available from less popular methods to compare with these leading protocols. Finally, floristic samples of ≥ 1 ha are suited to a variety of *additional* purposes such as monitoring forest dynamics, as well as phenological and ethnobotanical research (Condit 1998, Dallmeier & Comiskey 1998*a*, *b*; Malhi *et al.* 2002, Phillips *et al.* 1998, 2002*a*, *b*), which usually involve conversion to permanent plots by tagging, mapping and regular recensusing. However the 1-ha protocol is widely used in ecological research without becoming a site for long-term study, and many plots are in practice abandoned after yielding only inventory data. This appears to happen everywhere and to everyone, and in making this point we do not mean to criticize any individual research team. In the region that we are most familiar with (western Amazonia) we estimate this failure rate at > 50% (of 115 plots whose fate we know of, 64 plots have been abandoned, including 19 plots that we have had to abandon). Western Amazonia is the focus of a major international recensusing effort (RAINFOR: http://www.geog.leeds.ac.uk/projects/rainfor/; Malhi *et al.* 2002), so these data may underestimate the pantropical rate of failure to resample. At the pan-Amazon scale > 60% of 1-ha plots are abandoned: ≥ 270 × 1-ha plots had been inventoried by 1997 (based on a count of ≥ 204 plots inventoried *and* published by 1998, ter Steege *pers. comm.*, and RAINFOR unpublished data), but only 104 appear to have been recensused by 2002 (i.e. all floristically inventoried plots known to Malhi *et al.* 2002, Phillips *et al.* 1998, 2002*a*, *b*; RAINFOR unpublished data). Reasons for 1-ha plots to not become monitoring sites include: (1) inadequate funds to recensus; (2) impossibility of relocating the plot's position; (3) the threat of terrorism or war; (4) removal of aluminium nails by local residents; (5) forest disturbance by residents or commercial interests; (6) changing research interests of principal investigators; (7) rapid radial tree growth 'swallowing' tags; (8) liana or bamboo tangles discouraging access; and (9) death of the principal investigator. Clearly, not all these factors can be anticipated but they illustrate the need for a realistic appraisal of the risks and benefits before conducting any 1-ha inventory: conversion to permanent plot status is expensive, time-consuming and uncertain. Temporary and inadequate funding is the main reason that most 1-ha plots remain simply temporary floristic samples. We suggest that installation of 1-ha plots for *monitoring purposes* may only be worthwhile when long-term funding programmes are identified from the start.

However, as well as their key (but often unrealized) role in long-term studies, 1-ha plots may still be an appropriate method in some studies where the primary research purpose concerns floristic inventory of trees, and their principal attraction arguably lies in their reasonable suitability for many purposes. For example, researchers may wish to understand the floristic pattern only among the dominant biomass components, and the larger minimum diameter of the 1-ha protocol is better suited to this purpose since trees ≥ 10 cm dbh usually represent > 80% of

Table 7. A generalized comparison of the two major inventory protocols in terms of fitness for purpose. The table is not intended to be definitive, merely indicative of the likely advantages and disadvantages of each approach. A complete approach to selecting the optimal protocol for a particular study should involve a consideration of plot shape as well as size (Condit *et al.* 1996, Laurance *et al.* 1998), other, less popular protocols, and a finer definition of purpose that encompasses concerns of local people, target flora size-class, spatial and temporal extent of study, and the desired degree of statistical replication and precision (Wong *et al.* 2001).

