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BIODIVERSITY ASSESSMENT USING STRUCTURED INVENTORY: CAPTURING THE ANT FAUNA OF A TROPICAL RAIN FOREST

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Abstract. The goal of "strict inventory" (as opposed to community characterization) is to obtain species lists for specific sites. Quantitatively structured inventory can improve inventory efficiency (defined as the steepness of species accumulation curves). As part of the Arthropods of La Selva project (ALAS), a structured inventory of the ants of a lowland tropical rain forest was carried out. A novel method of sample processing was developed, in which parataxonomists prepared specimens based on their own sorting of morphospecies within samples (repeating the process for each sample, and thus not attempting to cross-reference morphospecies among samples), and a taxonomic specialist later sorted the resultant pool of prepared specimens. Efficacy of stratifying by sampling method (Berlese samples, Malaise traps, and canopy fogging), habitat, and time was investigated. Novel methods of analysis were used, including (1) curves depicting cost in prepared specimens of adding species to the inventory, as a function of number of species already captured, (2) within- vs. among-treatment species accumulation curves, and (3) matched rank-abundance plots. Over 400 species of ants are known from the site, of which the structured inventory captured 253. Projection of the species accumulation curve revealed that continuation of the same methods would not be an efficient method of capturing additional species, and that additional methods would be needed. Considered separately, Berlese, Malaise, and fogging samples were similarly efficient. Berlese samples combined with either Malaise or fogging samples were far more efficient than single methods because the faunas they sampled were highly complementary. Combining Malaise and fogging samples did not increase efficiency because the faunas they sampled had low complementarity. At the scale of our sampling, there was little evidence that spatial, temporal, or habitat stratification increased efficiency of inventory for Berlese and Malaise samples. For canopy fogging, processing a portion of the catch from multiple trees was more efficient than processing the entire catch from one tree. However, stratifying by tree species did not improve efficiency.

Key words: ants; Berlese funnels; biodiversity; canopy fogging; complementarity; Costa Rica; Formicidae; inventories; La Selva; Malaise traps; sampling methods; species accumulation curves; tropical rain forest.

INTRODUCTION

Biodiversity inventory documents the spatial distribution of biological elements (Kremen et al. 1993, Heywood and Watson 1995, Stork and Samways 1995). The goals of inventory can be divided into two broad categories: community characterization and "strict" inventory. Community characterization uses structured sampling to estimate the distribution of species abundances, community species richness, and complementarity (sensu Colwell and Coddington 1994) with other communities. Community characterization involves sorting specimens into species, but the authoritative identification of species may not be essential. Applications of community characterization include setting conservation priorities and monitoring, where various measures of community diversity (involving species richness and evenness) and complementarity are used to rank habitats or parcels of land, or to assess change over time. In contrast, strict inventory aims to obtain an accurate species list. Specimens are sorted into species because the actual identities of the species are valuable products, whereas relative abundance may be of minor interest. Strict inventory has application when phylogenetic measures of conservation value are considered (Raven and Wilson 1992, Humphries et al. 1995, Blackmore 1996). Unique traits of organisms have value because of their actual and potential contribution to human welfare (Reid 1994). For this kind of biodiversity value to be realized, the potential users of those unique traits (pharmaceutical companies, natural products chemists, producers of natural history films, agricultural researchers, etc.) must know where the traits are and how to collect or observe them (Gámez 1991, Janzen 1991). Strict inventory provides this information in the form of locality and collection data on the species that express those traits.

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Most studies that report quantitative results of field sampling have community characterization as the goal. The objective is to find particular, repeatable measurements that accurately reflect the patterns in the underlying ecological community. This approach is exemplified by the work of Oliver and Beattie (1996), who sought ways to make richness and complementarity assessment more efficient by evaluating the community characterization properties of: (1) large taxa vs. smaller surrogate taxa, (2) large sample sets vs. smaller surrogate samples, and (3) species sorted by nonspecialists vs. species sorted by professional taxonomists. In contrast, strict inventory, or efficiently producing accurate species lists, is a neglected area of investigation within the broader domain of biodiversity inventory. Our definition of efficiency for strict inventory is a rapidly rising species accumulation curve as a function of cost. Maximizing species obtained per unit of sampling effort reduces the cost of biological inventory in terms of personnel time, supplies, and environmental impact. Few studies have directly examined such efficiency issues (for examples, see Romero and Jaffe 1989, Brown and Feener 1995).

Techniques of efficient inventory are most urgently needed for hyper-diverse groups where our knowledge of diversity is rudimentary. Arthropods are a hyperdiverse group that is gaining increasing recognition in biodiversity surveys (Wilson 1987*a*, Wheeler 1990, Kim 1993, Kremen et al. 1993, Miller 1993, Samways 1993, Yoon 1993), because: (1) arthropods are major contributors to ecosystems processes, (2) they make up the bulk of macroscopic metazoan diversity, (3) they respond quickly to environmental change, and (4) they are small and abundant in nearly all habitats.

Strict inventory has traditionally been carried out by museum taxonomists, applying generally nonquantitative, unstructured sampling methods. Greater use and importance of inventory data and increasing reliance on field technicians demand increased structure and rigor in the inventory process (Coddington et al. 1991, Erwin 1991, Colwell and Coddington 1994, Ginsberg 1994, Longino 1994). In a structured inventory, species are recorded in the context of a set of replicated samples that are stratified with respect to a set of variables such as method, habitat, or time. Data from a structured inventory are an improvement over a traditional species list in several respects: (1) progress or completeness of the inventory, with respect to the sampling methods being used, can be assessed; (2) individual and joint efficiency of different sampling methods can be evaluated and methodology adjusted to maximize efficiency, allowing a better understanding of biotic complementarity; (3) quantitative data on individual species improve ecological knowledge of those species (e.g., habitat preferences, seasonality); and (4) the data may also be applied to community characterization.

We report here the results of a structured inventory of the ants (Hymenoptera, Formicidae) of a lowland tropical rain forest. We introduce new analysis methods that are generally applicable to assessing efficiency of biodiversity inventory. The results here apply primarily to efficiency of strict inventory; results pertaining to richness estimation and other aspects of community characterization will be treated elsewhere.

Methods

The study site is the La Selva Biological Station, Heredia Province, Costa Rica (McDade et al. 1993). The study area is ~1500 ha. Elevation ranges from 50 to 150 m. Mean annual rainfall is ~4 m. The habitat is a mosaic of mature lowland rain forest, second growth forest of various ages, and abandoned pastures.

The ant inventory was carried out as one component of a much more extensive arthropod survey project entitled Project ALAS (Arthropods of La Selva, see Longino 1994). For the project as a whole, a set of generalized sampling methods was applied to a broad range of arthropods, including spiders, katydids, and selected taxa of mites, Coleoptera, Lepidoptera, Diptera, and Hymenoptera. All field sampling and sample processing was carried out by a resident staff of four people recruited from surrounding communities and trained in entomological techniques (parataxonomists, sensu Janzen 1991). A relational database of collection, specimen, and identification data was managed using the biodiversity database application *Biota* (Colwell 1996).

The ongoing project is a collaboration with Costa Rica's National Biodiversity Institute (INBio; Gámez 1991). All specimens resulting from the project are labeled with INBio barcodes (in addition to standard locality labels) and are part of the INBio collection. Specimens are deposited in the INBio collections facility in Santo Domingo de Heredia, Costa Rica, with the exception of those distributed to taxonomic specialists, under INBio and Costa Rican regulations.

Field sampling methods

Extraction in Berlese funnels of litter/soil cores ("Berlese samples"), Malaise traps ("Malaise samples"), and fogging of tree crowns with pyrethrin insecticides ("fogging samples") were used to collect arthropods. All sample locations were spatially referenced with respect to the La Selva GIS grid system (Wentz and Bishop 1995). To place this paper within the context of other publications resulting from Project ALAS, the full field sampling program is described, even though only a portion of the samples were analyzed for this paper (see *Methods: Selection of samples to process*).

