

IMPROVING INVENTORY EFFICIENCY: A CASE STUDY OF LEAF-LITTER ANT DIVERSITY IN MADAGASCAR

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Abstract. For most invertebrates, ecologists lack efficient inventory methods for assessing geographic patterns of species richness, complementarity (distinctness), and areas of endemism. I evaluated the efficiency of quantitative inventory methods developed for leaf-litter ants in tropical rain forests in eastern Madagascar. The aim was to maximize the number of species captured per sampling effort in a systematic design subject to standard statistical analysis. I used species and complementarity accumulation curves to evaluate the efficiency of the inventory design based on all ant species sampled and based on four species-rich genera that could potentially act as surrogates for estimating total ant diversity. I evaluated: (1) efficiencies of pitfall and Winkler sifting methods to capture leaf-litter ant assemblages, (2) effects of sample size and spacing on completeness and ranking of species richness, (3) completeness of complementarity values, and (4) four species-rich ant genera that could potentially act as surrogates for estimating total ant richness. Inventories were conducted at 15 sites along elevational gradients at four localities. I collected 117 044 worker ants belonging to 381 species from pitfall and leaf-litter samples.

Species-accumulation curves showed decreased rates of species accrual with increased sampling but were still increasing slowly at the end of each transect. Leaf-litter samples had a greater rate of species accumulation than pitfall samples and were more cost effective. Rates of species accumulation were not improved by taking samples 10 or 15 m apart, compared with samples taken 5 m apart. Relative ranking of between-site patterns of species richness and complementarity stabilized before 25 samples and was not predicted to change with the addition of 50 more stations to each transect. The nonparametric incidence-based coverage estimator (ICE) of species richness was not useful for assessing sampling completeness because of a strong relationship between sample size and estimated species richness. Defining completeness based on the expected percentage increase in species from a doubling of sampling effort was more useful. To project the increase in species richness from increased sampling, I fit a nonasymptotic logarithmic model to the observed species accumulation curve.

Four potential surrogate genera (*Pheidole*, *Strumigenys*, *Tetramorium*, and *Hypoponera*, containing 68, 51, 51, and 50 species, respectively) were efficiently surveyed at each elevation; each was significantly correlated with the richness of species and complementarity values based on all other ant species. *Strumigenys* showed the highest correlation in both species richness and complementarity.

Key words: ants; complementarity; conservation; diversity; extrapolation; Madagascar; pitfall method; rain forest; species accumulation curve; species richness; surrogate taxa; Winkler method.

INTRODUCTION

Patterns of species richness, turnover, and endemism are three criteria for conservation assessment that require knowledge of species' spatial distributions (McNeely et al. 1990, Colwell and Coddington 1994). For most invertebrates, we lack both this information and the methods to obtain it. There are strong arguments to base conservation decisions on alternative criteria (such as threat or uniqueness of habitat or ecosystem), but there is often still the need to find out what

lives in threatened or unique habitats (e.g., Beissinger et al. 1996). In this paper, I assumed that discovering the spatial distribution of living organisms is important to the goals of ecology and conservation, and that rigorous, feasible, and efficient methods are needed, especially for species-rich taxa such as arthropods.

Inventories should contribute more than just species lists. They should provide information for measuring the completeness of the inventory at the site and the complementarity or turnover of species assemblages between sites. When inventory designs include replicable and quantitative sampling, goals of creating species lists are compatible with the goals of comparing species richness or complementarity between areas for use in monitoring or describing patterns of diversity. Therefore, effective inventory methods must be rapid,

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repeatable, and contain sufficient subsamples for statistical analysis of species richness and complementarity.

In this paper, I examine factors important for inventory design, in the context of an inventory of leaf-litter ants in tropical rain forest in eastern Madagascar (Fisher 1996, 1998; Fisher, *in press*). The objectives were to evaluate: (1) efficiencies of pitfall and Winkler sifting methods to capture leaf-litter ant assemblages, (2) effects of sample size and spacing on completeness and ranking of species richness, (3) completeness of complementarity values, and (4) four species-rich ant genera as surrogates for estimating total ant richness.

Designing inventories

Particular research objectives will determine the scope (taxonomic breadth and level of completeness) of an inventory. Development of a quantitative inventory design for a defined research objective and interpretation of results must take into account: (1) sampling biases due to particular collection or survey methods, habitat differences among sites, and seasonality, (2) effects of scale on species distributions and species turnover, (3) completeness of sampling for hyperdiverse groups such as insects, and (4) logistical and specimen processing effort (costs).

Results concerning patterns of species diversity will be limited by the collection or sampling methods used. Sampling methods do not collect all species equally (e.g., Remsen and Good 1996). Ants nest and forage in the soil, litter (leaf mold, rotten wood), rotting logs, dead branches, on the ground surface, and on vegetation. Nest site location and the proportion of time spent foraging in these habitats would determine the species-specific probability of capture for each type of inventory method employed. Ant species that are rare in pitfall and leaf-litter collections may be arboreal nesters that only occasionally forage on the forest floor and are abundant in canopy fogging samples (Longino and Colwell 1997). The decision to employ one or more techniques in a given habitat requires information on the number or kind of species obtained per unit of sampling effort. Species with a low probability of capture using one method may be more efficiently surveyed by switching methods, not by more intensive sampling with the same methods.

For most studies, especially for hyperdiverse taxa, inventory design for a particular method is not directed at collecting all species. Within the constraints of representativeness and statistical validity, inventory design should maximize species obtained per unit of sampling effort. General searching may provide a fast rate of species detection, but is often not suitable for statistical analysis. The efficiency of using one or more methods to create a species list, to estimate species richness, or to capture surrogate or indicator taxa, can be evaluated by the rate of species accrual for a given sampling effort (cost).

Species accumulation curves

For most taxa, sampled areas may be too small to include all microhabitats and all rare species in a region. Therefore, we expect an increase in the area sampled to produce a greater number of species. Likewise, we expect additional sampling methods to always collect more species. If increased sampling efforts or inclusion of additional methods always result in the collection of more species, how many subsamples should be taken using which method(s)? Species accumulation curves offer a potentially useful tool for comparing efficiencies of methods and alternative inventory designs; they may show which method or design is most efficient and give some indication of the completeness of the sampling (Colwell and Coddington 1994).