Purpose of sample		0.1-ha protocol		1-ha protocol	
		Pros	Cons	Pros	Cons
Floristic assessment	Floristic diversity and floristic composition	Includes all plants ≥ 2.5 cm diameter[1]		Includes larger plants (≥ 10 cm diameter) only[1]	
		Efficient inventory of tree and shrub species → relatively rapid replication across landscape (this study)			Inefficient inventory of tree species → slow replication across landscape (this study)
		Many neotropical data for comparison	Few palaeotropical data for comparison	Many neotropical and palaeotropical data for comparison	
			Small area → high sampling error (but outweighed by the advantage of rapid sampling of each locality) (this study)	Larger area → lower sampling error (but outweighed by the disadvantage of slow sampling of each locality) (this study)	
Physical structure		Includes all plants ≥ 2.5 cm diameter[1]		Includes larger plants (≥ 10 cm diameter) only[1]	
		Includes smaller species and stem-sizes		Focuses on plants which contribute > 90% biomass	Excludes many species and juveniles
		Sub-linear → not skewed by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)	Sub-linear → edge effects may create potential error and bias in estimating biomass (cf. Laurance *et al.* 1998)	Data from thinner plots not skewed by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)	Data from square plots may be dominated by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)
			Small area → high sampling error (outweighed by the advantage of rapid sampling of each locality?)[2]	Larger area → lower sampling error (outweighed by the disadvantage of slow sampling of each locality?)[2]	
		Many neotropical data for comparison	Few paleotropical data for comparison	Many neotropical and paleotropical data for comparison	
Monitoring dynamics		Sub-linear → easy to convert to growth and mortality studies if line marked	High edge:area ratio → difficult to convert for recruitment studies (edge effects, e.g. Sheil 1995)		
		Sub-linear → not skewed by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)		Data from thinner plots not skewed by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)	Data from square plots may be dominated by rare and stochastic big tree falls (R. Vásquez, *pers. obs*)
			Few data for comparison worldwide	Many data for comparison worldwide (Phillips *et al.* 1994)	
		Includes many lianas, which may contribute > 20% of productivity (e.g. Hegarty 1991)	Skewed by few larger plants	Includes almost all free-standing plant productivity	Excludes smaller lianas
			Small area → high sampling error	Large area → lower sampling error	
Matrix for other ecological studies	Phenological	Includes all plants ≥ 2.5 cm diameter[1] (disadvantage for tree phenological studies)		Includes larger plants (≥ 10 cm diameter) only[1] (advantage for tree phenological studies)	
		Sublinear → easy to convent to other plant-based research Small and quick → can be replicated more easily			Large → difficult to locate plants quickly Large and slow → difficult to replicate
			Few data for comparison	Some neotropical data for comparison (e.g. Phillips 1993)	
	Zoological	Includes all plants ≥ 2.5 cm diameter[1]		Includes larger plants (≥ 10 cm diameter) only[1]	
		Rapid → efficient assessment of resources available to frugivores (Sussman & Rakotozafy 1994)	Plot dimensions and size inappropriate scale for most animals	Plot dimensions and size appropriate scale for more animals (e.g. Dallmeier *et al.* 2002)	
	Canopy biology and remote sensing		Linear and small → not well suited to this purpose	Square, larger plots → better suited to purpose	
			< 10% of inventoried plants are in the canopy	Includes all canopy trees	< 30% of inventoried plants are in the canopy

[1] The lower size-class cut-off used in the 0.1-ha method may be an advantage or disadvantage depending on the precise nature of the purpose.

[2] Not yet tested to the authors' knowledge.

forest biomass (Araujo *et al.* 1999). Tenth-hectare samples may be less appropriate for canopy-oriented studies (e.g. involving ground-truthing remotely sensed measurements) than 1-ha samples, as long as the latter are replicated sufficiently, and canopy research can usefully occur even in 1-ha plots that are not destined for permanent study plot status (e.g. in Ecuador, N. Pitman *pers. comm.*). Further, if the research aims require comparison with existing data from elsewhere the availability of such data will also influence the choice of method. Thus in tropical Africa and Asia 1-ha inventories have been applied much more frequently than 0.1-ha inventories. Finally, judicious combination of 1-ha and 0.1-ha methodologies (and other protocols) can together meet a wider range of ecological objectives than either method alone. In Table 7 we have attempted to outline the advantages and disadvantages of each method with respect to the typical range of purposes in tropical forest ecology.