Sixteen areas were selected on a La Selva station map, stratified by soil type (alluvial vs. residual) and forest type (primary vs. secondary). This design yielded four replicates for each soil and forest type combination. Sites were easily accessible from a trail system, but widely dispersed (Fig. 1). A Malaise trap

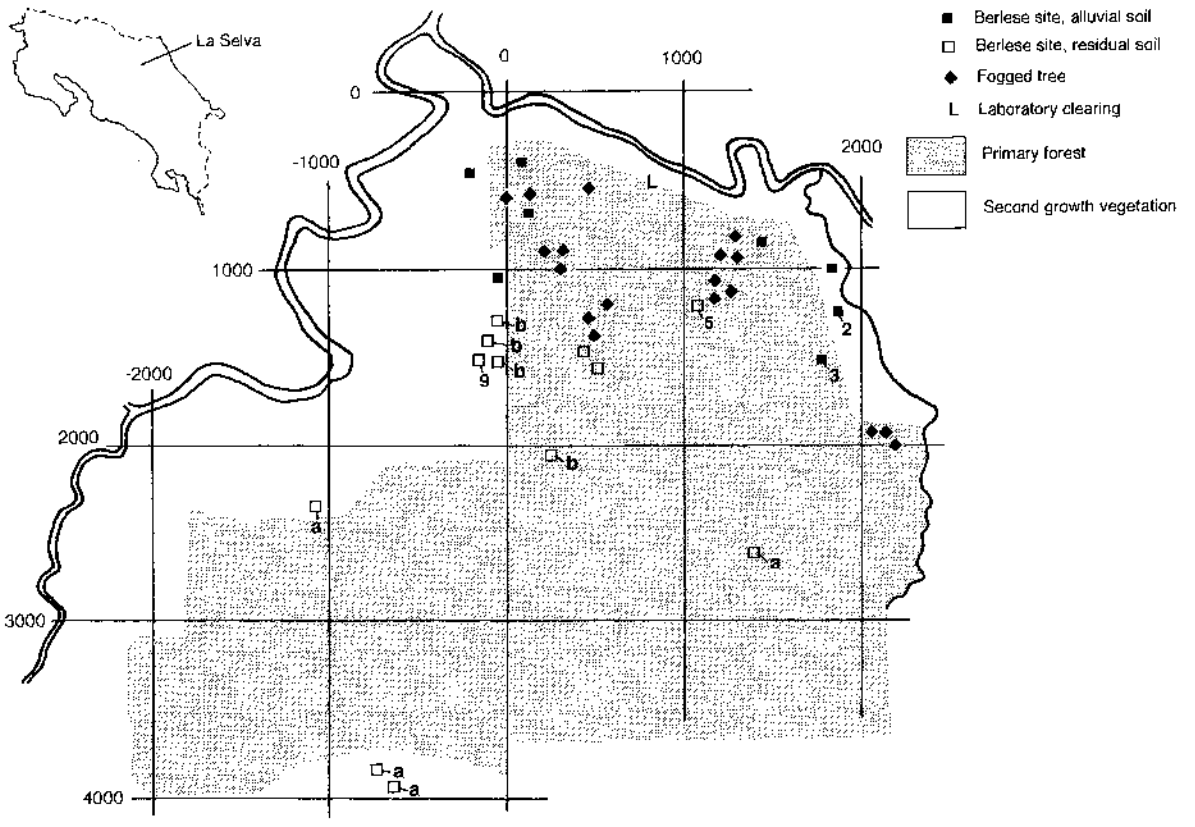

FIG. 1. Map of study site, showing location of sample sites within the La Selva Biological Station property. The sample points were referenced to the La Selva GIS (Wentz and Bishop 1995), shown on the figure as a grid of 1-km squares. The habitat beyond the river boundaries is largely pastures and young second-growth vegetation. Berlese sites subtended by "a" were moved to those subtended by "b" after three months of sampling, to reduce the time required to reach the sites to collect samples. Berlese sites subtended by a number show locations of four Malaise traps whose samples were examined for this study. The Malaise trap numbers (2, 3, 5, 9) are ALAS reference numbers from the full set of 16 traps that were deployed.

(Marris House, with black vertical panel and white roof) was erected in each area. Malaise traps are open-sided tents with a collecting head in which flying or crawling arthropods are trapped and accumulate (Matthews and Matthews 1971, Owen 1983, Darling and Packer 1988). The collecting head was a plastic bottle containing 75% ethanol. Malaise traps were placed in light gaps and potential flyways and maintained from March 1993 to March 1994, for a total of 13 mo. At the beginning and the middle of each month, the collecting bottle with accumulated arthropods was removed and replaced with a fresh bottle of ethanol.

At each harvest of a Malaise trap sample, a soil/litter core was taken from the vicinity, 10 m distant in a random direction from the central pole of the trap. The sample was taken by quickly placing a 14.5 cm inside diameter, 10 cm deep PVC ring on top of the leaf litter, driving it into the ground, dislodging it, and placing the ~1.5 L of soil and litter in a plastic bag. The samples were returned to the laboratory on the same day and placed in Berlese funnels. Because tropical soils are often wet, collapsible cloth funnels were used to avoid the condensation that often occurs on more traditional metal funnels. A breathable synthetic fabric (Ultrex) was used for funnel construction. The sample bed was a 35 × 35 cm piece of 6.6-mm mesh hardware cloth, overlain with several layers of cheesecloth. The soil sample was broken apart and spread out on the cheesecloth. An incandescent lightbulb was placed 15–20 cm above the sample bed and the bulb and the sample covered with a pyramidal aluminum-foil shield. Samples were left under a 25-W bulb for 2 d, then under a 50-W bulb for a third day. Arthropods were collected in a Whirlpac bag filled with 75% ethanol suspended from the bottom of the funnel.

After three months of sampling, the sampling regime at four distant sites (three primary forest residual soil, one secondary forest residual soil) was altered because it took too long to reach them. To replace the outlying Berlese sample sites, four new sites were established closer to the laboratory (maintaining the same habitat stratification) (Fig. 1). Berlese sampling commenced at these new sites, twice per month, 10 m distant in a random direction from a central point.

TABLE 1. Date of fogging and tree species for the 18 canopy fogging samples.

Pentaclethra macroloba	*Virola koschyni*	Third tree
6 Mar 1993	14 Jan 1993	*Carapa guianensis* Aubl. Meliaceae, 5 Mar 1993
6 May 1993	7 May 1993	*Conceveiba pleiostemona* Donn. Sm. Euphorbiaceae, 5 May 1993
4 Jul 1993	5 Jul 1993	*Goethalsia meiantha* (Donn. Sm.) Burret Tiliaceae, 3 Jul 1993
5 Sep 1993	4 Sep 1993	*Tapirira guianensis* Aubl. Anacardiaceae, 3 Sep 1993
6 Nov 1993	9 Nov 1993	*Sacoglottis trichogyna* Cuatr. Humiriaceae, 8 Nov 1993
8 Jan 1994	7 Jan 1994	*Vitex cooperi* Standl. Verbenaceae, 5 Jan 1994

Canopy fogging was carried out using the general procedures discussed in Erwin (1983), Adis et al. (1984), and Stork (1988). Eighteen trees were selected for canopy fogging: six individual trees of the most common tree species at La Selva [*Pentaclethra macroloba* (Willd.) O. Ktze., Fabaceae], six individual trees of a species of intermediate abundance (*Virola koschnyi* Warb., Myristicaceae), and one individual each of trees from six additional families (Table 1). Six areas were chosen on a La Selva station map, such that the areas were dispersed across the available primary forest, and at the same time accessible from the trail system. In each area three trees were selected: a *Pentaclethra*, a *Virola*, and one of the six unique species. We chose trees that had large crowns, little overlap with adjacent crowns, and good access for climbing. The three trees in a group were usually fogged on consecutive days, and the six groups were fogged at ~2-mo intervals over one calendar year (Table 1).

On the day prior to fogging a tree, the tree was rigged with mountain climbing ropes and a pulley system, so that the following day an operator could climb to the lower branches of the crown and the fogging machine could be hoisted on pulleys. Ropes were strung from trunk to trunk between the focal tree and neighboring trees to form an irregular network 2–3 m high above ground level. Forty 1-m^2 funnels were suspended from these ropes, distributed as evenly as possible in the area beneath the crown of the focal tree. The funnels were composed of ripstop nylon mounted on a metal hoop, with a threaded ring at the bottom for the attachment of a plastic sample bottle. Palm leaves and other vegetation immediately above the funnels were clipped or bent back, but otherwise the understory vegetation was left intact.