In this study, species accumulation curves are used to assess the completeness of the inventory with respect to sampling method and number of subsamples. The number of subsamples is evaluated with respect to estimated completeness of the inventory and the between-site ranking of species richness. Additional collecting methods or a survey in a different area or season at the same elevation would most certainly collect additional species. Species that are found to be rare when collected by one method, or at a particular site, or season, may be abundantly collected by another method or at a different site or season (Gaston 1994). Therefore, an accumulation curve is specific to an area, time, and the collecting techniques employed. If an observed or estimated species accumulation curve demonstrates a sufficient decrease in the rate of species accumulation, then the number of subsamples is arguably adequate for collecting the species in the area surveyed for the particular methods employed. Conversely, if the curves are rising rapidly, more intensive sampling may be necessary to accurately compare diversities between elevations. For hyperdiverse groups with large numbers of rare species, more intensive sampling (i.e., larger numbers of subsamples) typically never generates curves that completely flatten out and reach an asymptote. For these taxa, rates of species accumulation are expected to slowly decrease with more sampling. The entire area may need to be exhaustively surveyed before one can be sure that every species has been collected, but, in most cases, complete sampling is not possible and is often not the objective (see also Longino and Colwell 1997).

Sufficient sampling for a high level of completeness is the point, therefore, at which the accumulation curves show an adequate decrease in species accrual. The two problems are the frequent lack of existence of an asymptote for diverse taxa and the difficulty in quantifying "an adequate decrease in species accrual." I examine two alternative criteria for evaluating and defining the point of sufficient sampling (level of completeness): (1) sample until a certain percentage of the estimated number of species is obtained, and (2) sample

until additional sampling efforts achieve a defined percentage increase in the number of species sampled. The inventory objectives would determine the level of desired completeness. The increase in species richness with additional sampling would be set against the cost of sorting and identifying additional specimens and the importance of knowing the identity of the species at a site.

The aim of an inventory may be to compare the rankings of species-richness values between sites. In this case, sampling need only continue until the ranking between sites has stabilized. I use species accumulation curves to evaluate how many samples are necessary for comparisons of between-site ranking of species richness to compare the rate at which species are captured as a function of effort (cost) using different methods (pitfall and leaf litter) and different inventory designs (distance between subsamples and number of subsamples).

Defining subsample units

Species distribution patterns at a local scale can be spatially and temporally variable. At the scale of the area to be surveyed, local richness of an assemblage (i.e., subsample α -diversity) and complementarity between them will affect inventory design, notably the size of the subsample unit and the distance between subsamples. Spatial autocorrelation among samples is well-documented (Palmer and White 1994). Along a survey transect, adjacent points are more likely to share species than points further apart (Palmer 1995). If adjacent inventory units along a transect collect the same species, then a more efficient design would be to increase the distance between subsamples, but a greater distance must be set against the cost of missing species found between subsamples, and the greater difficulty and time spent placing transects. In this study, I use species accumulation curves to compare the species capture rates as a function of distance between subsamples.

Spacing of subsamples and the total number of subsamples taken are affected by the size of the sampling unit. Criteria to develop the size of the sampling unit must take into account the variance within subsamples (number of species and number of individuals per species) compared with the variance of species assemblages between subsamples, and set against the cost of taking and processing a few larger or many smaller subsamples. In this paper I do not directly analyze subsample unit size. I use field experience to provide what I think is a reasonable balance between variance and cost, based on the nature of the organism (ants). Based on this decision of subsample size, I evaluate the optimum distance between samples and the total number of samples.

Complementarity accumulation curves

Analysis of complementarity requires knowing the identity of species and is often compared between areas

where the species lists are assumed to be complete. For hyperdiverse taxa, however, complete sampling is often impossible. If increased sampling always collects more species, how many samples are necessary for comparisons of complementarity? If increased sampling collects rare species that are restricted to a particular site, then complementarity can be underestimated with limited sampling. Complementarity is initially overestimated, on the other hand, if additional sampling collects rare species that are also widespread and found at one or more other sites, or collects rare species at a site that are commonly found at one or more other sites. The problem is that we do not know the identity of the unsampled species or the direction of the bias.

Because it is impossible to estimate complementarity values from increased sampling of unknown species, I propose an analysis of the stability or direction of bias of the complementarity values from a successive pooling of subsamples. Completeness of sampling for comparing complementarity values can be evaluated by examining smoothed complementarity accumulation curves. Smoothed curves are produced by averaging complementarity values for successive pooling of subsamples chosen from each site with random reorderings of the samples.

Surrogate taxa

So far, cost-effective assessment has been directed at maximizing the efficiency of a particular inventory design or method for collecting all ant species. The same approach can be applied to effective and efficient use of surrogate taxa. This restricted set of taxa is surveyed based on their ability to represent relative differences among species richness and complementarity values at different sites. Identification of a surrogate taxon that is easier to survey and process compared with another target taxon would provide a powerful tool in diversity assessment (Hammond 1994, Kremen 1994, Oliver and Beattie 1996). Concordance between diversity patterns from unrelated taxa is not widely supported (Kareiva 1993, Prendergast et al. 1993). Unrelated taxa do not share evolutionary histories and may not share historical responses to ecological change and a priori one may expect no deterministic relationship between local species richness in unrelated groups (Goldstein 1997). A deterministic relationship may still be plausible, however, if all taxa responded to plant communities (Fisher 1997b).

I investigate concordance of species diversity patterns between related taxa, using each of four species-rich ant genera as a surrogate taxon for describing patterns of total ant species richness and complementarity. The efficiency of this approach is discussed based on analyses of species and complementarity accumulation curves.

STUDY SITES AND METHODS

Elevational gradients were surveyed at four localities in eastern Madagascar (Fig. 1): (1) Réserve Naturelle



FIG. 1. Map of Madagascar showing the four inventory localities, denoted by stars: the RNI d'Andohahela, the RNI d'Andringitra, the western Masoala Peninsula, and the RS d'Anjanaharibe-Sud.

Intégrale (RNI) d'Andohahela, 24°33'–34' S, 46°48'–49' E; elevational sites surveyed: 400, 800, and 1250 m. (2) RNI d'Andringitra, 22°12'–14' S, 46°58'–47°01' E; elevational sites surveyed: 785, 825, 1275, and 1680 m. (3) Western Masoala Peninsula, 15°34'–41' S, 49°57'–50°00' E; elevational sites surveyed: 25, 425, and 800 m. (4) Réserve Spéciale (RS) d'Anjanaharibe-Sud, 14°45' S, 49°26'–30' E; elevational sites surveyed: 875, 1200, 1280 (partial inventory of 26 samples), 1565, and 1985 m.

Field methods

At each of the 15 elevational sites, I used 50 pitfalls and 50 leaf-litter samples, in parallel lines 10 m apart, along a 250-m transect. Pitfall traps were placed and leaf-litter samples gathered every 5 m along the transect. Pitfall traps consisted of test tubes, 18 mm internal diameter by 150 mm long, partly filled to a depth of ~50 mm with soapy water and a 5% ethylene glycol solution, inserted into PVC sleeves, and buried with the rim flush with the soil surface. Traps were left in place for 4 d.