In conclusion, careful matching of inventory purpose to method has always been important for ecologists, and is especially so now in the tropical context of rapid environmental change. The need for efficient sampling is a dominant factor determining methodological decisions, but comparative analysis of efficiency has been lacking in the tropical eco-floristic literature. Our results show for the first time that conventional approaches to tropical floristic inventory vary greatly in their relative inventory efficiencies. These preliminary findings suggest that the urgent need for extensive plot-based floristic assessment in remote areas of the tropics can be addressed most simply by sampling small size-classes in narrow transects, but do not imply that this is the optimum approach for all inventory research. Further comparative analyses are needed using simulated and empirical results to explore how assessment techniques perform under different conditions.

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Appendix 1. List of sample sites using 0.1-ha and 1-ha methods.

(a) 0.1-ha method

Site	Code	S (degrees, minutes, seconds)	W (degrees, minutes, seconds)	Number of assistants	Person days in field = Effort	Species per person day in field = Efficiency	Species richness	Fisher's alpha	Plant individuals
LORETO									
Allpahuayo Yarinal 1	Allpgen1	3.57.17	73.25.26	2	14	19.6	275	386	401
Allpahuayo irapay sandy damp	Allpihan	3.57.03	73.26.06	4	12	14.1	169	152	312
Allpahuayo clayey soil irapay parcela A	Allpisac	3.56.55	73.26.09	4	9	18.7	168	157	302
Allpahuayo Varillal alto humedo 1, INEA Reserve	Allpvah1	3.57.06	73.24.38	5	4.9	10.0	49	13	579
Allpahuayo Varillal alto seco 2	Allpvas2	3.57.19	73.25.47	4	6	15.2	91	45	298
Allpahuayo Varillal alto seco 3	Allpvas3	3.57.09	73.26.13	4	6	20.7	124	79	302
Allpahuayo Yarinal 3	Allpyar3	3.57.12	73.25.17	4	9	16.2	146	129	271
Allpahuayo1 = Shapaja	Allp1	*c.* 3.57	*c.* 73.24	1	10.5	21.2	223	241	367
Allpahuayo2 = San Pedro	Allp2	*c.* 3.56	*c.* 73.26	1	9	18.0	162	104	390
Allpahuayo3 = Varillal alto seco 1	Allp3	3.57.16	73.25.43	1	6	15.5	93	39	391
Allpahuayo4 = Allpahuayo = Q. Shimbaico = Allpahuayo Yarinal 2	Allp4	3.57.21	73.26.28	1	9	27.6	248	243	432
Allpahuayo5 = Cinamillo, Sinamillal	Allp5	3.57.53	73.25.55	1	9	20.8	187	124	438
Constancia	CS-01	4.09.05	72.57.30	3	10.5	22.2	233	276	366