Funnels were left upside down on the ground overnight to avoid accumulation of debris before fogging. Before dawn the next morning the funnels were resuspended and the bottles filled with 75% ethanol. An operator climbed to the first branches at the base of the crown, 15 to 20 m above ground level, and commenced fogging at about 0600. We used a Golden Eagle DynaFogger, on setting 6, to fog 3.8 L of Pyrethrins 123 insecticide (Summit Chemical). This is a 3% solution of a natural pyrethrin insecticide with synergists, in a petroleum distillate carrier. The operator gradually fogged in a 360° circle, attempting to cover the crown evenly. Following fogging, a 2-h drop time was allowed, after which the sides of the funnels were washed down with ethanol and the bottles were collected.

Selection of samples to process

Only a subset of the field samples was processed for the results presented here, as follows:

Malaise samples.—Only samples from traps 2, 3, 5, and 9 (Fig. 1) were processed. Each trap was from a different soil type/forest type combination. Only the first sample from each month (~2 wk worth of accumulation) was processed. Thus, 52 samples were processed (4 sites × 13 mo).

Berlese samples.—The 16 samples from the beginning of each month were processed, for all 13 months, resulting in a total of 208 samples.

Fogging samples.—For one *Virola koschnyi* tree, all 40 funnels were processed. For the remaining trees, a minimum of 10 funnels was processed. For the analyses that involved all 18 trees, the results of 10 processed funnels were pooled and treated as one sample (note that specimens were not pooled prior to processing; funnels were processed individually, and the data pooled only for analysis). In the case of trees for which more than 10 funnel samples were processed, 10 samples were randomly selected for pooling.

Sample processing

For each taxon covered by Project ALAS (Longino 1994), including ants, the resident staff received training in how to recognize the taxon, what characters are often important in species differences, and how to prepare specimens for taxonomic study (dry-mounting on card points for ants). For each sample, they sorted specimens in alcohol to temporary morphospecies (temporary in the sense of pertaining only to that sample, and not being cross-referenced to other samples). For each temporary morphospecies, they prepared a series of 1–10 specimens, depending on their confidence in species separation (more specimens were prepared when they had doubts about the uniformity of their morphospecies). Thus, at the time of processing, decisions on what material to prepare were based on within-sample sorting by trained nonspecialists. The process was repeated for each new sample.

Using temporary morphospecies determinations to select material to prepare was intended as a compromise between (1) having staff prepare all specimens for study, and (2) having staff maintain a system of morphospecies across all samples and prepare only those specimens deemed new to the inventory. Preparing all specimens incurs a large cost for the most

common species, not only in terms of staff time, but also in terms of specialist sorting time and long-term collection maintenance. Having staff cross-reference morphospecies across samples was judged impractical, given the breadth of taxa for which they were responsible. Moreover, cross-referencing incurs a geometrically increasing cost per sample as the number of samples compared increases with time. The staff's determinations of temporary morphospecies were intended as a short-term process designed to maximize species obtained per prepared specimen.

Each mounted specimen was entered into the ALAS database by the staff, prior to study by the appropriate specialist. Staff entered identifications at the level of order, family, or subfamily. These higher level determinations aided greatly in data management (e.g., finding all records for ants, even if nothing more was known than that a specimen was an ant). (See Colwell 1996, Chapter 21, for details of the technique used for higher level specimen determinations in a relational database.)

At the time of selecting specimens to prepare, specimens of a morphospecies that remained in alcohol were counted to the nearest individual, ten individuals, hundred individuals, etc., and associated with the database record for one of the prepared specimens deemed conspecific, in the specimen abundance field for that record (Colwell 1996:152). All prepared material was subsequently sorted to species by a taxonomic specialist (Longino for ants). To obtain an abundance of a species in a sample, the abundance field was summed across the records for all specimens of that species in the sample (recognizing the likelihood of some error caused by discrepancies between staff and taxonomic specialist determinations of species, particularly lumping errors by staff).

For ants, only adult workers were included in the analysis. Data for two ant species were excluded from all results. These two (*Tapinoma melanocephalum* and a species in the *Camponotus abdominalis* complex) are common laboratory pests and most or all of the specimen records were probably laboratory contaminants.

Data analysis

Our analyses relied on patterns of species accumulation across samples or other measures of sampling effort (Soberón and Llorente 1993, Colwell and Coddington 1994). Usually smoothed species accumulation curves were examined, produced by averaging curves produced by repeated random reorderings of the samples (as in Colwell and Coddington 1994). The number of random reorderings averaged was the number necessary to produce a smooth curve; 10 replicates often produced a smooth curve, and 50 replicates always did. (A smooth curve is defined, for this purpose, as one not visually altered by additional randomizations.)

To allow projection of species accumulation curves, we fit a logarithmic model to smoothed species accumulation curves. Soberón and Llorente (1993) recommend the use of a logarithmic model for hyperdiverse taxa in open communities. This model assumes that species accumulation curves have no asymptote, and will increase indefinitely. However, the model allows statements about changes in inventory efficiency (in terms of species accrual rates) over time and/or sampling effort. The model takes the form

$$S(t) = \frac{\ln(1 + zat)}{z}$$

where t is the measure of effort such as time or number of samples, $S(t)$ is the predicted number of species at t, and z and a are curve-fitting parameters. We used nonlinear regression to estimate z and a, using the NONLIN procedure in SYSTAT Version 5.2. Model evaluation was based on least squares fit with quasi-Newton optimization (Wilkinson 1994). We modified the above equation to

$$t_s - t_{s-1} = \frac{e^{zs} - e^{z(s-1)}}{za}$$

and plotted it using estimated parameters a and z. This equation defines the effort required to add the s^{th} species to the inventory.

In most of our analyses the measure of effort is the number of samples. However, samples from the three methods we used (Berlese, Malaise, and fogging) differed greatly in actual cost to the inventory, because they differed in the average number of mounted specimens per sample (Table 2). Ant specimens must be dry-mounted for accurate identification and future value as voucher specimens. By far our largest cost was staff time in the laboratory, mounting specimens. Mounted specimens have a cost not only in staff processing time, but also in taxonomist handling time during sorting, data entry, museum space commitments, and future curatorial handling. Thus, number of mounted specimens was a good measure of actual cost to the inventory and became a currency by which to measure the relative cost of different sampling methods. Thus, when comparing the efficiency of different sampling

TABLE 2. Number of samples, specimens, and species taken during the 1993–1994 Project ALAS structured inventory; results for Formicidae.

Method	Mounted specimens	Estimated specimens†	No. of samples	No. mounted per sample	No. of species	Cost per species‡
Malaise	835	1300	52	16.1	89	24
Berlese	1653	3500	208	8.0	113	45
Fogging	3092	13 800	18	171.8	137	74
All methods	5580	18 600	278	20.1	253	78

† Mounted specimens plus unprocessed duplicates remaining in sample residue.

‡ Cost in mounted specimens to add an additional species, based on logarithmic curve fit to species accumulation curve (see *Methods: Data analysis*).

methods, our measure of effort was number of mounted specimens.

When developing a sampling program, choices must be made regarding which sampling methods to employ and how to distribute sampling with respect to space, time, and habitat variables. How can efficiencies of different sampling programs be compared? For example, is using a combination of Berlese samples and Malaise samples more efficient than putting all effort into just one of the methods? Does stratifying Berlese samples by soil type or forest type improve inventory efficiency? We develop here a novel use of species accumulation curves that allows us to answer questions such as these.

The method is best illustrated with an example. The 208 Berlese samples were stratified with respect to both space and time, with samples from 16 sites taken each month for 13 months. A smoothed species accumulation curve (as defined earlier) can be produced for each month individually, each curve containing 16 samples. A smoothed species accumulation curve can also be produced for all 208 samples together, and the first 16 samples of this "combined" curve compared to the within-month curves. If species turnover between months is high, then the combined curve will be steeper than the within-month curves. Such a result would recommend temporal stratification of sampling. Alternatively, if the combined curve is similar to within-month curves, then stratifying by time does not improve inventory efficiency, at least for the first 16 samples. The process is analogous to analysis of variance, but with conclusions based on visual inspection of curves rather than rigorous hypothesis testing and explicit probability models. We use this method to investigate whether inventory efficiency is increased by (1) using a variety of sampling methods instead of a single method, (2) distributing Berlese samples over several kilometers rather than over tens of meters, (3) distributing Berlese samples over 13 months instead of over one month, (4) stratifying Berlese samples by forest type and soil type rather than sampling within a single forest or soil type, (5) using four malaise traps instead of one, and (6) fogging different species of trees instead of repeatedly fogging one species of tree.