I extracted invertebrates from samples of leaf litter (leaf mold, rotten wood) using a modified form of the Winkler extractor (Fisher 1998; Fig. 1). The leaf-litter samples involved establishing fifty, 1-m² plots, separated by 5 m along the transect line. The leaf litter inside each plot was collected and sifted through a wire sieve of 1-cm grid size. Before sifting, the leaf-litter material was minced using a machete to disturb ant nests in small twigs and decayed logs. Approximately

2 L of sifted litter was taken from each 1-m² plot. At the low elevations (<800 m) litter was occasionally sparse and <2 L was sometimes taken. If the subsample plot contained a large rotten log or thick litter, 2 L was the maximum amount taken at each subsample site. This 2-L limit was imposed because of the size limit of the Winkler extractor. Those sites where 1 m² provided an excess of leaf litter, the plot was subsampled until 2 L of litter was obtained. Ants and other invertebrates were extracted from the sifted litter during a 48-h period in mini-Winkler sacks (for a detailed discussion of the mini-Winkler method, see Fisher 1998).

Sample processing

For every 50-station transect, which took from 5–7 field days to conduct, 1 mo on average was spent in the laboratory sorting, identifying, and curating specimens. After each locality was inventoried, ant specimens were sorted from the pitfall and leaf-litter samples. Saltwater extraction (Fisher, *in press*) was used to remove organic matter from inorganic matter in the leaf-litter samples before initial sorting began. Next, trained student assistants (parataxonomists, *sensu* Wheeler 1995) sorted and identified all ant specimens to the genus level. All ant specimens from a single genus and locality were then sorted to species by the author by examining specimens sequentially from each elevational site. This method allowed the greatest number of specimens within an elevational site to be identified while in alcohol and, thus, limited the cost in time of mounting specimens. A total of 6867 ants were mounted, pinned, and labeled during this identification phase. Data for specimens were managed using the database program Biota (Colwell 1996).

The cost of mounting specimens did not vary with collection method. The number of specimens mounted per sample was irrespective of whether a species was collected by pitfall or mini-Winkler methods. The number of individuals that had to be examined, however, was affected by the collection method. An efficient method collects a high number of species but a low number of individuals. To compare the relative cost of obtaining species from pitfall and leaf-litter samples, I compared the accumulation of species as a function of the number of individuals collected.

Data analysis

To assess survey completeness for the elevations sampled, I plotted species accumulation curves for each elevation. Species accumulation was plotted as a function of the number of leaf-litter and pitfall-trap samples taken. For most analyses, each leaf-litter sample was paired with the adjacent pitfall sample, collectively termed a station sample or paired sample. To compare efficiencies of pitfall and Winkler methods, pitfall and litter samples were combined, for a total of 100 samples per transect (50 of each type). Only records of ant workers were used in data analysis since the presence

TABLE 1. Number of worker individuals and species of ants collected in the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and on the western Masoala Peninsula in Madagascar.

Locality	Elevation (m)	Method	Individuals (no.)	Species (no.)
Andohahela	430	Pitfall	852	18
		Winkler	4032	46
		Both	4884	49
	800	Pitfall	1038	30
		Winkler	3679	63
		Both	4717	71
	1250	Pitfall	430	20
		Winkler	2254	53
		Both	2684	59
		All elevations		12 285
Andringitra	785	Pitfall	218	19
		Winkler	8582	76
		Both	8800	77
	825	Pitfall	255	19
		Winkler	6479	64
		Both	6734	67
	1275	Pitfall	238	15
		Winkler	5467	36
		Both	5705	41
	1680	Pitfall	127	8
		Winkler	6500	23
		Both	6627	23
		All elevations		27 866
Masoala	25	Pitfall	884	29
		Winkler	14 980	76
		Both	15 864	76
	425	Pitfall	569	33
		Winkler	21 827	98
		Both	22 396	101
	825	Pitfall	1661	20
		Winkler	12 386	106
		Both	14 047	109
		All elevations		52 307
Anjanaharibe	875	Pitfall	175	20
		Winkler	6661	92
		Both	6836	97
	1200	Pitfall	440	22
		Winkler	6033	85
		Both	6473	86
	1280	Pitfall	1741	14
		Winkler (26 samples)	1393	52
		Both (26 stations)	3134	53
	1565	Pitfall	293	12
		Winkler	6130	47
		Both	6423	50
	1985	Pitfall	48	5
		Winkler	1672	8
		Both	1720	9
	All elevations		24 586	180
All sites			117 044	381

Note: At each elevation, 50 pitfall and 50 mini-Winkler sacks were used (except at 1280 m in the RS d'Anjanaharibe-Sud where only 26 mini-Winklers were used). See (Fisher 1996, 1998; Fisher, *in press*) for species list and relative abundances.

of queens or males in samples does not necessarily signify the establishment of a colony of that species within the transect zone.

Since the form of the species accumulation curve can depend on the ordering of samples (Palmer 1990, Colwell and Coddington 1994), curves were smoothed. Sample order was randomized 100 times and means were computed for each succeeding station using the

program EstimateS (R. K. Colwell, *unpublished software, Version 5*).

Differences in processing time between the two sampling methods were compared by species accumulation curves plotted against the number of individuals sampled. The number of individuals sampled was calculated by multiplying the number of stations sampled by the average number of individuals per sample.

