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THE ANT FAUNA OF A TROPICAL RAIN FOREST: ESTIMATING SPECIES RICHNESS THREE DIFFERENT WAYS

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Abstract. Species richness is an important characteristic of ecological communities, but it is difficult to quantify. We report here a thorough inventory of a tropical rain forest ant fauna and use it to evaluate species richness estimators. The study was carried out in ~1500 ha of lowland rain forest at La Selva Biological Station, Costa Rica. Diverse methods were used, including canopy fogging, Malaise traps, Berlese samples, Winkler samples, baiting, and manual search. Workers of 437 ant species were encountered. The abundance distribution was clearly lognormal, and the distribution emerged from a veil line with each doubling of sampling effort. Three richness estimates were calculated: the area under the fitted lognormal distribution, the asymptote of the Michaelis-Menten equation fit to the species accumulation curve, and the Incidence-based Coverage Estimator (ICE). The performance of the estimators was evaluated with sample-based rarefaction plots. The inventory was nearly complete because the species accumulation curve approached an asymptote, the richness estimates were very close to the observed species richness, and the uniques and duplicates curves were both declining. None of the richness estimators was stable in sample-based rarefaction plots, but regions of stability of estimators occurred. The explanation of rarity is one key to understanding why richness estimates fail. Fifty-one species (12% of the total) were still uniques (known from only one sample) at the end of the inventory. The rarity of 20 of these species was explained by ''edge effects'': ''methodological edge species'' (possibly abundant at the site but difficult to sample because of their microhabitat), and ''geographic edge species,'' known to be common in habitats or regions outside of La Selva. Rarity of 31 species remained unexplained. Most of the 51 rare species were known from additional collections outside of La Selva, either in other parts of Costa Rica or in other countries. Only six species were ''global uniques,'' known to date from only one sample on Earth. The study demonstrates that patterns of species occurrence early in an inventory may be inadequate to estimate species richness, but that relatively complete inventories of species-rich arthropod communities are possible if multiple sampling methods and extensive effort are applied.

Key words: abundance distribution; ants; biodiversity; Costa Rica; Formicidae; incidence-based coverage estimator; inventories, species; La Selva; lognormal; Michaelis-Menten; richness estimation; species accumulation curves; tropical rain forest.

INTRODUCTION

There is an abiding interest in the number of species in local communities, because species are the fundamental particles of biodiversity (Bisby 1995, Gaston 1996). A major research agenda in ecology is to explain geographic patterns of species richness (Rosenzweig 1995). Many studies address the latitudinal change in species richness and why there are so many species in the tropics. Others examine change with elevation, asking whether there is a mid-elevation peak in diversity, and if so, why. Conservation biologists examine whether species richness changes with land use history or degree of landscape fragmentation, and whether richness changes over time. When an investigator is carrying out a taxon inventory of a site, the first question asked by visitors is always ''How many species do you have?'' One can show them a list of the species observed and count them up, but that does not answer the question of how many species are present at the site. Observed number of species is a biased estimate of community species richness, because observed richness can never be higher than true richness (barring identification errors), but it can be and usually is lower. Although many studies rely on taxonomists' species lists, with the assumption that the taxonomic work is exhaustive and the lists are complete, ecologists have also devised methods for estimating species richness based on quantitative sampling (e.g., Soberón and Llorente 1993, Colwell and Coddington 1994, Palmer 1995, Peterson and Slade 1998). This study reports on a relatively thorough inventory of the ants (Hymenoptera: Formicidae) in a Costa Rican rain forest, and evaluates the efficacy of three richness estimation methods.

There are several reasons for choosing ants as a sur-

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TABLE 1. Field sampling techniques and definitions of sampling methods used in the inventory of the ants (Formicidae) of La Selva Biological Station, Costa Rica.

		Sample distribution		
Method	Sample unit	No. samples	No. subsites	Duration
Fogging	1-m^2 funnel	10–40/tree	24 trees	
Malaise	2-wk catch	8–15/trap	7 traps	13 mo
Berlese	1.7 L litter/soil core	20 sites		13 mo
Winkler	6 L sifted litter	41 sites		14 yr
Barger	transect of 20 baits	10 sites		1 mo
Thompson	1 nest	30-m^2 area of forest floor		1 mo
Longino	various temporally and spatially restricted samples	multiple sites		14 yr
Other	various temporally and spatially restricted samples	multiple sites		23 yr

vey taxon. Ants and other invertebrate taxa should be included in biodiversity studies because of their high diversity and rapid response to environmental change (Kim 1993, Kremen et al. 1993, Miller 1993, Samways 1993, Basset et al. 1998). When choosing invertebrate taxa to survey, the relative merits of different taxa are often discussed (e.g., Basset et al. 1998). Agosti et al. (2000) have made a strong case for the inclusion of ants. In most terrestrial ecosystems ants are a conspicuous presence, and they are among the most commonly studied terrestrial invertebrates. They are mostly scavengers and predators, and they have large impacts on soil formation, seed predation and dispersal, and invertebrate community structure (Folgarait 1998). They are particularly good candidates for monitoring community changes that may occur due to climate change or habitat fragmentation. Ants are also an important group to monitor for the arrival and impact of invasive species.

Ecological studies of ant communities are very common but in most cases are the result of relatively small-scale sampling programs using one or few sampling methods. There are increasing numbers of very thorough inventories of leaf litter ants (Belshaw and Bolton 1994, Fisher 1996, 1998, 1999*a*, *b*, 2000, Delabie et al. 2000). Other studies involve sampling the whole community with a variety of methods, in the context of answering particular ecological questions, but they do not purport to be exhaustive inventories of a local ant fauna (e.g., Andersen and Majer 1991, Andersen 1992, Andersen and Reichel 1994, Armbrecht and Ulloa-Chacón 1999, Gadagkar et al. 2000). Inventories involving both sustained effort and a variety of sampling methods, with the express purpose of capturing the entire fauna, are relatively rare. Notable examples include Van Pelt (1956) for the Welaka Reserve, Florida; Talbot (1975) for the E. S. George Reserve, Michigan; and Deyrup and Trager (1986) for Archbold Biological Station, Florida. Tropical rain forest studies include Verhaag (1990, 1991) for Panguana Reserve, Peru, and Brühl et al. (1998) for Kinabalu National Park, Sabah, Borneo. Here we report the results from a thorough inventory of the ants of La Selva Biological Station, an active research station located in a lowland tropical rain forest in Costa Rica (McDade et al. 1993). Earlier work on the ant fauna of La Selva includes Olson (1991) and Roth et al. (1994), but these were smaller studies that did not attempt to sample the entire ant community.