When analyzing the effect of collection method, species accumulation curves from different methods cannot be compared using number of samples as a common horizontal axis, because the samples from different methods vary greatly in number of individuals captured, and thus vary in cost. Instead, we plotted the curves on a common horizontal axis based on number of mounted specimens rather than number of samples. Each individual curve, for the three methods and four combinations of methods, was "stretched" along the horizontal axis based on the average number of mounted specimens per sample, for that particular method or combination of methods (fifth column of Table 2). For combinations of two methods (not shown in Table 2) the total number of mounted specimens for both methods was divided by the total number of samples for both methods to obtain the scaling factor. In other words, the points of a species accumulation curve for a particular method or combination of methods were still based on sample-wise accumulation, but the points were spaced along the horizontal axis according to the average number of specimens mounted.

We introduce here the use of "matched rank-abundance plots," another graphical method of examining overlap of species between sampling methods. These plots consist of a standard rank-abundance plot for one sampling method (the "reference method") and, for the species present in the reference method, the corresponding abundances in a second method. Matched rank-abundance plots allow a quick visual inspection of the degree of correspondence between two methods. This method also reveals species that are very rare (often singletons) in samples produced by one method but very common in samples produced by another method.

Results

Logarithmic curve fitting

The structured inventory captured 253 species of ants. The known ant fauna of La Selva, based on the sampling reported here and additional focused collecting by a taxonomic specialist (Longino), is over 415 species. Thus, the ALAS staff obtained ~60% of this known ant fauna using a combination of Berlese samples of soil/litter cores, Malaise trap samples, and canopy fogging. The smoothed species accumulation curve as a function of number of samples, when the 278 samples from all three methods were used, showed a gradually decreasing slope, indicating that the number of new species encountered per sample was decreasing as sample size grew larger (Fig. 2). A logarithmic equation provided an excellent fit to the observed curve (Fig. 2), and projecting the curve predicts that eight times greater sampling effort would be required to obtain the known fauna, if the same sampling methods were continued. Many of the species not captured by the structured inventory, however, are easily sampled with other methods. These species include: (1) army ants, (2) specialized plant-ants living in myrmecophytes, (3) tramp species in and around buildings, and (4) cryptic leaf litter ants.

Complementarity and efficiency of collecting methods

When viewed separately, the three methods analyzed here—Berlese samples, Malaise traps, and canopy fogging—were equally efficient in terms of species obtained per mounted specimen (Fig. 3). The three methods combined were far more efficient, however, with a much steeper species accumulation curve than any method considered singly. Pairwise combinations of methods revealed that Berlese samples combined with

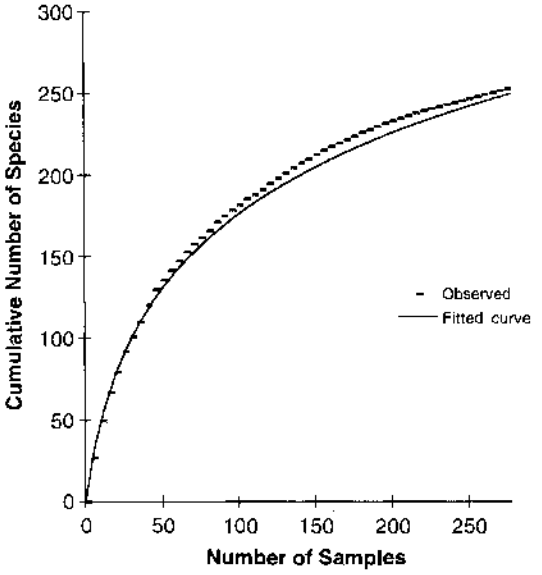

FIG. 2. The ant fauna of La Selva as revealed by quantitative sampling. The smoothed species accumulation curve for all 278 samples (every fifth point is shown) is well fit by a logarithmic curve with parameters $a = 6.818$ and $z = 0.013$ ($r^2 > 0.99$).

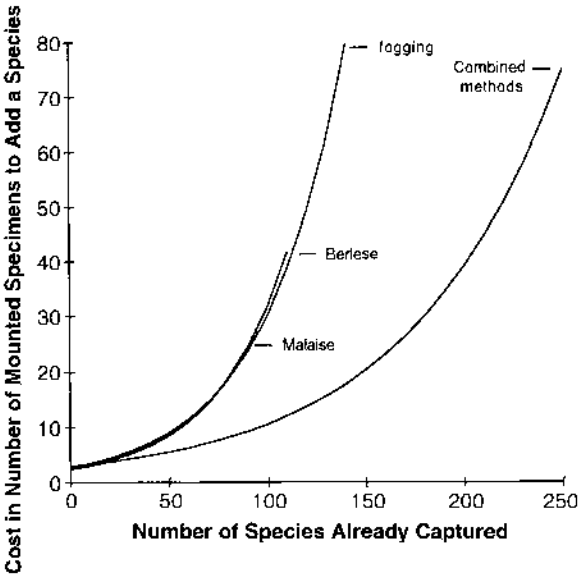

FIG. 4. Cost, in terms of number of mounted specimens, of adding additional species to the inventory. Curves are the cost equation described in the *Methods*, using parameters of logarithmic curves fitted to the smoothed species accumulation curves.

either Malaise traps or fogging were far more efficient than any method considered singly, but that combining Malaise and fogging samples had relatively little effect on efficiency. Relative to single methods, processing a combination of Malaise and fogging samples slightly reduced efficiency below 1000 mounted specimens, and slightly increased it above 1000 specimens. Similarly, efficiency was highest for the combination of Berlese and Malaise samples up to ~1500 mounted specimens, above which efficiency was higher for the combination of Berlese and fogging samples and for the combination of all three methods.

Cost per species curves vividly reveal the exponential nature of cost increase and also the complementarity of sampling methods (Fig. 4). At the beginning of an inventory, it only costs one specimen to obtain the first species. By the time 253 ant species were obtained using all methods combined in the ALAS project, it cost 78 mounted ant specimens for each additional species obtained (Table 2). Values for individual

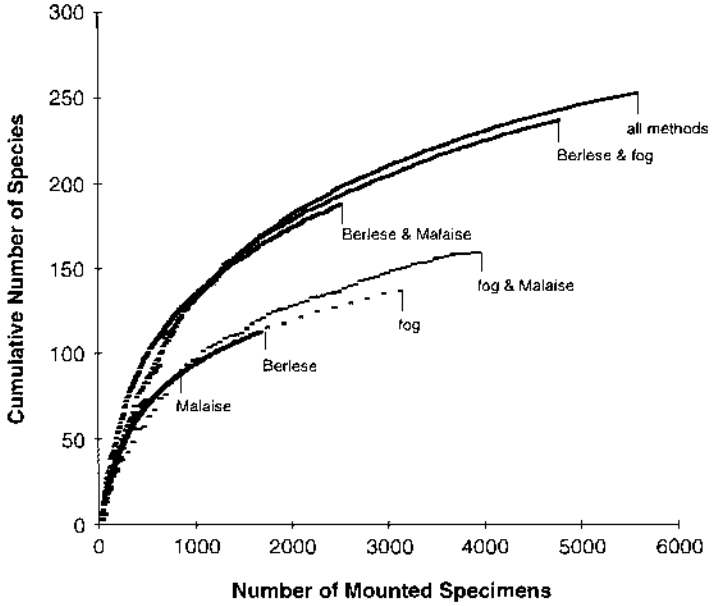

FIG. 3. Efficiency of different collecting methods as revealed by smoothed species accumulation curves. All curves are scaled to a common horizontal axis, scaled by the number of mounted specimens. For each method or combination of methods, the original smoothed species accumulation curve as a function of the number of samples is modified by multiplying the number of samples by the average number of specimens mounted per sample *for that particular method or combination of methods* (Table 2). For example, the points for the canopy fogging curve are widely spaced, because each fogging sample cost on average 172 mounted specimens. Labels mark the end points of the different curves. The basal portions of the individual Malaise, Berlese, and fogging curves almost perfectly coincide and thus are indistinguishable in the figure.

methods reveal that by the end of the sampling period, cost of species accrual when processing fogging samples was about three times greater than the cost for Malaise samples (Table 2). Thus, the inventory could have been more efficient (at least for ants) by decreasing the effort on fogging samples and increasing the effort on Malaise samples.

Matched rank-abundance plots support the results from the species accumulation curves (Fig. 5). There is very little similarity between Berlese and fogging samples. Only two species are similarly abundant in Berlese and fogging samples. In contrast, matched abundance plots for fogging and Malaise samples show a great deal of overlap. Many of the species common in one are common in the other.