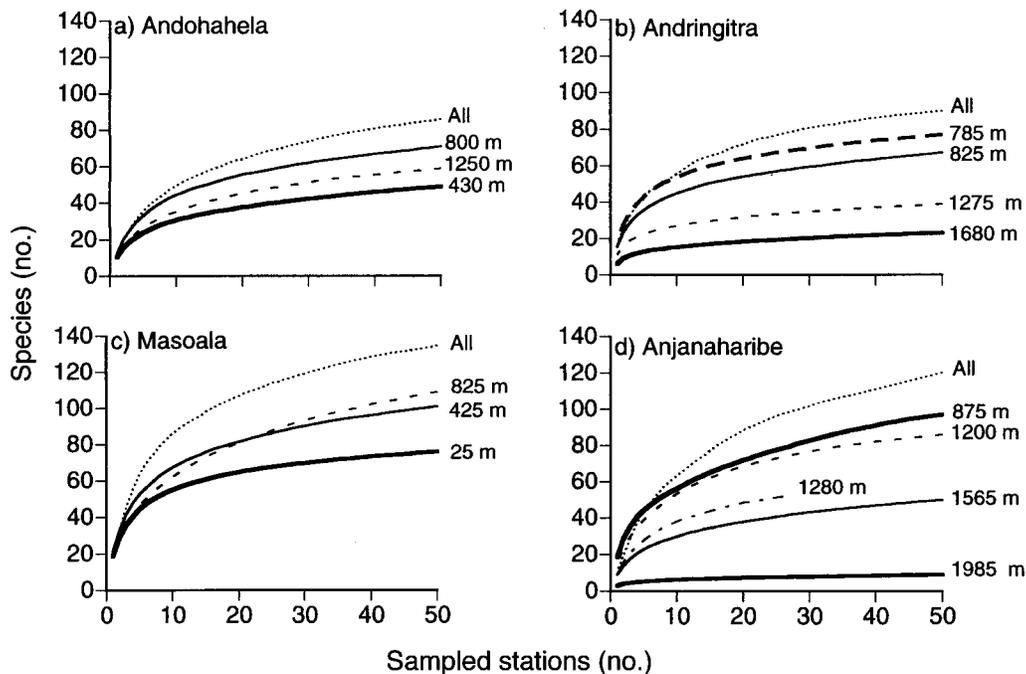


FIG. 2. Assessment of the leaf-litter and pitfall ant inventory technique for each elevation and for all elevations combined at (a) the RNI d'Andohahela, (b) the RNI d'Andringitra, (c) the western Masoala Peninsula, and (d) the RS d'Anjanaharibe-Sud. The species accumulation curve in each chart plots the observed number of species as a function of the number of stations sampled. Curves are plotted from the means of 100 randomizations of sample accumulation order. Only the first 50 pooled stations are shown for the "All" elevations curve within each locality.

As a potential criterion for evaluating completeness, I examined the protocol of sampling until a certain percentage of the estimated species was sampled. Colwell and Coddington (1994) review three types of methods for estimating species richness from quantitative sampling data: (1) extrapolation of species accumulation curves, (2) parametric methods, and (3) nonparametric methods (see also Chazdon et al. 1998). I used the nonparametric incidence-based coverage estimator (ICE) of Lee and Chao (1994) (see Chazdon et al. 1998; R. K. Colwell, *unpublished software, Version 5* for description of ICE). Chazdon et al. (1998) found this estimator to be the least sensitive (out of eight richness estimators) to sample size for woody plants in Costa Rica. ICE is based on the assumption that for data where some species are very common and others very rare, the useful information about the undiscovered species lies in the rarer discovered species. ICE estimates of species richness are based on the number of species found in 10 or fewer sampling units (Lee and Chao 1994, Chazdon et al. 1998). I plot species accumulation curves for ICE estimates of the total number of species in the local community from which the samples were taken for each succeeding station sampled.

An alternative criterion for assessing the level of completeness is to sample until additional sampling achieves a defined increase in the number of species sampled and is no longer cost effective. Depending on

the study objectives, the cost of sorting and identifying additional samples using the same method at one site could be compared with sampling at another site or switching methods. I use extrapolation of species accumulation curves to project the increase in species richness expected for a doubling of sampling effort (Lamas et al. 1991, Soberón and Llorente 1993).

Species accumulation curves based on randomization of sample accumulation order can be extrapolated by asymptotic or nonasymptotic functions (Palmer 1990, Lamas et al. 1991, Soberón and Llorente 1993, Colwell and Coddington 1994, Mawdsley 1996, Longino and Colwell 1997). The predicted species richness values are based on extrapolating from subsamples from an increasingly larger total area. Since sampled areas along the transect are too small (or too few) to include all microhabitats and all rare species at a given elevation in the region, we expect more area (or more samples) to contain more species. As pointed out by Lamas et al. (1991) and Colwell and Coddington (1994), statistical properties of the estimates are questionable due to non independence of the data and because a good fit between a model and the observed part of a species accumulation curve may not indicate the reliability of the extrapolated estimates (Keating and Quinn 1998). Nonetheless, this method may be the best alternative to estimate the increase in richness expected for a given level of additional sampling effort (Soberón and Llorente 1993, Colwell and Coddington 1994).

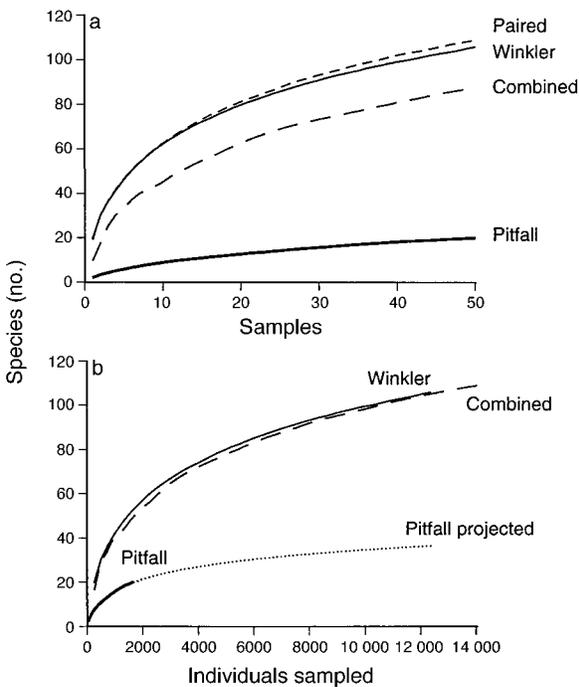


FIG. 3. Efficiency of pitfall and leaf-litter (mini-Winkler) methods assessed using species accumulation curves at the most species-rich site, 825 m on the western Masoala Peninsula. Species richness is plotted as a function of (a) the number of stations sampled and (b) the number of individuals collected. The number of individuals is calculated by multiplying the number of samples by the average number of worker individuals collected in each sample. "Paired" refers to the pairing of pitfall and Winkler collections to form a single sample (50 total). "Combined" refers to combining pitfall and Winkler collections as separate samples (100 total). Only the first 50 samples of the combined curve are shown. In (b), the pitfall curve is projected out to the number of individuals collected by mini-Winklers by fitting the logarithmic curve ($r^2 > 0.999$).

There is also the consideration as to the area limits of the species richness estimates predicted from extrapolation since the location of the additional samples are not known. For example, extrapolation of species richness based on 50 samples taken 5 m apart does not necessarily mean the 51st sample (the first extrapolated sample) is taken 5 m from the 50th along the same transect. Extrapolation estimates the number of species for a given sampling effort and assumes a uniform sampling process from an area where the pattern of relative abundance among species does not change. The predicted increase in species richness, therefore, is not an estimate of the total species richness for a specific area.