The results reported here are part of a larger arthropod inventory at La Selva, Project ALAS (Longino and Colwell 1997; also see the project ALAS web site).[5] The project combines the methods of museum taxonomists and field ecologists (Longino 1994), with the primary goal of achieving thorough inventories as efficiently as possible. An additional goal is to apply quantitative sampling procedures that allow the investigation of inventory efficiency and richness estimation. Longino and Colwell (1997) analyzed inventory efficiency; this second report addresses estimation of species richness.

METHODS

La Selva Biological Station, Heredia Province, Costa Rica, is approximately 1500 ha, with an elevation range of 50–150 m and ~4 m mean annual rainfall. The habitat is a mosaic of mature lowland rain forest, second growth forest of various ages, and abandoned pastures (McDade et al. 1993).

The data set on which this paper is based is a species × sample incidence (presence–absence) matrix. The samples fall into eight categories: *fogging* and *Malaise* sample the arboreal fauna; *Berlese, Winkler, Barger,* and *Thompson* sample the soil and litter fauna; *Longino* and *Other* sample a combination of microhabitats (Table 1; also see the Appendix).

Samples were processed by the four Project ALAS Parataxonomists, or by J. T. Longino (see the Appendix). All quantitative results in this paper were based on the worker caste; males and queens were excluded

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[5] URL: <viceroy.eeb.uconn.edu/alas/alas.html>

(much like excluding seeds from a vegetation survey). Most ant taxonomy is based on the worker caste, and the presence of a worker is clear evidence of colony establishment. All specimens were examined and identified by Longino, with the exception of one species record from the literature (Supplement).

Richness estimation and evaluation of estimators

Bunge and Fitzpatrick (1993) and Colwell and Coddington (1994) reviewed methods for estimating the number of species in a community. Three broad categories of estimators are (1) fitting a lognormal abundance distribution and estimating the hidden or unsampled portion of the curve, (2) fitting asymptotic equations to species accumulation curves, and (3) using nonparametric estimators that use the relative abundances of rare species to estimate the number of species not seen. We used these three methods to estimate species richness of the La Selva ant fauna.

Abundance distributions.—Various methods have been proposed for fitting sample data to a lognormal distribution and for estimating species richness by calculating the total area under the fitted curve, including the portion of the curve hidden behind the ‘‘veil line’’ (Preston 1948, Williams 1964, Ludwig and Reynolds 1988, Magurran 1988, Lobo and Favila 1999). We followed the method of Preston, in which abundance classes or ‘‘octaves’’ had boundaries 0.5, 1, 2, 4, 8, etc. If a species fell on a boundary, then its abundance was evenly split between the two adjacent octaves, adding 0.5 to each one. The first visible octave was 1–2, which contained one half the singletons plus one half the doubletons (the other half of the singletons necessarily ignored in analyses). Richness was estimated by assuming a truncated lognormal distribution for the observed data, estimating the parameters of the complete distribution, and calculating the area under the curve of that complete distribution. The lognormal distribution is given by

$$S(R) = S_0 e^{(-a^2 R^2)}$$

where $S(R)$ is the number of species in the Rth octave, S_0 is the number of species in the modal octave, and a is a parameter related to the width of the distribution. $R = 0$ for the modal octave; 1, 2, 3, etc. for higher octaves; -1, -2, -3, etc. for lower octaves.

The parameters of the lognormal were estimated using a modified version of the method in Ludwig and Reynolds (1988). Octave numbers were assigned to each observed abundance class, and the parameters S_0 and a were estimated using the Nonlin module of Systat 5.2, with Quasi-Newton estimation and least-squares fit. Octave numbers were assigned such that they maximized the corrected r^2 value from the model estimation. Traditionally, S^*, the estimate of total species richness, is the area under the entire estimated curve. However, this contains not only the species behind the veil line, but also that portion of the estimated curve that extends beyond the highest observed abundance class. Since all the very abundant species are being observed (there are no ‘‘hidden’’ species with abundances greater than the most abundant observed species), the estimated curve should be truncated at the octave with the highest observed abundance. We followed that procedure here.

Projecting species accumulation curves.—This method requires a series of samples, so that a species accumulation curve can be observed as additional samples are added to the pool. An asymptotic equation is then fit to this curve, and the estimate of the asymptote parameter is the estimate of species richness. The function most often used, and the one used in this report, is the Michaelis-Menten equation (Clench 1979, Soberón and Llorente 1993, Colwell and Coddington 1994, Chazdon et al. 1998, Keating and Quinn 1998). Parameter values were estimated using Raaijmakers’ (1987) maximum likelihood estimators for the Eadie-Hofstee transformation, as outlined in Colwell and Coddington (1994).

Nonparametric estimators.—Nonparametric methods show promise for richness estimation (Bunge and Fitzpatrick 1993, Colwell and Coddington 1994). Chao and colleagues developed a set of nonparametric methods for estimating the number of classes in a sampling universe (Chao 1984, 1987, Chao and Lee 1992, Chao et al. 1993, Lee and Chao 1994). These methods have now been evaluated for a number of biological data sets (e.g., Colwell and Coddington 1994, Fisher 1996, 1998, 1999*a*, *b*, Chazdon et al. 1998, McKamey 1999, Anderson and Ashe 2000). An estimator that shows considerable promise is the Incidence-based Coverage Estimator (ICE). Details of its calculation may be found in Chazdon et al. (1998) and R. K. Colwell’s EstimateS (Version 6) web site.[6] We used ICE for nonparametric richness estimation in this paper.

Two parameters that are components of nonparametric estimators and that are often examined as indicators of inventory completeness are the number of ‘‘uniques’’ and ‘‘duplicates.’’ Uniques are species known from a single collection; duplicates are species known from only two.