Constancia norte 1	CN-01	4.07.19	72.55.25	4	6	31.0	186	262	271
Constancia norte 2	CN-02	4.07.22	72.55.31	4	6	27.7	166	247	237
Constancia norte 3	CN-03	4.07.04	72.55.17	4	6	27.8	167	206	258
Constancia sur 2	CS-02	4.09.29	72.57.41	4	12	16.3	196	243	302
Constancia sur 3	CS-03	4.09.13	72.57.41	4	12	14.7	176	153	331
Indiana	IN-01	3.31	72.51	1	9	24.6	221	210	391
Jenaro Herrera	JH-01	4.55	73.44	3	15	16.4	246	259	411
Sucusari	SU-01	3.14.48	72.55.32	1	6	32.8	197	234	309
Yanamono tahuampa	YT-01	3.26.36	72.50.48	1	10	16.2	162	115	356
MADRE DE DIOS									
Alegria	AL-01	12.02.28	69.06.20	1	3	32.3	97	64	226
Alegria	AL-02	12.02.10	69.05.56	1	3	28.3	85	42	277
Alegria	AL-03	12.01.55	69.06.15	1	3	22.7	68	29	268
Alegria	AL-04	12.01.55	69.06.15	1	3	30.3	91	57	226
Alegria	AL-05	12.06.43	69.08.16	1	3	31.7	95	66	211
Alegria	AL-06	12.05.59	69.10.31	1	3	28.3	85	52	216
Alegria	AL-07	12.06.43	69.08.16	1	3	23.3	70	60	132
Alegria	AL-08	12.10.51	69.07.50	1	3	38.7	116	86	246
Alegria	AL-09	12.07.53	69.06.22	1	3	29.0	87	55	213
Alegria	AL-10	12.10.30	69.02.54	1	3	23.3	70	36	217
Alegria	AL-11	12.10.56	69.02.45	1	3	22.3	67	34	211
Boca Pariamanu	BO-01	12.23.25	69.18.28	0	2	40.5	81	46	221
Boca Pariamanu	BO-02	12.23.50	69.19.35	0	2	49.0	98	70	214
Boca Pariamanu	BO-03	12.25.23	69.16.44	0	2	42.0	84	66	169
Boca Pariamanu	BO-04	12.24.52	69.19.13	0	2	45.5	91	75	178
Boca Pariamanu	BO-05	12.23.06	69.18.28	0	2	47.5	95	76	189
Boca Pariamanu	BO-06	12.25.43	69.16.31	0	2	25.0	50	27	144
Boca Pariamanu	BO-07	12.24.57	69.19.37	0	2	39.5	79	47	207
Boca Pariamanu	BO-08	12.25.46	69.17.27	0	2	40.5	81	57	178
Boca Pariamanu	BO-09	12.25.33	69.17.32	0	2	42.0	84	56	196
Cusco Amazonico	CA-01	12.35	69.09	0	6	28.0	168	124	357
Jorge Chavez	JC-04	12.40.07	69.00.54	2	5	13.4	67	40	174
Jorge Chavez	JC-05	12.39.20	69.04.35	2	5	13.4	67	35	204
Jorge Chavez	JC-06	12.38.35	69.06.05	3	4.8	18.8	90	47	269
Jorge Chavez	JC-07	12.40.35	69.06.43	2	4	28.0	112	59	334
Jorge Chavez	JC-08	12.41.42	69.06.54	2	4	24.0	96	50	293
Jorge Chavez	JC-09	12.40.35	69.10.53	2	4	29.5	118	62	357
Jorge Chavez	JC-10	12.40.46	69.10.53	2	2	10.5	21	5	313
La Torre	LT-01	12.49.07	69.21.02	2	8.8	14.0	123	102	238
La Torre	LT-02	12.48.16	69.20.06	2	8	15.9	127	101	255
La Torre	LT-03	12.50.26	69.17.35	3	5	23.2	116	75	276
La Torre	LT-04	12.50.04	69.16.17	3	5	23.6	118	91	242
La Torre	LT-05	12.49.18	69.21.00	3	7.5	17.3	130	99	270