Matched abundance plots graphically reveal some of the species that are accidentals or transients, caught in the "wrong" microhabitat (Fig. 5). They are revealed as species that are singletons or represented by very few individuals in samples from one method, but very abundant in samples from another method. For example, ~25% of the singletons in Berlese samples are common in the canopy, and vice versa.

Spatial and temporal contributions to species richness

Berlese.—Individual months varied nearly tenfold in number of individuals sampled and nearly twofold in number of species, but there was no pronounced association with rainfall (Fig. 6). The smoothed species accumulation curve for 1 to 16 Berlese samples (based on the full set of 208 samples) fell in between the highest and lowest within-site curves, and in between the highest and lowest within-month curves (Fig. 7). Thirteen samples within a 10 m radius of a central point, or 16 samples taken from dispersed sites within one 2-wk period, were thus little different, in terms of cumulative species richness, from a similar number of samples spread hundreds to thousands of meters apart and collected over 13 months. Moreover, species accumulation over space (within-month curves) was little different from species accumulation over time (within-site curves).

The smoothed species accumulation curve for sites (pooling the 13 monthly samples within a site) in second-growth habitats was slightly steeper than the curve for old-growth forest, and the curve for alluvial soil slightly steeper than the curve for residual soil (Fig. 8). Sampling four to eight sites in one forest or soil type was little different, in terms of cumulative species richness, from a similar number of sites stratified by forest or soil type.

Malaise traps.—Malaise traps varied over a hundredfold in the number of individuals captured each month, and over tenfold in number of species (Fig. 9). Unlike Berlese samples, there was a slight trend toward a decline over time in both abundance and richness of sampled ants.

Individual Malaise traps varied in the steepness of smoothed species accumulation curves (Fig. 10). The smoothed species accumulation curves for 1 to 13 samples (based on the full set of 52 samples) fell among the curves for individual traps (Fig. 10). Thus, processing 13 samples from one Malaise trap could be better or could be worse than processing 13 samples randomly drawn from a year's catch of four Malaise traps, depending on the siting of the trap.

Unsmoothed species accumulation curves were higher than the smoothed curve for three of the four traps (Fig. 11), which shows that Malaise trap efficiency declined over time (i.e., richer samples tended to occur early in the sampling period, elevating the species accumulation curve). Three of the four traps show the same temporary plateau in species accumulation for August through November, the height of the wet season. For individual Malaise traps, number of species captured in the first sample was highly predictive of the number of additional species captured in the subsequent 12 samples ($n = 4$ traps, $r^2 = 0.95$, $p < 0.03$; Fig. 12).

Fogging.—For the first tree fogged, a *Virola koschnyi*, all 40 funnels were processed for ants. The species accumulation curve as a function of number of funnels reached 32 species at 40 funnels (Fig. 13).

Examining only 10 funnels per fogged tree, the mean number of species per tree was 31 (13.3 SD) and ranged from 8 to 55 (Fig. 14). The three treatments (*Virola, Pentaclethra,* and diverse) did not differ significantly in the number of ant species per tree (Kruskal-Wallis test). In the species accumulation curve pooling all 18 trees (Fig. 3), the smoothed curve reached 76 species after four trees (and consequently 40 funnels processed overall). This was far higher than the 32 species observed in the single *V. koschnyi* tree for which all 40 funnels were processed. This result suggests that individual trees vary in species composition, such that processing fewer samples from multiple trees is more efficient than higher processing effort in one tree (a conclusion which assumes that the one extensively processed *V. koschnyi* sample was typical).

Smoothed species accumulation curves for the three treatments, each combining data from six trees, were highest for *Virola koschnyi,* intermediate for the "diverse" treatment (trees of six different plant families), and lowest for *Pentaclethra macroloba* (Fig. 15). The smoothed species accumulation for 1–6 trees, based on all 18 trees, fell among the three treatment curves (Fig. 15). Thus, ant species accumulation rate was not strongly affected by host tree species.

Discussion

The inventory

The results presented here illustrate the effectiveness with which an inventory can be undertaken by trained field personnel who are not specialists in the group

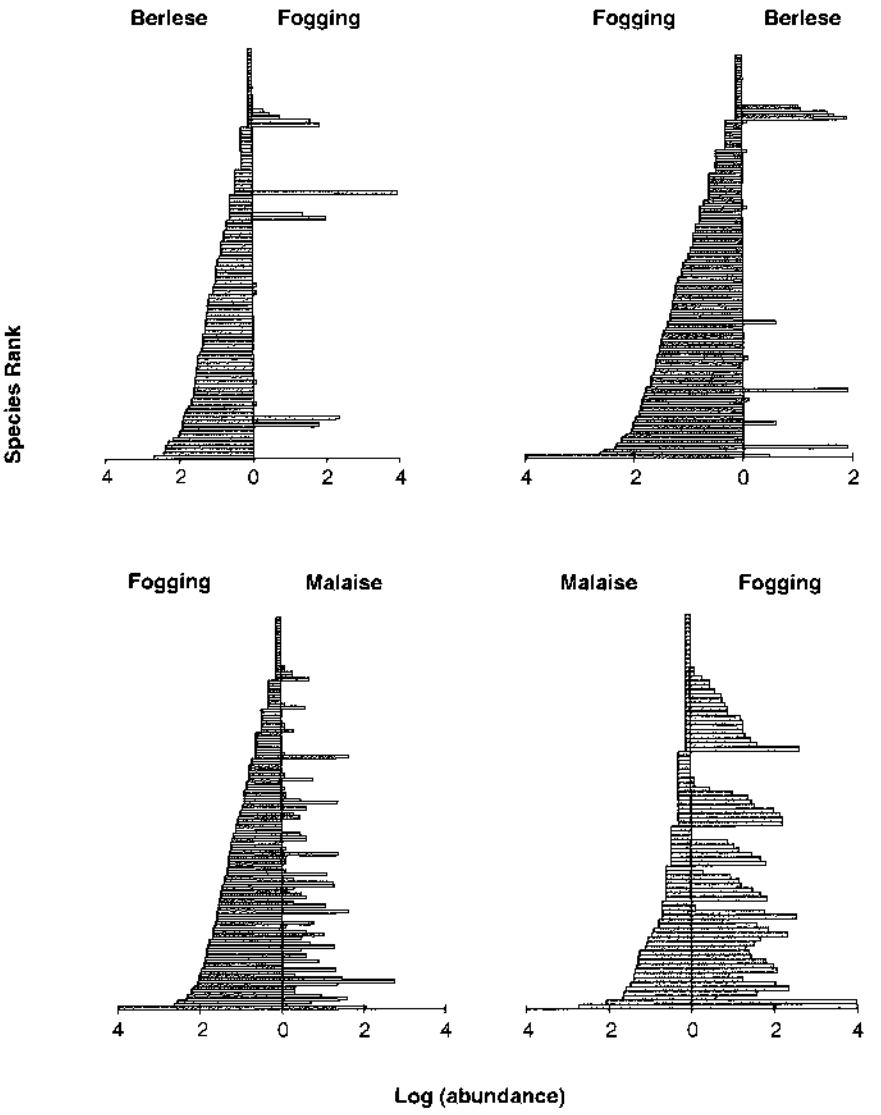

FIG. 5. Comparing collection methods with matched abundance plots. In each plot, the left side is a standard rank-abundance plot for one method, oriented vertically with the most abundant species at the bottom. A log scale is used for abundance. The right side shows, for all the species on the left, the corresponding abundance for a different method. For example, the upper left figure reveals that only two species were abundant in both Berlese and fogging samples, and that 5 of the 22 singletons in the Berlese samples were species common in the canopy.

under study, and they provide specific recommendations and guidance for similar inventories undertaken elsewhere. The ALAS staff obtained ~60% of the known ant fauna using a combination of Berlese samples of soil/litter cores, Malaise trap samples, and canopy fogging. The overall species accumulation curve had achieved a relatively shallow slope by the end of the sampling process. The fact that the structured sampling in this study undershot the known minimum fauna simply reveals the incompleteness of the methods, not the inadequacy of effort. The methods used in the project efficiently sampled the subset of the ant fauna susceptible to the methods used, but other methods (e.g., Winkler extraction from sifted leaf litter, specialized search for army ants and ants in myrmecophytes) could be added to reveal additional elements of the ant fauna. The use of small soil/litter cores and Berlese funnels by Project ALAS was a compromise to allow the simultaneous sampling of mites. Winkler extraction of sifted leaf litter (Besuchet et al. 1987) is a proven and highly efficient sampling method for litter ants (Ward 1987, Olson 1991, Belshaw and Bolton 1994). Olson (1991) obtained 117 ant species from five Winkler samples of sifted litter at La Selva, compared to 113 species from 208 ALAS Berlese samples, and the species composition was very similar. Thus, Winkler samples should perhaps replace Berlese sampling if ants are the sole focus of an inventory.