Sample-based rarefaction curves and associated estimator curves.—A key attribute of a richness estimator is that it become independent of sample size above some minimum sample size. As additional species are discovered during a survey, the species accumulation curve can be viewed as an increasingly accurate assessment of community species richness. As additional samples are pooled and the observed species richness curve stabilizes beyond a particular number of samples, then observed species richness is deemed an adequate estimate of community species richness for that number of samples. Pielou (1966, 1975) first suggested assessing diversity index measures (although not species

[6] URL: <http://viceroy.eeb.uconn.edu/estimates>

richness), at progressively larger numbers of pooled samples, by adding samples to the pool in random order from an existing sample set, then computing a diversity index measure for each level of sample pooling. Pielou's ''pooled quadrat method'' (Magurran 1988) was generalized by Lloyd et al. (1968), who suggested multiple re-orderings to account for variation among sample re-orderings, and by Colwell and Coddington (1994), who extended this approach to richness estimators. If the estimate of species richness is unstable or rises with sample size, it is not a reliable estimate of total richness. (A rising Chao estimator can nonetheless be regarded as a valid estimator of minimum richness, given the available data [A. Chao, *personal communication*]). If the estimate stabilizes and is independent of sample size, it is more likely to be a reliable estimate of total species richness. Gotelli and Colwell (2001) refer to this random resampling procedure as ''sample-based rarefaction,'' since it is analogous to the individual-based rarefaction of Sanders (1968; see also Simberloff 1978), but it differs from the latter in retaining the pattern of aggregation of species within samples.

To investigate the effect of number of samples on richness estimates using Michaelis-Menten and ICE, R. K. Colwell's program EstimateS (Version 5) was used.[7] This program calculates sample-based rarefaction curves and associated values for a variety of richness estimators, presenting the mean of a user-designated number of random re-orderings of the samples. Sample-based rarefaction plots were produced for each data set. For all calculations involving multiple random orderings of the samples, 50 randomizations were used. The ICE calculations were carried out using the EstimateS default ''cut-point'' of 10, as suggested by Lee and Chao (1994). EstimateS calculates Michaelis-Menten estimates in two ways: (1) for each of the 50 sample re-orderings, then averaged (''MMRuns''), or (2) once using the smoothed species accumulation curve (''MMMeans''). MMMeans is used in this report.

To compare sample-based rarefaction curves, the units of the abscissa should, in general, be number of individuals when examining community species richness, whereas the units should be number of samples when examining species density (Gotelli and Colwell 2001). Because this report is concerned with species richness, the abscissa of rarefaction curves should, in principle, be number of individuals. However, ants present a problem because of their sociality, resulting in an extreme spatial clumping of individuals within samples. In addition, some of the data from Project ALAS are incidence data (presence/absence data). To circumvent this problem, all data were converted to incidence data, and number of species occurrences (not number of samples) is used throughout as a measure of abundance and sampling effort. All rarefaction curves are plotted with number of occurrences on the abscissa.

We use a log scale for the abscissa of most sample-based rarefaction plots. This technique reveals patterns in estimator curves that are not easily seen in arithmetic plots. Arithmetic plots make it difficult to distinguish asymptotic curves from logarithmic curves. In a semilog plot the former will appear sigmoidal and the latter will approach linearity. Also, curves of number of uniques that appear flat on arithmetic plots may appear more distinctly humped on log plots.

Data subsets.—We applied richness estimators to a variety of data partitions, ranging from small, uniform subsets to the entire data set. Richness estimators were applied to (1) each of the eight methodological subsets, considered separately; (2) within-month, among-site subsets of the Berlese samples; (3) the quantitative data set, which is the combined data set for all the methods using structured sampling (i.e., ''Longino'' and ''Other'' excluded); and (4) the full data set, consisting of the samples from all eight methods.

We used the quantitative and full data sets to evaluate richness estimates based on the lognormal method and to assess the prediction that the abundance distribution would emerge from behind a veil line one octave for each doubling of sample size. Samples were pooled to yield subsets with 12.5%, 25%, 50%, and 100% of the samples. Samples were randomly selected from within each of the eight methods so that proportional representation of methods did not change as sample size increased. For each subset we observed the abundance distribution and calculated a richness estimate based on the truncated lognormal distribution.

We used all data partitions and sample-based rarefaction plots to evaluate ICE and Michaelis-Menten estimates.

Examination of rarity.—Richness estimates are highly influenced by rare species. Often an attempt is made to partition rare species into those that are low density elements of local communities and those that somehow do not belong. The latter are often referred to as ''tourists,'' reflecting their transitory, nonresident status (Moran and Southwood 1982, Stork 1988, Basset and Kitching 1991, Gaston et al. 1993, Gaston 1994, Novotny and Basset 2000). To better understand rarity in the La Selva ant fauna, the unique species (those found in only one sample) were partitioned according to additional knowledge of their natural history and distribution.

First, ''edge'' species were identified: species known or surmised to be common but not easily sampled with the methods reported here. Edge species were further divided into ''methodological'' vs. ''geographic'' edge species. The former are assumed to be common at La Selva but not readily sampled by the methods employed. In particular, this category consisted of specialized inhabitants of the soil, a subsurface community that is not easily collected. Geographic edge species

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[7] URL: <http://viceroy.eeb.uconn.edu/estimates>

TABLE 2. Summary statistics for different types of samples used in the inventory of the ants of La Selva Biological Station, Costa Rica.

Method	No. samples	No. species occurrences†	No. species	No. local uniques‡	No. uniques§
Fogging	459	3262	165	21	2
Malaise	62	455	103	39	0
Berlese	217	775	117	33	1
Winkler	41	1416	197	50	11
Barger	40	275	65	26	3
Thompson	222	255	52	19	0
Longino	528	894	283	96	16
Other	335	573	235	111	18
Total	1904	7904	437		51

† Ants are social, and entire colonies may occur in single samples. To reduce the effect of this extreme spatial aggregation, only incidence data are used in this report.

‡ Number of species found in only one sample for a particular method, but not necessarily for the study as a whole (following terminology of Novotny and Basset 2000).

§ Number of species found in only one sample in the entire study.

are known to be abundant outside of La Selva yet occurred in only one sample at La Selva. Geographic edge species were further subdivided into those more common at higher elevation, those more common in the tropical dry forest habitats on the Pacific side of Costa Rica, and ''tramp'' or synanthropic species that are common in open or highly disturbed habitats (most La Selva sampling occurred in mature or second growth forest). The rarity of the remaining unique species remained unexplained. Finally, ''global uniques'' were identified: those known only from the one sample reported here, and as yet from nowhere else on Earth.