I fitted the observed species accumulation curves using the Soberón and Llorente (1993) logarithmic model: $S(t) = \ln(1 + zat)/z$, where t is the measure of sampling effort (samples or individuals), and z and a are curve-fitting parameters. Log models do not have an asymptote and are considered appropriate for spe-

cies-rich taxa (Soberón and Llorente 1993, Mawdsley 1996). That is, I use a nonasymptotic model because I assume the curves will never completely flatten, even with complete sampling. Using a nonasymptotic model, therefore, may result in a conservative estimate of the number of species predicted with increasing effort. I fitted the log model using the nonlinear least squares method of regression in JMP (SAS 1994).

Complementarity of ant assemblages at different elevations and localities was assessed using the proportion of all species in two sites or localities that occurred in only one or the other of them. Complementarity was calculated using the Marczewski-Steinhaus (M-S) distance index: $C_{MS} = (a + b - 2j)/(a + b - j)$ where j = number of species found at both elevations, a = number of species at elevation A, and b = number of species at elevation B (Pielou 1984, Colwell and Coddington 1994). M-S was chosen because of its simple and statistically valid approach to comparing two biotas (Pielou 1984, Colwell and Coddington 1994). Smoothed complementarity accumulation curves were produced by calculating mean complementarity values for each value of n between 1 and 50 chosen from each site, with 100 random reorderings of sample order (J. A. Umbanhowar, unpublished program). For example, for $n = 5$, five samples were chosen from each site and the complementary value calculated. This was repeated 99 times, and each time sample order was randomized. These 100 complementary values were used to compute the mean for $n = 5$.

To assess the spatial dependence and efficiency of the technique as a function of distance between samples, I investigated faunal similarity (Jaccard index) between samples along the 250-m transect and compared species accumulation curves with samples taken 5, 10, and 15 m apart. Jaccard index is the complement of M-S (i.e., $j/(a + b - j)$).

RESULTS

Leaf-litter and pitfall methods yielded 117 044 worker ants belonging to 30 genera and 381 species. Detailed discussions of the species collected, their relative abundance, faunal similarity, and species turnover are presented in Fisher (1996, 1998; Fisher, *in press*). The number of worker individuals and species collected by method at each elevation in the four localities is presented in Table 1.

Species accumulation curves of observed species showed decreased species accrual with increased sampling, but were still increasing slowly at the end of each transect (Fig. 2). The rate of accumulation was greatest for combined samples taken from all elevations (at least for the first 50 samples shown, Fig. 2). Across all localities together, midelevation sites (~ 800 m) usually had the highest rate of species accumulation and always had the greatest species richness.

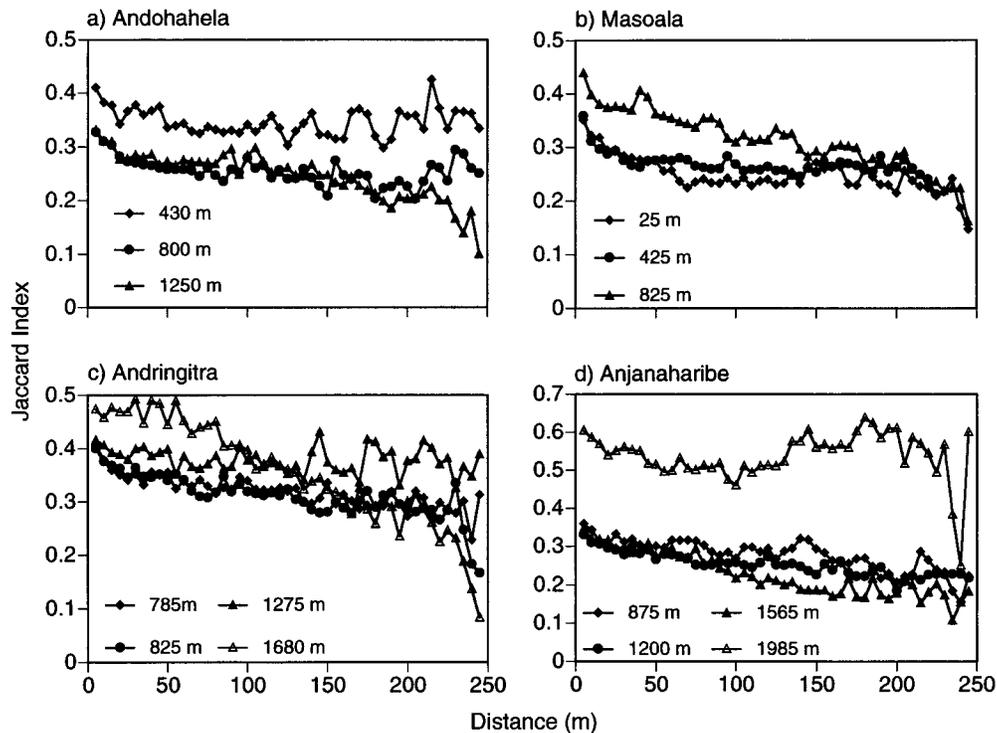


FIG. 4. Relationship between faunal similarity (Jaccard index) and distance (m) for the 50 samples collected along each 250-m transect: (a) in the RNI d'Andohahela; (b) on the western Masoala Peninsula; (c) in the RNI d'Andringitra; and (d) in the RS d'Anjanaharibe-Sud. The mean faunal similarity of each distance class is presented.

Efficiency of methods

Visual inspection of species accumulation curves showed that litter samples had a higher rate of species accumulation than pitfall samples and were more cost effective (Fig. 3). Comparisons of species accumulation curves as a function of the number of stations sampled (Fig. 3a) showed that leaf-litter samples had a higher rate of species accumulation than did pitfall samples and collected similar species. If cost of processing samples is calculated as the number of individuals collected per species, then it was still more efficient to collect leaf-litter samples than it was to collect pitfall samples (Fig. 3b). Pitfall collections and leaf-litter samples were redundant. Fewer individuals were collected per species in pitfalls, but the rate of collection of new species with increased sampling was much higher for leaf-litter samples.

Species richness of pitfall samples and leaf-litter samples at each elevation at the 15 sites was significantly correlated (Pearson's $r = 0.747$, $n = 15$, $P < 0.005$). The relative ranking of species richness between elevations within a locality, however, was not always the same. For example, on the western Masoala Peninsula, the 825-m site had the smallest number of species collected by pitfalls, but it had the greatest number of species collected by mini-Winkler and by both methods combined.