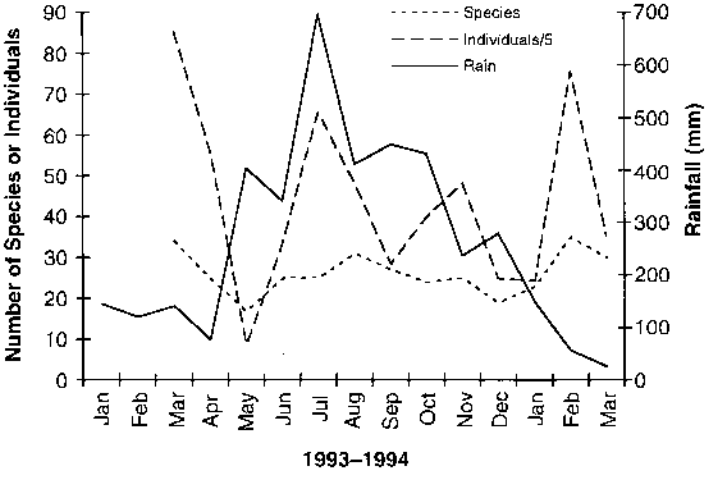

FIG. 6. Berlese results; seasonal changes in rainfall, ant abundance, and species richness. Ant data for each month are totals from 12 Berlese samples across the 12 sites that were sampled over the full 13-mo sampling period. Rainfall data are from the La Selva meteorological station.

Rarity

There remained a set of rare species for which there is no current explanation of their rarity. A portion of the resident ant community may not easily be collected by any of the commonly used methods. For example, P. Ward (*personal communication*) and other myrmecologists have speculated that the subterranean ant community may be more abundant and more diverse than generally thought. The presence of subterranean species is sometimes revealed by occurrence of male ants at lights. For example, the number of species of army ants known from males collected at lights is often higher at a site than the number of species known from workers. Ant males are sometimes encountered that cannot be easily associated with known genera. Workers of a large eyeless ponerine, *Centromyrmex alfaroi*, have been collected only once at La Selva, when they appeared briefly at the soil surface as alates were being released (S. Cover, *personal communication*), yet males are moderately common at blacklights. Workers of a species of *Acropyga* (Formicinae) are only rarely encountered because they nest beneath the soil, tending Homoptera on plant roots. Nonetheless, the species must be very abundant at La Selva because heavy rains

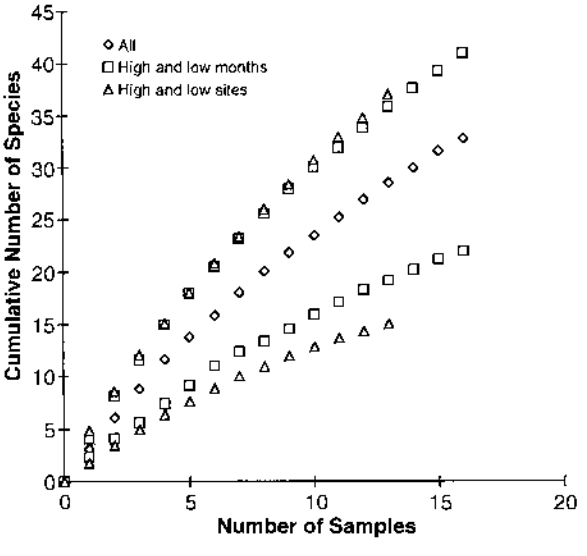

FIG. 7. Berlese results; spatial and temporal contributions to species accumulation. High and low site curves are for richest and most depauperate sites, respectively (among the 12 sites that were sampled over the full 13-mo sampling period; 13 monthly samples per site). High and low month curves are for richest and most depauperate months (16 samples per month from 16 different sites). The combined curve is the mean, randomized species accumulation curve for 1 to 16 samples, based on the full set of 208 samples.

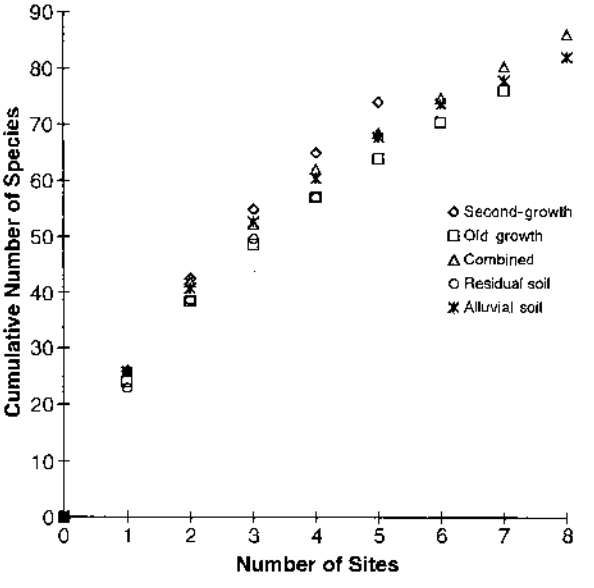

FIG. 8. Berlese results; habitat and soil effects on species accumulation curves. Berlese samples were combined to give one pooled sample for each site. Only the 12 sites with a full complement of 13 monthly samples were included, yielding 5 second-growth sites compared to 7 old-growth sites, and 4 residual soil sites compared to 8 alluvial soil sites. The combined curve is the smoothed species accumulation curve from all 12 sites.

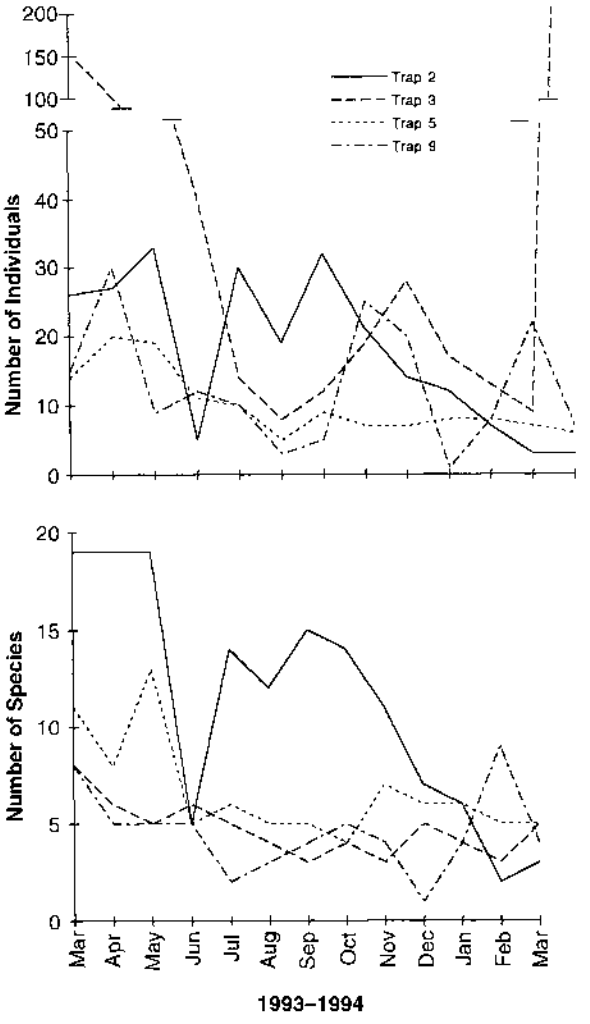

FIG. 9. Malaise results; temporal distribution of within-sample ant abundance and richness, by trap. The top figure shows the number of individuals caught per month. Total trap catches were 232 for trap 2, 665 for trap 3, 131 for trap 5, and 167 for trap 9. The bottom figure shows the total number of species caught per month.