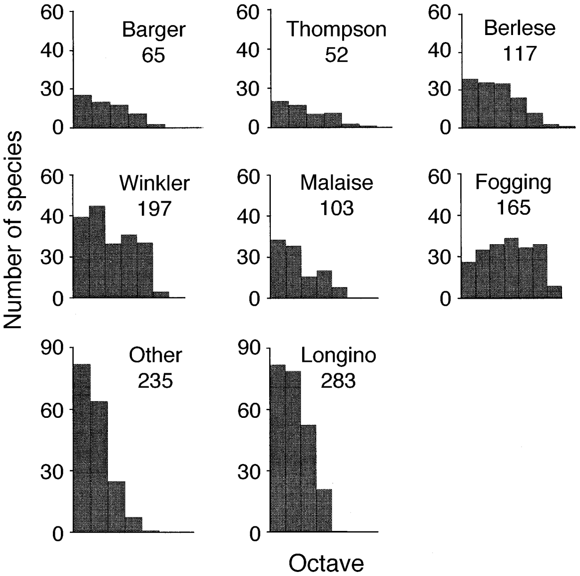

FIG. 1. Abundance distributions of ants at La Selva Biological Station, based on eight different sampling methods (see the Appendix). Octaves are standard Preston abundance classes, with boundaries 1, 2, 4, 8, etc. Species falling on a boundary are split between the two adjacent octaves (see *Methods: Abundance distributions*). Abundance of each species is the number of samples in which a species occurred. The number below the name of each method is the total number of species collected by that method.

Background information on ant species was obtained from existing taxonomic literature, and from J. T. Longino's ongoing survey of Costa Rican ants (available online).[8] Although no other site in Costa Rica has been surveyed as intensively as La Selva, Longino has carried out smaller scale collecting in many different regions of Costa Rica and has relied on the nationwide collection at INBio.

RESULTS

Workers of 437 species of ants were found at La Selva (Supplement). In the data set presented here, 7904 species occurrences are distributed among 1904 samples (Table 2). Eighteen additional species were collected as queens and/or males only (discussed below but not included in the quantitative analyses).

Individual methods

Octave-based relative abundance plots for most of the methodological subsets, plotted independently, failed to reveal a mode (Fig. 1). Canopy fogging clearly revealed a mode, however, and produced a convincing lognormal distribution. The Winkler method had a mode in the second octave, but the distribution was irregular and not convincingly lognormal. All others showed distributions typical of tropical insect surveys: the mode was in the first octave. Most species were rare, and the distribution would fit a log series distribution or the right tail of a lognormal distribution equally well. The quantitatively structured samples had lower, broader distributions than the two nonquantitative methods (Longino and Other), as might be expected, given the tendency of nonquantitative collectors to ignore additional specimens of species already collected.

Richness estimates based on the Michaelis-Menten equation and ICE usually did not stabilize (Fig. 2). The exception was the ICE estimate for Other, which stabilized at ~360 species. In general, final observed rich-

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[8] URL: <www.evergreen.edu/ants>

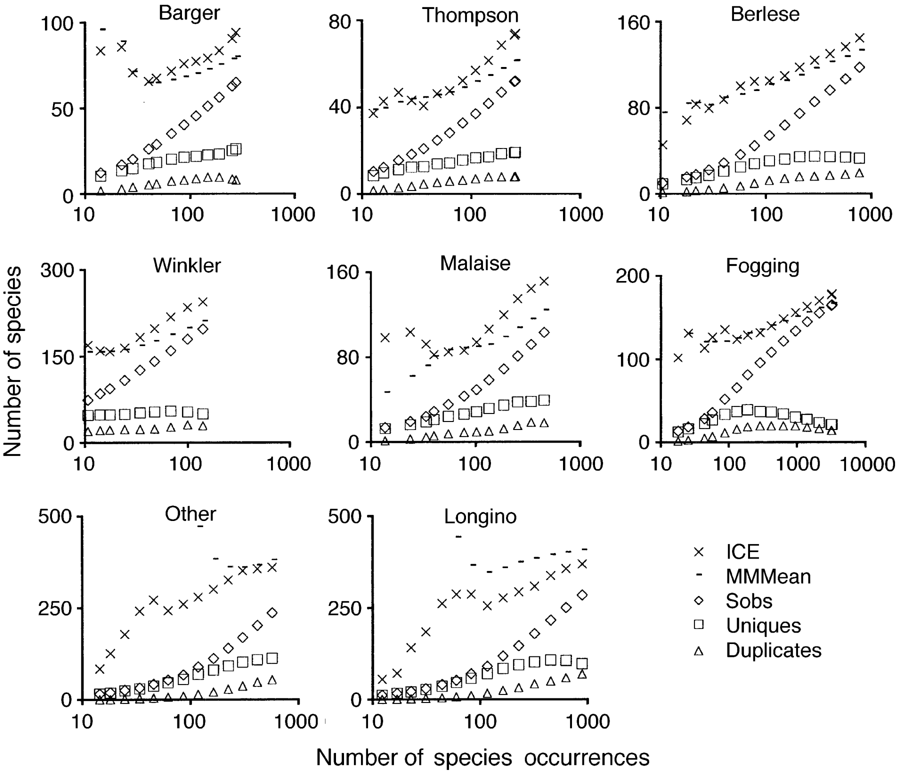


FIG. 2. Sample-based rarefaction curves and corresponding estimators, based on eight different sampling methods. The abscissa is the number of species occurrences, on a logarithmic scale. Key definitions are: ICE, incidence-based coverage estimator; MMMean, asymptote of Michaelis-Menten curve estimated from the sample-based rarefaction curve; Sobs, observed species richness; Uniques, number of species each known from only one sample; Duplicates, number of species each known from exactly two samples.

ness and richness estimates were still widely separated. For canopy fogging samples, both estimates closely converged on observed richness, and in the Winkler method, the Michaelis-Menten estimate closely converged on the observed richness. The uniques and duplicates curves were generally rising as the maximum number of samples was approached. For canopy fogging, both curves peaked and declined. For the Longino samples, the uniques curve was beginning to decline (Fig. 2).

Within-month Berlese samples

Richness estimation using ICE and Michaelis-Menten can produce stable richness estimates for uniform subsets of the data. When the Berlese samples from 16 different sites were examined within months ($n=16$ samples within each month), the ICE estimates stabilized in six of the 13 mo, Michaelis-Menten in four (Fig. 3). But the behavior of ICE and Michaelis-Menten was not correlated: no months showed stabilization of both estimators.

Quantitative data set

The combined data set, using only the six methods based on structured sampling, produced a lognormal distribution (Fig. 4, left column of histograms). Random subsets representing successive doublings of effort showed a lognormal distribution emerging from behind a veil line. For the first two doublings of sample effort, fitted lognormal curves had similar size and shape and appeared as one curve that was revealed one octave at a time. However, the best-fit curves for the third doubling, from 50% to 100%, did not differ in position. Instead the 100% curve differed in shape, being lower and broader than the 50% curve (Fig. 4, lower left histogram). Richness estimates based on the lognormal method were thus stable for 12.5%, 25%, and 50% of sampling effort, but at a value that was clearly an underestimate of the total species richness. The estimate based on 100% of sampling effort was much higher (Fig. 5), exceeding the observed total of 437 species.