Spatial autocorrelation of subsamples along the 250-m transect showed that in most cases, nearby samples were more similar than the most distant samples (Fig. 4). In 13 of the 14 curves, there was an upwards inflection at scales < 30 m. Adjacent samples, however, were not very similar. For example, mean Jaccard index for all samples 5 m apart (excluding the species-poor 1985 m site) was 0.38 (1 SD = 0.117). For samples 30 m apart, the mean Jaccard index had declined to 0.33 (1 SD = 0.112). In RNI d'Andringitra, the 785- and 825-m sites were located 3 km apart and provide an estimate of species turnover at a larger scale than 250 m. The mean Jaccard index between all pairwise comparisons of samples at the 785 and 825 m sites was 0.25 (1 SD = 0.091), which is comparable to mean values for samples within the 250-m transect at 785 m (mean = 0.33, 1 SD = 0.090) and 825 m (mean = 0.33, 1 SD = 0.102). The rate of observed species accumulation or ICE-estimated species richness did not improve by taking samples 10 or 15 m apart compared with samples taken 5 m apart (Fig. 5).

How many samples are needed for between-site comparisons of species richness?

The relative ranking of between-site patterns of species richness for all localities stabilized after 22 stations

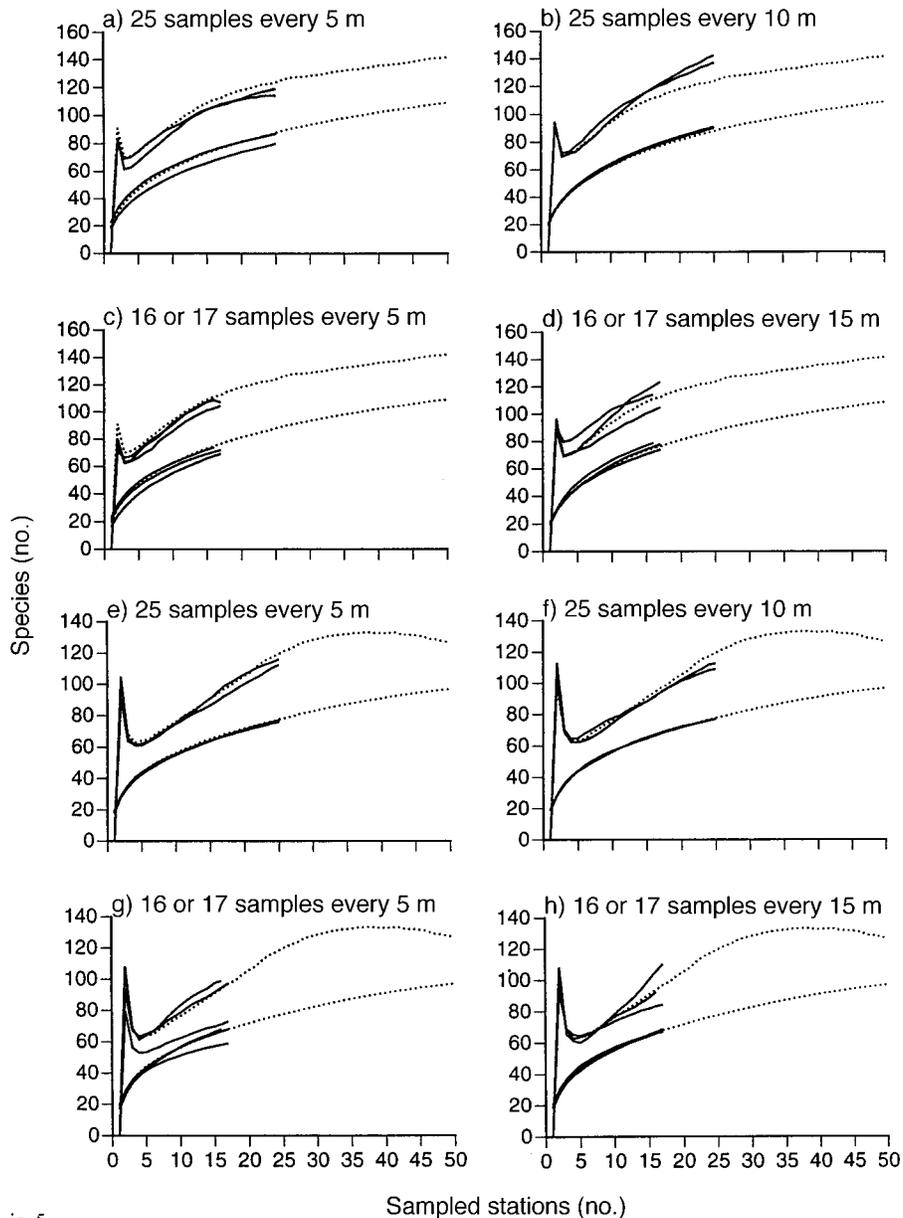


FIG. 5. Influence of distance between samples on efficiency, assessed using species accumulation curves for: (a–d) 825 m on the western Masoala Peninsula, and (e–h) 875 m in the RS d’Anjanaharibe-Sud. The lower set of curves in each chart plots the observed number of species as a function of the number of stations sampled. The upper set of curves displays the nonparametric incidence-based coverage estimator (ICE) estimated total species richness based on successively larger numbers of samples from the data set (Lee and Chao 1994). Dashed lines in each chart plot the ICE (upper line) or observed species richness (lower line) for all 50 stations sampled and are plotted from the means of 100 randomizations of sample accumulation order. The solid lines show samples taken 5, 10, or 15 m apart based on the actual sequence of samples taken in the field (without randomization). In charts (a) and (e), solid lines show results for the first 25 and last 25 stations sampled 5 m apart. Charts (b) and (f) show 25 stations sampled every 10 m. Charts (c) and (g) show 16 or 17 stations sampled every 5 m. Charts (d) and (h) show 16 or 17 stations sampled every 15 m. Note difference in scales.

(Fig. 2) and was not predicted to change with the addition of 50 more stations at each transect (see *Results: Assessing completeness*). The two sites with the greatest diversity (425 m, 98 total spp. and 825 m, 109 total spp.) on the Western Masoala Peninsula required the

greatest number of samples to reach a stable ranking. For the communities sampled in this study, I conclude that 25 samples is a sufficient level of completeness for comparison of species richness values. The total number of species collected from the first 25 samples

TABLE 2. The observed number of species for 25 and 50 samples, projected species richness at 100 samples, and nonparametric estimates for combined Winkler and pitfall methods in the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula in Madagascar.