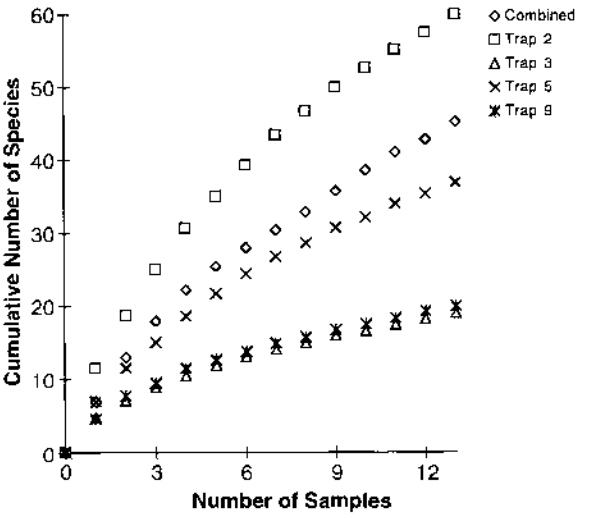

FIG. 10. Malaise results; trap contribution to species accumulation. Smoothed species accumulation curves for each trap are from the 13 monthly samples. The combined curve is the mean, randomized species accumulation curve for 1 to 13 samples, based on the full set of 52 samples.

bring out dense clouds of lekking males over every shrub in the laboratory clearing (*personal observation*).

Alternatively, rare species may have absolutely low densities at the site for a variety of reasons. They may be rare immigrants from a nearby source population. For example, *Stenamma felixi* (Myrmicinae) is known from one collection at La Selva, from its usual nesting site under loose bark of a rotten log. *Stenamma felixi,* however, is a relatively common species in mid-montane and cloud forests of Costa Rica, and thus higher density populations occur on the mountain slopes a few kilometers south of La Selva. Alternatively, rare species could result from temporal changes in populations, representing either the remnant of a declining population or the first examples of an increasing population. Although one might expect perennially nesting ants to be less prone to seasonal or long-term population fluctuations than solitary insects, studies by Levings (1983) show considerable seasonal variability in tropical ant communities.

Our inventory results for La Selva ants may be explained by the heuristic model depicted in Fig. 16. Some species will be resident and accessible to a particular sampling method (or methods). Others will be nonresident or otherwise not typically accessible to a particular sampling method. The model assumes that resident species will have locally reproducing populations, and will approach a lognormal or otherwise hump-shaped distribution of relative abundances (and thus probabilities of encounter). The number of resi-

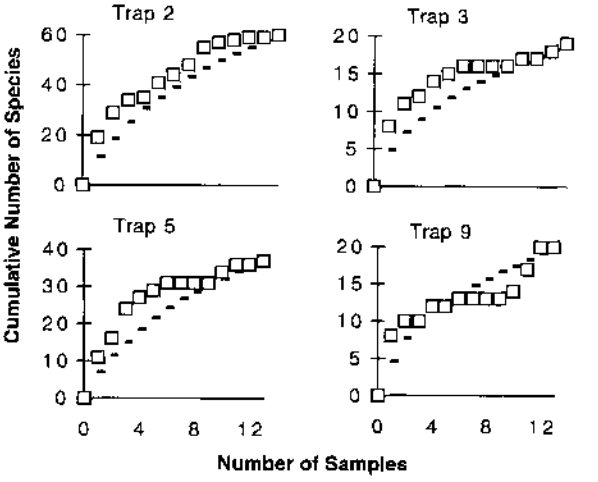

FIG. 11. Malaise results; unsmoothed (open squares) compared to smoothed (dashes) species accumulation curves for each trap.

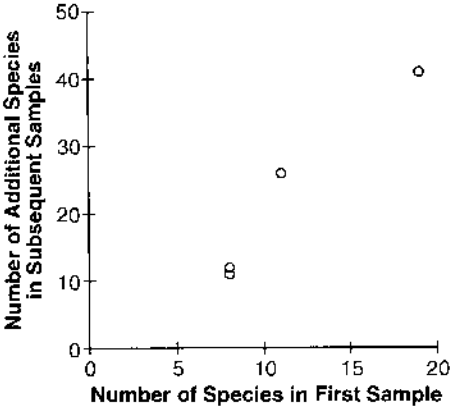

FIG. 12. Malaise results; relationship of species richness of the first sample to the number of additional species obtained in all 12 subsequent samples. Each point is one trap.

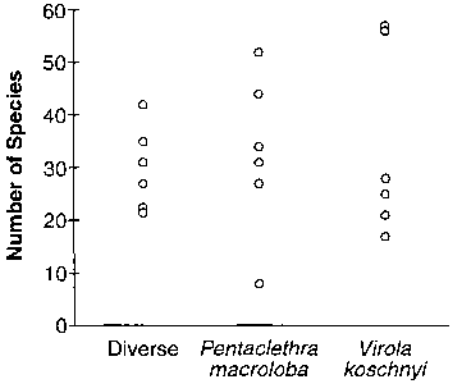

FIG. 14. Fogging results; number of species per tree, by treatments.

dent species will be limited. In contrast, there may be a very large number of nonresident species that disperse into the study site from other source areas. At low probability of encounter, the number of potential nonresident species increases. For example, Berlese samples capture the resident fauna in the leaf litter, but they also occasionally capture species from the forest canopy. The source pool for this influx includes more than a hundred species that are common in the canopy. There is great faunal turnover with elevation in Costa Rica, and some of the rare species in the ALAS inventory are species more common at higher elevation. The source pool for this kind of influx into La Selva includes perhaps a thousand or more species of ants predicted for Costa Rica as a whole. Thus, inventories of hyperdiverse groups can almost never "get them all." Singletons continue to appear indefinitely. With increased sampling effort, some singletons will cease to be singletons as additional specimens are obtained, but new singletons will appear in the sampling effort. Inventories of hyperdiverse groups may, perhaps, never be complete in a strict sense; they can only reach some arbitrarily defined low rate of new species accrual per unit effort.

Complementarity of methods

Berlese samples were highly complementary to both Malaise trap samples and fogging samples. Thus any ant inventory should focus collecting on both the litter/soil fauna and the arboreal fauna. Malaise traps and canopy fogging were largely redundant. This result was surprising, given the vertical stratification of ant species that is obvious to a general collector. Apparently there is a rain of workers from the high canopy, either falling from the canopy or walking down as the occasional long-distance forager, and these ants walk into Malaise traps. Malaise traps can be surprisingly good at capturing even high canopy ants, and should not be discounted as an ant-collecting method. In some inventory applications, ground-based Malaise traps could be a substitute for canopy fogging. If resources for preparing ant specimens are limited and nonspecialists

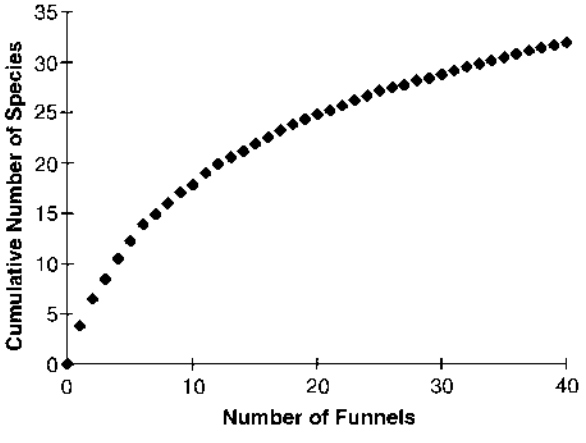

FIG. 13. Fogging results; smoothed species accumulation curve for one *Virola koschnyi* tree.

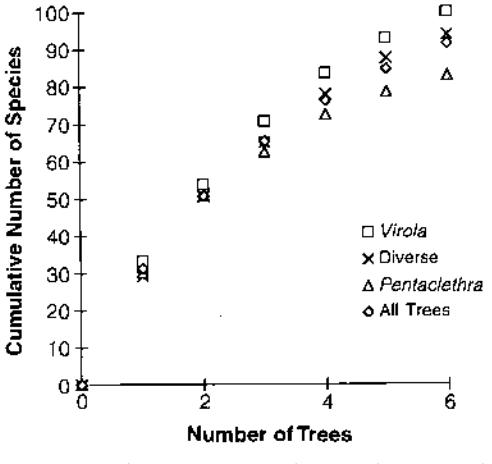

FIG. 15. Fogging results; smoothed species accumulation curves for *Virola koschnyi*, *Pentaclethra macroloba*, and trees of six different plant families. The All Trees curve is the first six values from the smoothed curve for the full set of 18 trees.