The Michaelis-Menten estimates were unstable but closely approached the total observed richness (Fig. 5). The ICE estimates produced a double plateau, one at ~275 species and 100–500 species occurrences and one at ~390 species and 4000–6500 species occurrences. The observed species accumulation curve was slightly sigmoidal, ending at 364 species. The uniques curve was broadly hump-shaped and declining at higher sampling intensity. The duplicates curve was flat.

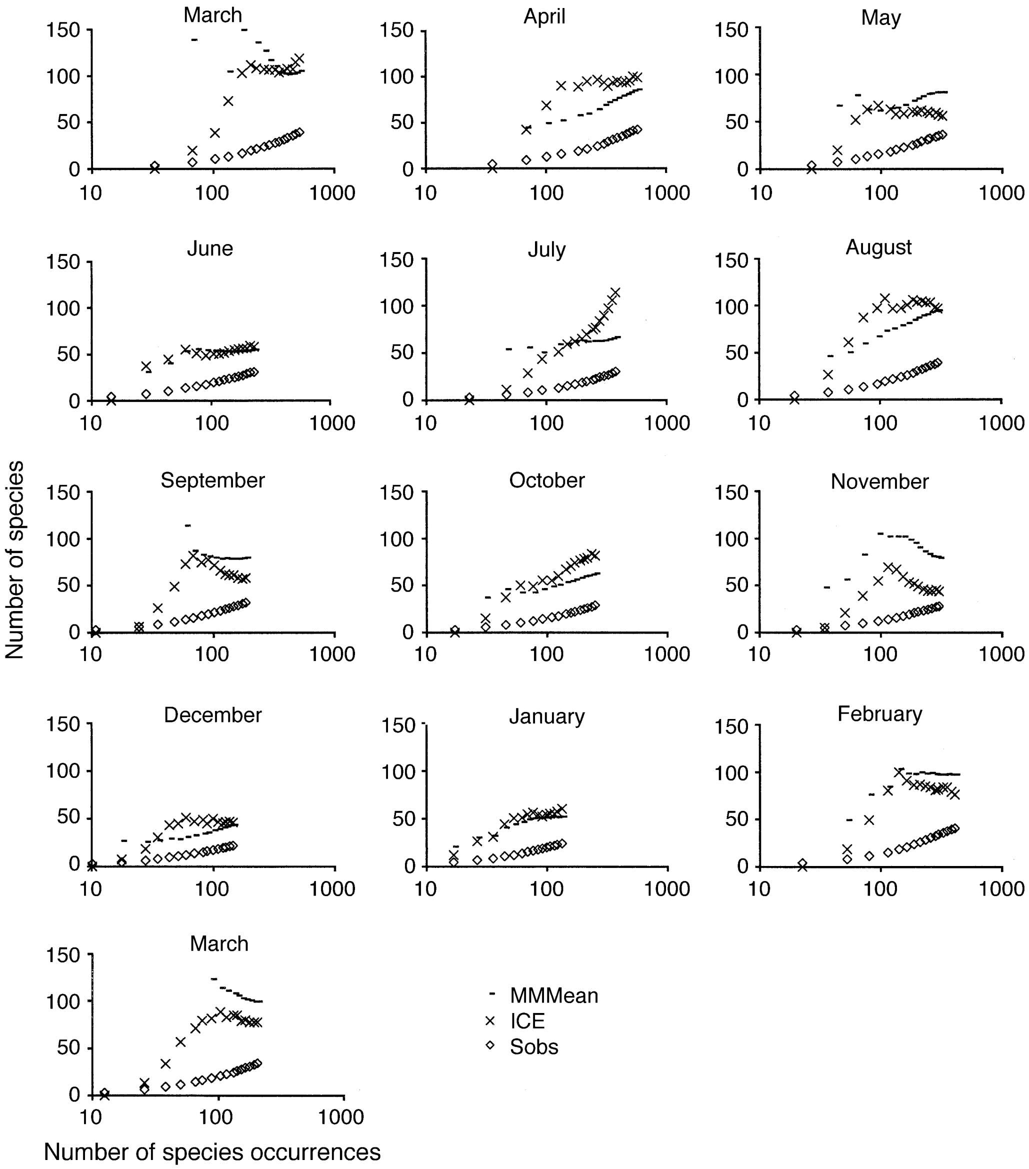


FIG. 3. Sample-based rarefaction curves and corresponding estimators, based on Berlese samples across sites within months. Abscissa, MMMean, ICE, and Sobs are defined as in Fig. 2.

Full data set

The entire data set, for all methods combined, produced a distribution even more clearly lognormal than for the quantitative data set; the fitted curves for the subsamples approximated one underlying distribution, revealed one octave at a time (Fig. 4, right column of histograms). However, richness estimates based on the lognormal method were not stable, reflecting subtle changes in distribution size and shape with increasing sampling intensity. The richness estimate was stable for the two lowest sampling intensities, but then rose with and closely approximated observed species richness (Fig. 5).

The Michaelis-Menten estimates behaved very differently than the quantitative data set. They rose along with observed species richness but formed two line segments with different slopes. The transition to shallower slope occurred at about 340 species and 400 species occurrences (Fig. 5). The ICE estimates also appeared to have two different ''phases,'' somewhat offset from the Michaelis-Menten estimates, accelerating from a shallower to a steeper curve. Neither estimator stabilized with sample size. However, the estimates and the observed richness closely converged at the highest observed richness: 437, 453, 463 for observed richness, Michaelis-Menten, and ICE, respectively. The species accumulation curve was slightly sigmoidal. Both uniques and duplicates curves peaked and began to decline.