Locality	Obs. at 25 samples	Obs. at 50 samples (% increase from 25 samples)	Extrap. at 100 samples (% increase from 50 samples)	ICE at 25 samples (% increase from 25 samples)	ICE at 50 samples (% increase from 50 samples)
Andohahela					
430	40.2	49 (18.0)	56.2 (12.8)	51.4 (21.8)	61.7 (20.5)
800	59.0	71 (16.9)	82.7 (14.1)	74.1 (20.3)	90.3 (21.4)
1250	48.8	59 (17.2)	69.4 (15.0)	66.7 (26.7)	71.9 (18.0)
Andringitra					
785	67.4	77 (12.5)	88.3 (12.8)	78.1 (13.8)	88.2 (12.7)
825	56.9	67 (15.1)	76.4 (12.3)	69.0 (17.5)	82.6 (18.7)
1275	34.4	41 (16.0)	43.9 (6.6)	42.7 (19.4)	53.4 (23.6)
1680	19.4	23 (15.6)	25.9 (11.2)	26.5 (26.5)	29.1 (21.0)
Masoala					
25	67.6	76 (11.0)	87.3 (12.9)	76.5 (11.6)	84.8 (10.3)
425	86.3	101 (14.6)	116.5 (13.3)	104.7 (17.6)	120.3 (16.0)
825	87.7	109 (19.5)	128.4 (15.1)	123.6 (29.0)	141.7 (23.1)
Anjanaharibe					
875	77.6	97 (20.0)	112.8 (14.0)	119.6 (35.1)	126.7 (23.5)
1200	73.3	86 (14.8)	102.5 (16.1)	91.0 (19.5)	97.4 (11.7)
1565	40.7	50 (18.7)	58.3 (14.2)	54.2 (25.0)	66.3 (24.6)
1985	7.6	9 (15.1)	10 (10.0)	8.9 (14.5)	11.3 (20.3)
Total species	324 (1–25) 333 (26–50)	374			

Notes: The projected species richness for an additional 50 stations (100 samples) is based on the extrapolation of observed species accumulation curves using the logarithmic model. The percentage increase in species richness from 25 to 50 samples or from 50 to 100 samples is given in parentheses. Incidence-based coverage estimator (ICE) estimated species richness is presented for 25 and 50 samples. The percentage increase in species richness for the ICE estimated species richness is given in parentheses. Numbers of species for each sample size represent the mean of 100 randomizations of sample pooling order. The total number of species is also presented for 25 samples (based on stations 1–25 and 26–50 at each elevation) and for all 50 samples at these elevations.

from each site with 50 samples (14 total sites) was 324, while 333 species were collected from samples 26–50 (Table 2). Based on these sample subsets, a doubling of sampling effort increased species richness only by 11–13%.

Assessing completeness

Nonparametric estimates of species richness and extrapolation were used to calculate an index of completeness. Based on incidence-based coverage estimator (ICE) estimates of the actual number of species that could be collected using these methods in each transect area, between 75 and 90% of the species were sampled after 50 stations at each elevation in the four localities (Table 2; ICE accumulation curves for two elevations are shown in Fig. 5; see Fisher 1996, 1998; Fisher, *in press* for curves of additional nonparametric estimates). For all elevations combined within each locality, between 84 and 87% of the ICE-estimated species richness was sampled. The problem with using this approach as an index of completeness is that ICE and other nonparametric estimated values (see Fisher 1996, 1998; Fisher, *in press*) were often sensitive to sample size (e.g., Fig. 5a). Therefore, the percentage sampled of the estimated species based on nonparametric methods was not a reliable indicator of completeness. For

example, at 825 m on the Masoala Peninsula (Fig. 5a), the ICE and observed curves between 10 and 50 stations are parallel. ICE estimates predict comparable levels of completeness within this range of samples (10–50) even though species accumulation was still rising rapidly after 10 stations (Fig. 5a). Sensitivity to sample size prevents using this method for assessing the level of completeness of these inventories.

The relationship between sample size and estimated species richness resulted in part because the number of rare species did not necessarily decrease with increasing sample size. ICE belongs to a class of nonparametric estimators of species richness that are based on the number of rare species found in samples (e.g., species found in 10 or fewer sampling units for ICE) and assumes that the number of rare species decreases with increased sampling (Colwell and Coddington 1994, Chazdon et al. 1998). The estimated species richness will approach the observed when the number of rare species declines to an estimate-specific level. In this study, the number of rare species of ants was generally constant with increased sampling (Fig. 6). Singletons (species that occurred in only one station) and doubletons (species that occurred in only two stations) did not necessarily decline with increased sampling.