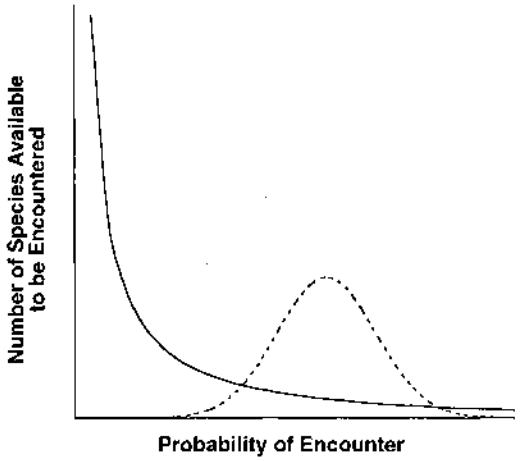

FIG. 16. Model of underlying processes producing inventory results. Resident species are represented by the dotted line, and nonresidents by the solid line. As sampling effort increases, an ever larger pool of rare species is encountered. With this model, species accumulation curves never reach a plateau.

will be processing the material, it may even decrease inventory efficiency to process ants from both Malaise traps and fogging samples.

For inventory purposes, fogging has the advantage of generating a large number of specimens in a short period of time. In contrast, Malaise traps generate relatively few specimens of each species, and must be left in the field a long time to obtain them. The similar efficiency we observed between fogging and Malaise traps was probably due to our processing protocol, in which we mounted examples of each species from each funnel. Within a tree, common species are duplicated over many funnels, and as a result many duplicate specimens of the same species are mounted. A change in the protocol might be to pool the contents of 10 funnels into one sample and mount examples of each species after pooling. This would increase the efficiency by decreasing the number of mounted specimens of the more abundant species. However, it has the potential to decrease efficiency if nonspecialist lumping errors are common (multiple species interpreted as a single species at the time of mounting). The apparently redundant mounting effort by the nonspecialist may increase the number of cryptic species obtained from the sample, which are later discovered when the taxonomist sorts the mounted material.

Spatial and temporal contributions to richness

Berlese samples showed little effect of habitat or seasonality on the rate of species accumulation in our data. To the degree that our results are typical, if time and resources permit only 16 samples, they can all be clustered within a few meters of one another in an easily accessible place. In this study, no increase in species accrual rate was gained by dispersing samples with respect to habitat or time. If 12 sets, with 13 samples in each set, can be taken, there is no advantage in stratifying them with respect to forest stage (primary vs. second growth) or soil type (alluvial vs. residual).

Individual Malaise traps were highly variable in their catch rates, ranging from 19 to 60 species captured over the 13-mo sampling period. The number of species caught during the first month of trap sampling was predictive of the overall success rate for the trap (Fig. 12). This result suggests that a more efficient inventory procedure would be to assess the first month's catch rate and relocate traps with low catch rates.

When a sequence of Malaise trap catches shows a decreasing rate of species accrual over time, the decrease can be from two causes: (1) gradual sampling of species in a stable community, a pure sampling phenomenon that does not rely on change in the trap or the local community, and (2) a reduction in trap function over time due to some change in trap characteristics and/or community characteristics. These causes can be examined by comparing smoothed (randomized) to observed (time-sequential) species accumulation curves. If decreasing species accumulation curves are purely the result of community sampling, then smoothed and time-sequential curves should be roughly the same. If trap function declines over time, then the observed curve should be initially steeper than the time-sequential curve, because the richest samples will be clustered in the earliest sampling periods. We observed that smoothed curves were below time-sequential curves for three of four traps, which suggests a reduction in trap function over time. Two processes that could cause a reduction in trap function are (1) increased visibility of the trap over time as it accumulates debris on the roof and fungi on the walls, and (2) a decrease of local arthropod populations. Three of the four traps showed evidence of a plateau in species accumulation for the wet season months of August to November. Thus, an efficient ant inventory at La Selva might suspend Malaise trap operation during these months. Considering these results together, an efficient inventory in the La Selva climatic regime might place Malaise traps in December, relocate low catch rate traps in January, and suspend operations at the end of July.

Canopy fogging revealed significant among-tree heterogeneity in species composition. Thus spreading effort across multiple trees rather than concentrating effort in a few trees was more efficient, in terms of species accrual per specimen. However, there was no evidence of any host specificity, a result similar to that found by Wilson (1987*b*) in his study of ants in a Peruvian forest canopy. Our samples from multiple trees of the same species accumulated ant species at a rate similar to samples from trees of different species. After 18 trees, the rate of species accrual was considerably less than the initial rate.

The similarity of species occurrences between habitat types found for ants at La Selva might suggest that

habitat stratification be abandoned in other inventories. However, it is also true that stratifying by habitat did not actually depress species accumulation curves based on number of samples. Thus, in designing an efficient inventory, there is no reason *not* to stratify by environmental variables if it does not incur a large cost in terms of additional field time. However, if estimation of species richness or more complete inventory of a particular habitat is desired (community characterization goals), then stratifying by habitat variables can be detrimental, resulting in undersampling of particular, individual habitats (Coddington et al. 1991).

Interpretation of combined species accumulation curves

When combined vs. within-treatment species accumulation curves were compared, the combined curve often fell among the within-treatment curves. How should this pattern be interpreted? It reveals that stratifying a sampling regime with respect to the treatments will not greatly increase inventory efficiency. If there is no a priori knowledge of relative steepness of species accumulation curves in different treatments, then stratifying sampling would be a risk-avoiding option. It would not be as bad as the worst treatment, but it might not be as good as the best treatment. For example, when designing a fogging program, one has a choice between fogging trees of many species, or fogging multiple trees of the same species. If there is no a priori knowledge of which tree species produce the most ant species, then a mixed-species strategy would be best. If the results from the La Selva fogging program are generalizable to other lowland sites, then concentrating fogging effort on *Virola koschnyi* trees might be more efficient than a mixed-species strategy. And, of course, some other tree species at La Selva might have proven even richer than *V. koschnyi*.

An important caveat is that comparing combined vs. within-treatment species accumulation curves does not necessarily reveal underlying differences or similarities in community richness and/or species composition. This analysis method applies purely to inventory efficiency, and not to community characterization. Consider the case of two habitats that have high complementarity (low species overlap) but one habitat is far richer than the other. Common sense might dictate that sampling occur in both habitats because the species in the two habitats differ. However, a combined species accumulation curve might nevertheless be lower than the curve of the richer habitat. Even though the species in the depauperate habitat are distinct, expending sampling effort in this habitat may reduce sampling efficiency (more specimens processed for fewer species), such that fewer species are obtained overall than if all effort had been concentrated in the richer habitat.

Conclusions

This study clarifies the distinction between community characterization and strict inventory. The goal of strict inventory is an accurate species list for a site, obtained in the most efficient way possible. This objective may best be met by sampling and sample processing methods that do not accurately reveal relative abundances. It may require concentrating sampling in rich habitats and ignoring depauperate ones.

We must stress that the findings reported here may not be true for other taxa, other sample processing procedures, other habitat types, or other spatial scales. Project ALAS surveyed many other taxa simultaneously with the ants, using the same methods, so assessment of the generality of our findings to other taxa (for La Selva) should be forthcoming. The generality of the findings for other methods, sites, and spatial scales must await new studies. Moreover, we wish to stress that the results of a strict inventory may not meet the needs of conservation biologists or decision-makers in resource and wildland management, for whom community characterization data may be required, instead of or in addition to strict inventory results. Habitat or seasonal specificity, relative abundance, endemicity, and population size and density are often crucial data in conservation biology, requiring or benefiting from in-depth community characterization.

Rain forest ant communities throughout the lowland neotropics are relatively similar in terms of generic composition, relative richness of different genera, and behaviors of different species (J. T. Longino, *personal observation*). Thus, our findings should have immediate application to similar ant surveys in other neotropical forests. An ant inventory in a neotropical forest should sample both the litter/soil zone and the vegetation. Litter/soil ants may be sampled with Berlese or Winkler methods, but the latter are probably superior. Arboreal ants can be sampled with Malaise traps or canopy fogging. Mass sampling techniques such as Berlese sampling or Malaise traps should be accompanied by direct visual search for army ants and ants in myrmecophytes. Malaise trap sampling may be a low cost and logistically simpler alternative to canopy fogging for capturing the arboreal ant fauna. Malaise traps should be assessed for capture rates after a month of sampling, and low catch rate traps relocated. Stratifying by forest type, soil type, tree species, or time do not dramatically increase inventory efficiency at the spatial scale considered here, and thus might be dispensed with if such stratification incurs much cost.

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