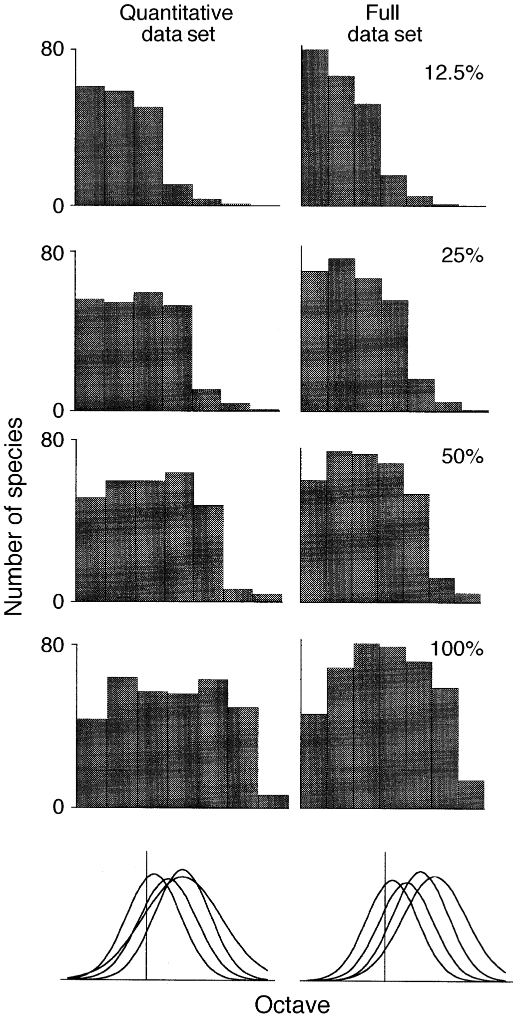


FIG. 4. Abundance distributions of ants at La Selva. The left column of histograms is for the combined data set, containing all data from quantitatively structured sampling; the right column is for the full data set, pooling data from all methods, both quantitative and nonquantitative. Rows represent successive doublings of sampling effort, beginning with 12.5% of samples randomly drawn from the respective data set. In each column the bottom graph shows the superimposed curves of the lognormal distributions estimated from the four histograms; the vertical line there is the veil line.

When plotted on an arithmetic abscissa (the traditional representation of species accumulation curves), the gradual nature of the approach to inventory completion is revealed (Fig. 6). For the majority of the inventory (between 2000 and 8000 species occurrences), the Michaelis-Menten and ICE estimates are similar and outperform the estimates based on the lognormal method.

Rarity

Of the 437 species known from workers, 51 (12%) were uniques. Rarity of 20 of them could be explained by edge effects. Six were methodological edge species, known or suspected to be common at La Selva but not easily sampled by the methods used. These were all ants that nest and forage in the soil but apparently do not forage into the leaf litter or higher. Most of them are eyeless or have greatly reduced eyes. Geographic edge species included three species that are common in synanthropic habitats around La Selva, four species that are abundant in the wet montane forests at higher elevations above La Selva, three species that are common in the seasonal dry forests of Costa Rica's Pacific lowlands, two species that are generally common in Costa Rica but inexplicably rare at La Selva, one species that is near the southern limit of its geographic range and is much more common in countries to the north, and one species that is near the northern limit of its range and is more common in countries to the south. The remaining 31 uniques have no known or suspected area of high abundance.

Among the 51 uniques, 45 were known from additional collections outside of La Selva. Among the remaining six global uniques, five were morphospecies from taxonomically difficult genera, and global uniqueness cannot be stated with certainty. Only one species was certainly a global unique. This can be claimed with confidence because it is in a genus with a recent taxonomic revision.

Sixteen species in the La Selva inventory are known from queens or males only. Two species of *Crematogaster* are known from queens only. These are species known from other sites and have been associated with workers, but they are always extremely rare, and the queen morphology suggests that they are temporary or facultative social parasites. At La Selva, the queen of one species was found in the nest of another *Crematogaster* species, and an alate queen of the other species was found in a canopy fogging sample. Both these species make small carton nests, and there is no explanation why they have not been collected, other than low density. Two species of *Cylindromyrmex* are known from alate queens only. *Cylindromyrmex* are known to be rare in general, and nests are probably in narrow beetle galleries in solid wood. None of the collecting methods used so far is efficient at sampling insects inside of solid wood. One species of *Discothyrea* is known from two alate queens obtained in canopy fogging samples. The workers of this genus are extremely small. Workers of what may be the same species have been collected in Winkler samples from other Atlantic lowland sites, but not from La Selva.

The remaining 11 species are all army ant (Ecitoninae) males. Army ants have a parallel taxonomy for workers and males. Apart from a few common species that forage on the surface, workers of most species are rarely encountered. They are largely nocturnal, and many appear to be largely or entirely subterranean. In contrast, the males are large and conspicuous, and they are common at blacklights and in Malaise traps. In many cases males have never been associated with

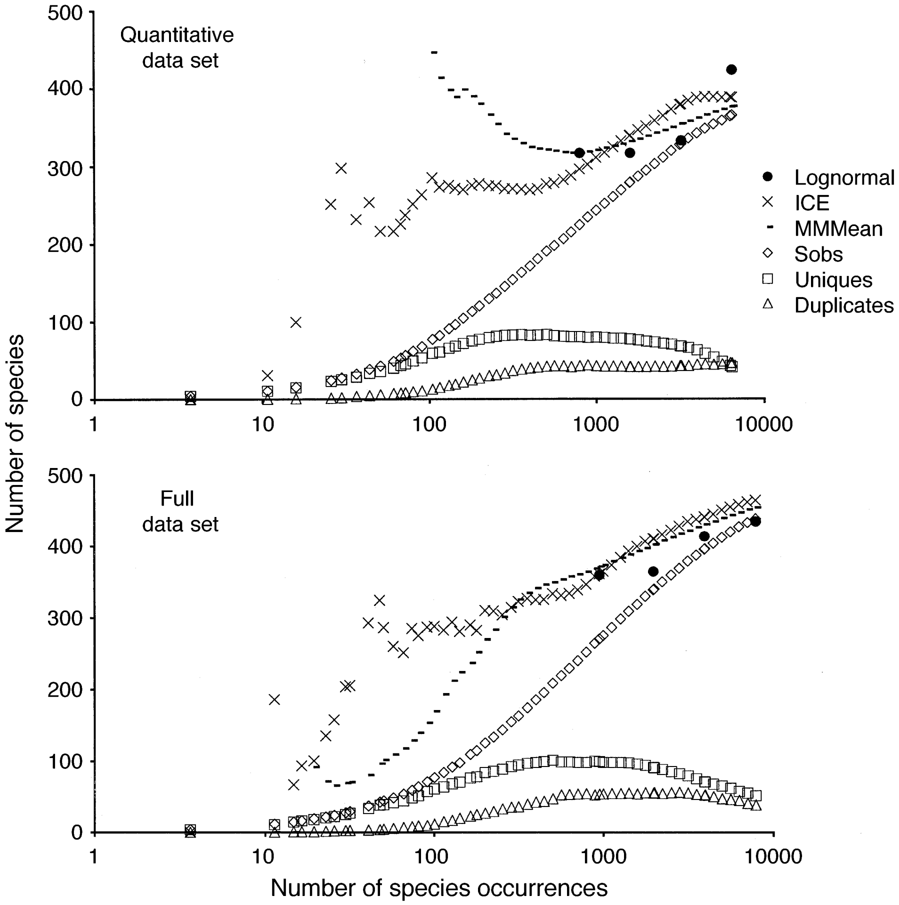
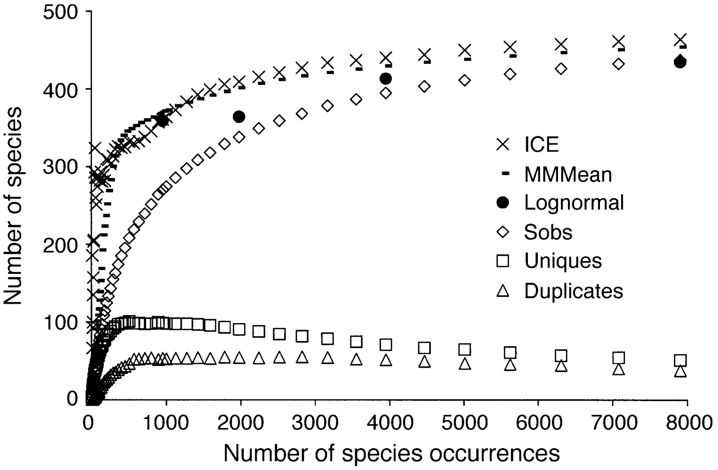