Appendix 1. Continued.

(a) 0.1-ha method

Site	Code	S (degrees, minutes, seconds)	W (degrees, minutes, seconds)	Number of assistants	Person days in field = Effort	Species per person day in field = Efficiency	Species richness	Fisher's alpha	Plant individuals
La Torre	LT-06	12.53.03	69.16.41	3	5	20.0	100	62	251
La Torre	LT-07	12.50.52	69.17.37	3	5	18.0	90	51	249
La Torre	LT-08	12.49.32	69.15.40	2	4	24.3	97	64	229
La Torre	LT-09	12.49.24	69.18.12	2	4	23.0	92	74	183
Lago Valencia	LV-01	12.23.58	68.49.11	1	3	40.0	120	85	264
Lago Valencia	LV-02	12.23.09	68.47.39	1	3	45.3	136	91	314
Lago Valencia	LV-03	12.24.43	68.51.29	1	3	31.3	94	47	302
Lago Valencia	LV-04	12.21.49	68.47.59	1	3	30.0	90	53	238
Lago Valencia	LV-05	12.26.01	68.48.07	1	3	35.7	107	61	291
Lago Valencia	LV-06	12.27.36	68.48.18	1	3	28.7	86	50	228
Lago Valencia	LV-07	12.28.14	68.48.06	1	3	31.0	93	60	223
Lago Valencia	LV-08	12.26.47	68.48.46	1	3	37.7	113	70	283
Palma Real	PR-01	12.30.45	68.44.42	1	3	27.3	82	44	241
Palma Real	PR-02	12.31.17	68.43.57	1	3	32.0	96	56	257
Palma Real	PR-03	12.30.17	68.46.40	1	3	19.0	57	32	157
Palma Real	PR-04	12.30.18	68.45.02	0	2	45.0	90	49	257
Palma Real	PR-05	12.32.54	68.46.18	0	2	34.5	69	27	323
Palma Real	PR-06	12.29.22	68.45.42	0	2	31.5	63	30	211
Palma Real	PR-07	12.30.18	68.46.48	0	2	43.0	86	60	192
Palma Real	PR-08	12.31.17	68.45.02	0	2	45.0	90	47	272
Palma Real	PR-09	12.32.05	68.45.28	0	2	47.0	94	56	245
Palma Real	PR-10	12.31.17	68.43.26	0	2	38.0	76	36	266
Palma Real	PR-11	12.28.53	68.45.40	0	2	27.5	55	27	182
Pampas del Heath	PH-01	12.39	68.45	0	6	22.5	135	77	367
PNBS	PN-01	12.39.03	68.44.25	1	3	33.3	100	55	283
PNBS	PN-02	12.39.46	68.45.16	1	3	26.0	78	46	206
PNBS	PN-03	12.43.54	68.46.58	1	3	25.3	76	46	195
PNBS	PN-04	12.43.10	68.48.21	1	3	25.0	75	35	263
Puerto Arturo	PA-01	12.28.02	69.12.25	2	4	25.3	101	60	263
Puerto Arturo	PA-02	12.28.40	69.12.16	2	4	28.8	115	79	265
Puerto Arturo	PA-03	12.28.02	69.13.38	2	4	23.0	92	55	236
Puerto Arturo	PA-04	12.29.05	69.12.53	2	4	29.0	116	75	277
Puerto Arturo	PA-05	12.27.02	69.12.05	2	4	28.3	113	83	240
Puerto Arturo	PA-06	12.27.27	69.12.09	2	4	21.0	84	56	295
Puerto Arturo	PA-07	12.28.58	69.13.26	2	4	30.3	121	99	239
Puerto Arturo	PA-08	12.29.46	69.13.22	2	4	22.8	91	53	247
Puerto Arturo	PA-09	12.29.05	69.12.06	2	4	28.5	114	77	263
Sabaluyoc	SA-01	12.19.48	69.16.16	1	1.5	46.0	69	48	155
Sabaluyoc	SA-02	12.21.46	69.17.04	0	2	46.5	93	64	209
Sabaluyoc	SA-03	12.20.45	69.15.17	0	2	35.5	71	45	173
Sabaluyoc	SA-04	12.18.12	69.18.16	0	2	44.5	89	63	196
Sabaluyoc	SA-05	12.20.07	69.18.16	0	2	40.5	81	66	160
Sabaluyoc	SA-06	12.15.60	69.19.20	0	2	47.0	94	71	195
Sabaluyoc	SA-07	12.17.20	69.15.03	0	2	40.5	81	53	193
Sabaluyoc	SA-08	12.17.52	69.16.28	0	2	46.5	93	61	220
Sabaluyoc	SA-09	12.18.36	69.16.05	0	2	40.0	80	66	156
Sabaluyoc	SA-10	12.20.21	69.15.10	0	2	39.0	78	49	193
Sabaluyoc	SA-11	12.16.58	69.16.50	0	2	42.0	84	57	191
Sandoval	SJC-01	12.36.18	69.00.59	1	3	27.7	83	48	222
Sandoval	SJC-02	12.35.59	69.00.54	1	4.5	18.2	82	42	251
Sandoval	SJC-03	12.36.38	69.01.04	1	3	25.0	75	46	188
Sonene	SO-01	12.33.36	68.42.39	2	3.5	22.3	78	39	249
Sonene	SO-02	12.33.46	68.41.54	1	3	30.7	92	61	214
Sonene	SO-03	12.33.46	68.43.03	1	3	26.7	80	45	219
Sonene	SO-04	12.35.07	68.43.59	1	3	21.7	65	31	224
Sonene	SO-05	12.35.48	68.43.30	1	3	30.3	91	45	291
Sonene	SO-06	12.36.22	68.44.05	1	3	31.7	95	51	277
Sonene	SO-07	12.36.22	68.44.49	1	3	31.7	95	61	229
Sonene	SO-08	12.35.28	68.41.54	1	3	29.3	88	51	237
Sonene	SO-09	12.37.32	68.45.13	1	3	26.7	80	39	261
Sonene	SO-10	12.38.55	68.44.36	1	3	34.0	102	63	254
Tambopata Swamp Trail	TA-ST	12.51	69.17	0	4	39.5	158	109	355
Tambopata Upland Sandy	TA-US	12.50	69.17	1	3	43.7	131	79	336