FIG. 5. Sample-based rarefaction curves and associated estimators for the ants of La Selva. The top figure is for the combined data set containing all data from quantitatively structured sampling; the bottom figure is for the full data set, pooling data from all methods, both quantitative and non-quantitative. Key definitions are: Lognormal, richness estimate based on the area of an estimated lognormal distribution; ICE, incidence-based coverage estimator; MMMean, asymptote of Michaelis-Menten curve estimated from the smoothed sample-based rarefaction curve; Sobs, observed species richness; Uniques, number of species each known from only one sample; Duplicates, number of species each known from exactly two samples. The abscissa is scaled logarithmically.

FIG. 6. Sample-based rarefaction curve and associated estimators for the combined data set, with the abscissa scaled arithmetically.



workers, because it is extremely rare to find them together. At La Selva, 11 species of army ant are known from males only.

DISCUSSION

The inventory

The 1500-ha La Selva Biological Station contains at least 437 resident ant species (known from workers at the site). This is one of the most thorough inventories of an entire ant community ever carried out. The observed abundance distribution is a truncated lognormal, with three revealed abundance classes below the mode. Richness estimates using a variety of methods are at most 6% above the observed richness. Uniques comprise only 12% of the observed species.

Similarly thorough inventories for temperate and subtropical sites show the expected lower species richness outside of the tropics. Talbot (1975) reported 87 species for the 518-ha E. S. George Reserve in Michigan, a result of 24 summers of field work. Van Pelt (1956) found 72 species (12.5% uniques) for the 882-ha Welaka Reserve in Florida. Deyrup and Trager (1986) found 102 species (9% uniques) for the 1771-ha Archbold Biological Station in Florida. Studies in the wet tropics have reported much higher species richness. Brühl et al. (1998) found 524 species in a 400-ha area at Poring Hot Springs in Kinabaloo National Park, Borneo. Verhaagh (1990, 1991) reported 520 species for a 1000-ha area in Panguana Reserve, Peru. These tropical studies do not provide relative abundances or other measures of inventory completeness, but they employed diverse sampling methods and involved a major collecting effort. The results for La Selva are of the same order of magnitude as these other tropical sites.

Richness estimation

Our results for individual collection methods reveal the inadequacy of single methods for insect inventories. Most show high proportions of rare species, species accumulation curves that do not show signs of approaching a plateau, uniques and duplicates curves that are rising or flat, and richness estimates that rise steeply and remain well above observed species richness. The exceptions were canopy fogging, which showed a close convergence of estimated and observed species richness, and Berlese samples for some months, which showed stable richness estimates.

Even for combinations of methods, the three richness estimators evaluated here showed a variety of behaviors when plotted together with sample-based rarefaction curves (Fig. 5), and none showed a stable plateau. After a region of highly fluctuating or declining richness at very low sample sizes, they all increased along with observed species richness as sample size increased. However, some showed intervals of temporary stability, and all tended to converge with observed species richness at large sample size. What causes regions of temporary stability in richness estimates is unknown and would benefit from further study. They may represent subcommunities that are efficiently sampled by the combination of methods used. If true, richness estimators might best be thought of as linked to a particular set of methods. Instead of assuming that our richness estimates are of the whole community at a site, we should expect them to be of the subcommunity available to the particular combination of methods we have used.

Coverage-based estimators are relatively new in the field of richness estimation, and are in a trial period. Sample-based rarefaction plots with corresponding coverage estimators have now appeared in numerous publications. In nearly all cases the estimates have shown variable behavior, stabilizing for some data sets and failing to stabilize in others. Anderson and Ashe (2000) sampled montane leaf litter beetles, McKamey (1999) sampled Homoptera at a site in Africa, and Fisher (1996, 1998, 1999*a, b*) sampled ant communities in Madagascar. All of these studies involved large sampling efforts, with diminishing returns revealed by species accumulation curves. In these studies most coverage-based estimators have steadily risen with sampling effort. Colwell and Coddington (1994) emphasized the untested nature of coverage-based estimators. Chazdon et al. (1998) evaluated a range of nonparametric estimators, using a tropical tree data set. They found ICE to be one of the best, but even ICE was inconsistent, stabilizing in some cases and not in others. These estimators are valuable additions to the ecologist's toolbox for richness estimation, and they are seeing increasing usage (e.g., Feener and Schupp 1998, Sayre et al. 2000), but continued evaluation of their performance is advised, they should not be used uncritically, and they should be viewed as yielding *minimum* estimates of true richness.

Some of the variation in the performance of these estimators perhaps can be explained by a consideration of what is being estimated. When we set out to measure species richness, we assume that the community we are sampling is like a jar of candy, from which we draw samples and attempt to estimate the number of kinds of candy. The hard fact is that there is no jar. We attempt to define a jar by the spatial, temporal, and methodological boundaries of our sampling program, but we must accept the fact that the jar leaks. The leaks are from various kinds of edge effects, which can be spatial, temporal, or methodological. Methodological edge effects are perhaps the most serious problem in arthropod inventory. Species vary in probability of capture in ways that are not necessarily related to their absolute abundance. This problem is less severe for studies of large or highly visible organisms such as trees and birds (e.g., Hubbell and Foster 1986, Terborgh et al. 1990, Clark et al. 1999, Pitman et al. 1999) but is particularly vexing for small organisms that must be extracted from the environment using a variety of traps, extraction methods, and search techniques.

It is unrealistic to expect species accumulation curves and richness estimates to stabilize completely, but combinations of methods and large enough sample sizes may sample a particular ‘‘jar’’ in ways that reduce the effects of edge species. If observed and estimated richness closely converge, this is evidence that a relatively thorough inventory of a spatially, temporally, and methodologically bounded community has been achieved.

Abundance distributions

A persistent question is what the abundance distribution of organisms would be if one could collect all individuals of all species in an area and count them. The abundance distribution reported here is lognormal. The lognormal distribution has been demonstrated numerous times and is often assumed (Preston 1948, May 1975, Sugihara 1980, Magurran 1988). However, Lambshead and Platt (1985) and Hughes (1986) argued that there was no a priori reason that species should have a lognormal distribution in nature. They claimed that reported lognormal distributions were mostly the result of combining multiple samples and thus could be explained by the central limit theorem alone (see also Preston [1981], Ugland and Gray [1982], and Wilson [1993] for further critiques of the lognormal). The data set reported here is certainly the result of multiple, combined samples from disparate methods and no single sample in this inventory comes even close to revealing a nonsingleton mode. What the abundance distribution would look like if one could record and identify every ant colony in La Selva’s 1500-ha remains unknowable. However, we argue that even though sampling artifacts certainly influence the shape of the observed distribution, this inventory still strongly supports the presence of an approximately lognormal distribution in nature.

The upper part of the true abundance distribution (the right hand tail) must be similar to what was observed here, because it contains the most abundant species that are routinely encountered in samples. They are the most conspicuous part of the whole community, and their abundances can be more accurately assessed, much like trees or birds. The distribution of rare species is the more difficult problem. Are species with few captures really less abundant, or are there features of their nesting and foraging behavior that make them harder to capture? If one could capture all the ants at La Selva, would there still be uniques? Would any species be represented by one colony (or a lone worker foraging across the border from a nest outside of La Selva)? Or would all species be represented by multiple colonies?

The specialized collecting by Longino makes it very unlikely that there is a large pool of rare, unseen ant species at La Selva. In fact, the combination of nonquantitative taxonomist collecting and quantitatively structured sampling may result in biases at opposite ends of the abundance distribution that tend to cancel each other out, resulting in a relatively accurate estimation of the true distribution. The specialized collecting of a taxonomist may reveal relative abundances of rare species, because a very broad spectrum of methods is used, and every sample of every rare species is kept. However, after a few collections of a species are obtained, subsequent encounters are ignored. Thus common species are underrepresented. In contrast, quantitatively structured sampling does a good job of estimating relative abundances of common species, but underrepresents rare species due to the limited scope and number of methods. These compensating tendencies may explain why the full data set more closely approximates a lognormal than the quantitative data set.

Rarity

Rarity in a sample may be caused by methodological edge effects. These are cases in which species are abundant at the study site but are undersampled due to the inadequacy of the sampling methods. It is easy to recognize edge species within one sampling technique when multiple techniques are used in an inventory (Longino and Colwell 1997). For example, specialized plant-ants that live only in myrmecophytes are very rarely obtained in canopy fogging samples, yet manual searching can make them as abundant as one might wish.

In this inventory, the combination of methods covered nearly every imaginable niche for ants in the leaf litter or above. The one portion of the habitat that was poorly sampled was the subsoil. Only one method, Berlese samples, extended into the soil, and the volume of material sampled was relatively small. A number of species were relatively abundant in the Berlese samples and nearly or entirely absent from all other collecting methods, including Winkler samples of litter lying directly on top of the soil. Subterranean species that were even moderately abundant would appear extremely rare in this survey. Six of the uniques in this inventory were species either manually excavated from soil or obtained in a Berlese sample. They are part of the undersampled soil fauna and might, in fact, be relatively abundant.

Rarity at a site may also be caused by mass effects (Shmida and Wilson 1985). Species may arrive at a site by dispersal from nearby source areas where they are more abundant. Since this survey was based entirely on workers, rarity cannot be caused by a ‘‘rain’’ of long-distance dispersers that immediately die. For each species, at least one colony has to be established at La Selva. However, source–sink population dynamics may nonetheless apply, with a continual influx of immigrant queens necessary to maintain a low density population. Fourteen of the uniques at La Selva are known to have high population densities elsewhere, ranging from synanthropic species with high density immediately adjacent to La Selva, to species at the limits of their ranges and with high densities hundreds or thousands of kilometers north or south. An unanswered question, and one relevant to conservation biology, is whether these low-density species rely on continual immigration for population persistence or are capable of persisting at a low density, with immigration insignificant or non existent.

Rabinowitz (1981) and Rabinowitz et al. (1986) examined rarity at larger spatial scales for British plants. Similar analyses of rarity have been done for Amazonian birds (Terborgh et al. 1990), Amazonian trees (Pitman et al. 1999), and benthic marine organisms (Carney 1997). All have found that species rare in small-scale ecological samples often have broad ranges and are frequently known to be abundant elsewhere. Species rare in ecological samples are often not rare to museum taxonomists. For insect taxonomists, rare species are often methodological edge species. The findings reported here are consistent with these observations. Only seven species out of 437 are currently known from only one collection in the world. For many of the La Selva ant species we can say little about their ranges outside of Costa Rica and even less about their abundances outside of La Selva. But it was nonetheless striking how many of the La Selva uniques were known from additional collections outside of La Selva.

Rarity will continue to be an important research topic in ecology, because of its obvious relevance to conservation biology. A challenging task is to understand patterns of abundance at larger spatial scales, extending to the entire geographic range of species. Finally, an important question to address is whether rare but widespread species are nonetheless relatively prone to extinction as the habitat becomes increasingly fragmented throughout their range.

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APPENDIX

Descriptions of methods used in the inventory of the ants of La Selva Biological Station, Costa Rica, are available in ESA's Electronic Data Archive: *Ecological Archives* E083-011-A1.

SUPPLEMENT

An inventory of species occurrences of ants at La Selva Biological Station in both viewable and downloadable form is available in ESA's Electronic Data Archive: *Ecological Archives* E083-011-S1.