Appendix 1. Continued.

(a) 0.1-ha method

Site	Code	S (degrees, minutes, seconds)	W (degrees, minutes, seconds)	Number of assistants	Person days in field = Effort	Species per person day in field = Efficiency	Species richness	Fisher's alpha	Plant individuals
Tres Islas	TI-01	12.29.59	69.25.08	1	3	35.0	105	81	216
Tres Islas	TI-02	12.29.31	69.24.30	3	4.5	22.4	101	79	204
Tres Islas	TI-03	12.32.20	69.25.33	3	4.5	9.6	43	21	146
Tres Islas	TI-04	12.32.20	69.23.11	3	4.5	15.8	71	47	167
Tres Islas	TI-05	12.29.59	69.22.14	1	3	36.0	108	75	242
Tres Islas	TI-06	12.28.51	69.23.07	1	6	17.0	102	61	266
Tres Islas	TI-07	12.31.31	69.28.36	1	3	34.0	102	76	215
Tres Islas	TI-08	12.35.18	69.34.15	1	3	23.7	71	23	471
Tres Islas	TI-09	12.37.12	69.34.07	1	3	35.0	105	74	231
Tres Islas	TI-10	12.37.55	69.33.52	1	3	31.3	94	68	203

(b) 1-ha method

Site	Code	S (degrees, minutes, seconds)	W (degrees, minutes, seconds)	Number of assistants	Person days in field = Effort	Species per person day in field = Efficiency	Species richness	Fisher's alpha	Plant individuals
LORETO									
Allpahuayo A		03.56.59	73.26.02	3	75	3.9	293	208	643
Allpahuayo B		03.57.11	73.26.12	3	75	4.1	311	242	634
Mishana		*c.* 3.47	*c.* 73.30	2	32	9.0	289	154	858
Sucusari A		3.16	72.54	4	63	5.2	325	270	630
Sucusari B		3.16	72.54	4	63	4.8	302	234	617
Yanamono		3.26	72.51	1	30	10.0	300	236	606
MADRE DE DIOS									
Tambopata	PLOT #0	12.51	69.17	2	16	12.3	197	101	604
Tambopata	PLOT #1	12.50	69.17	2	19	8.4	160	75	564
Tambopata	PLOT #2	12.50	69.17	1.5	18	3.3	59	16	710
Tambopata	PLOT #3	12.50	69.17	2	16	10.3	165	79	560
Tambopata	PLOT #4	12.50	69.18	2	16	11.7	187	92	611
Tambopata	PLOT #6	12.50	69.16	1.5	28.5	6.2	177	87	580
Cusco Amazonico	1-E	12.35	69.09	0	26	6.7	174	90	534
Cusco Amazonico	1-U	12.35	69.09	0	26	6.3	164	80	541
Cusco Amazonico	2-E	12.34	69.08	0	26	5.8	151	73	509
Cusco Amazonico	2-U	12.34	69.08	0	26	7.0	182	87	619