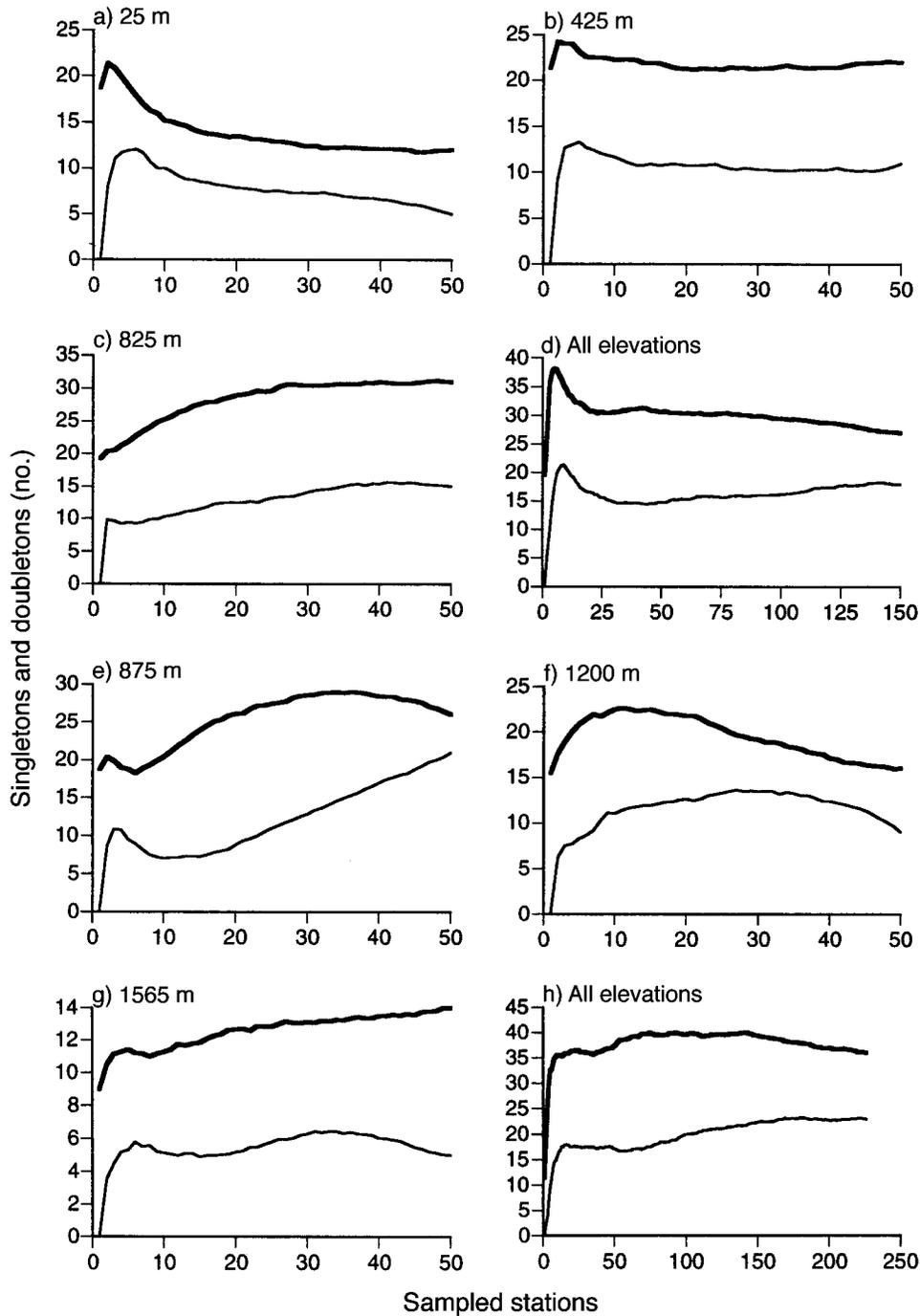


FIG. 6. Accumulation of singletons (upper thick line; species that occurred in only one station) and doubletons (lower line; species that occurred in only two stations) for: (a–d) the western Masoala Peninsula, and (e–h) select elevations in the RS d'Anjanaharibe-Sud. Curves are plotted from the means of 100 randomizations of sample accumulation order. Note difference in scales.

An alternative approach to evaluating completeness of an inventory is to estimate the effect of additional sampling. Based on the extrapolation of observed curves using the logarithmic model, a doubling of sampling effort (an additional 50 stations) would

achieve a 7–16% gain in species richness at sites sampled by an initial 50 stations (Table 2; Fig. 7). Relative between-site and between-locality patterns of species richness would not change if an additional 50 stations had been collected at each elevation (Table 2). If in-

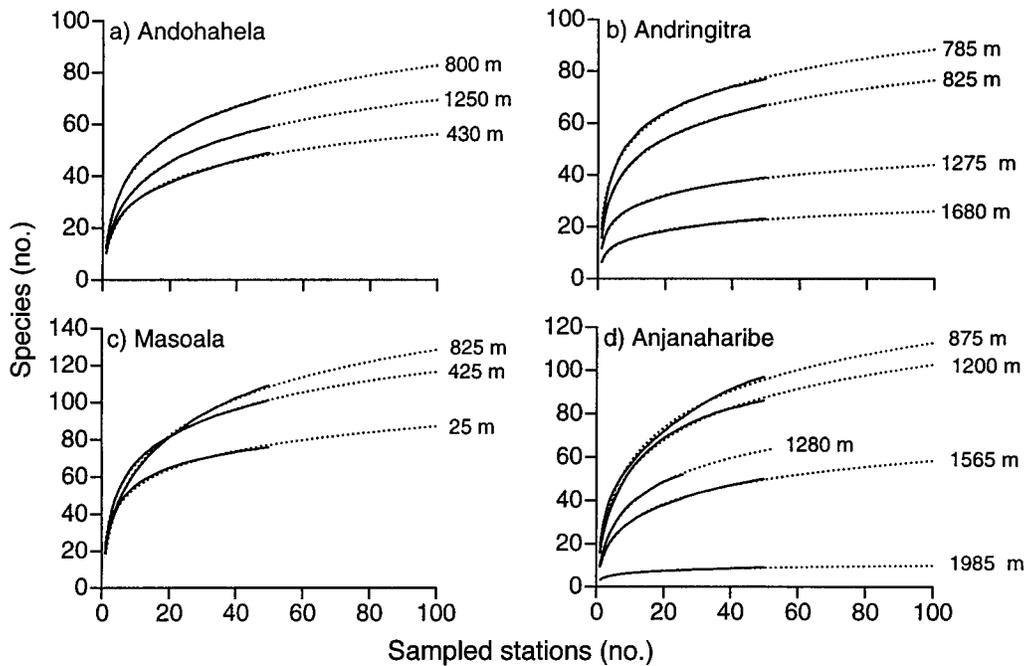


FIG. 7. Projection of species accumulation curves for each elevation at (a) the RNI d'Andohahela, (b) the RNI d'Andringitra, (c) the western Masoala Peninsula, and (d) the RS d'Anjanaharibe-Sud. For each elevation, the solid line corresponds to the observed species richness for the 50 stations sampled. The dashed line is the logarithmic function fitted to the observed species curve by the standard least squares method. The logarithmic curves predict the number of species expected from a doubling of sampling effort (100 stations) ($r^2 > 0.999$). Note difference in scales.

inventories at all altitudes within a locality are combined, 11–13% more species are predicted from a doubling of sampling effort at each locality. At 25 samples, the extrapolation method index of completeness for each site was between 11–20% for a doubling of sampling size (Table 2).

Complementarity

Additional species from 100 station transects did not affect the between-site ranking of species richness; however, they could affect the relative between-site pattern of complementarity. The problem is that the identities of the unsampled species are not known.

For all localities, relative rankings of between-site complementarity values stabilized after 5 stations for within-locality comparisons and after 20 stations for between-locality comparisons (Fig. 8). The relative magnitude of between-site complementarity generally stabilized after about 25 samples. With increased sampling, however, a few comparisons (see curves in Fig. 8a, c, e) show an almost linear decrease in complementarity. The analysis of complementarity accumulation curves suggests that at the scale of this inventory, the rate of accumulation of rare and shared species is relatively constant and will change little with additional collecting after 25 stations. Therefore, 25 subsamples was complete enough for comparisons of both species richness and complementarity between sites.

Surrogate taxa

The four richest ant genera, *Pheidole* (68 spp.), *Tetramorium* (51 spp.), *Strumigenys* (51 spp.), and *Hyponoponera* (50 spp.) accounted for 58% of the 381 species collected in leaf litter and pitfall samples (Table 3). Species accumulation curves of each genus demonstrated that the leaf-litter inventory technique was very effective at sampling each of these genera. For example, on the western Masoala Peninsula (Fig. 9), most of the species accumulation curves for these four genera showed a slow rate of species accumulation after 25 samples were pooled. Doubling sampling effort produced a similar increase in species richness for each genus as for all species. For example, *Strumigenys*, showed a predicted 11–15% increase in species richness for 100 samples based on the logarithmic model ($r^2 > 0.99$).

The species richness of each of these genera was highly correlated with species richness of all other ant species, with *Strumigenys* having the highest correlation (Table 4). Little improvement in the correlation was attained by combining two of the genera (Table 4). Compared with results from all ant species, sampling all species in a single genus produced similar relative ranking of species richness between elevations within a locality and total species richness between localities.

Complementarity values between elevations within

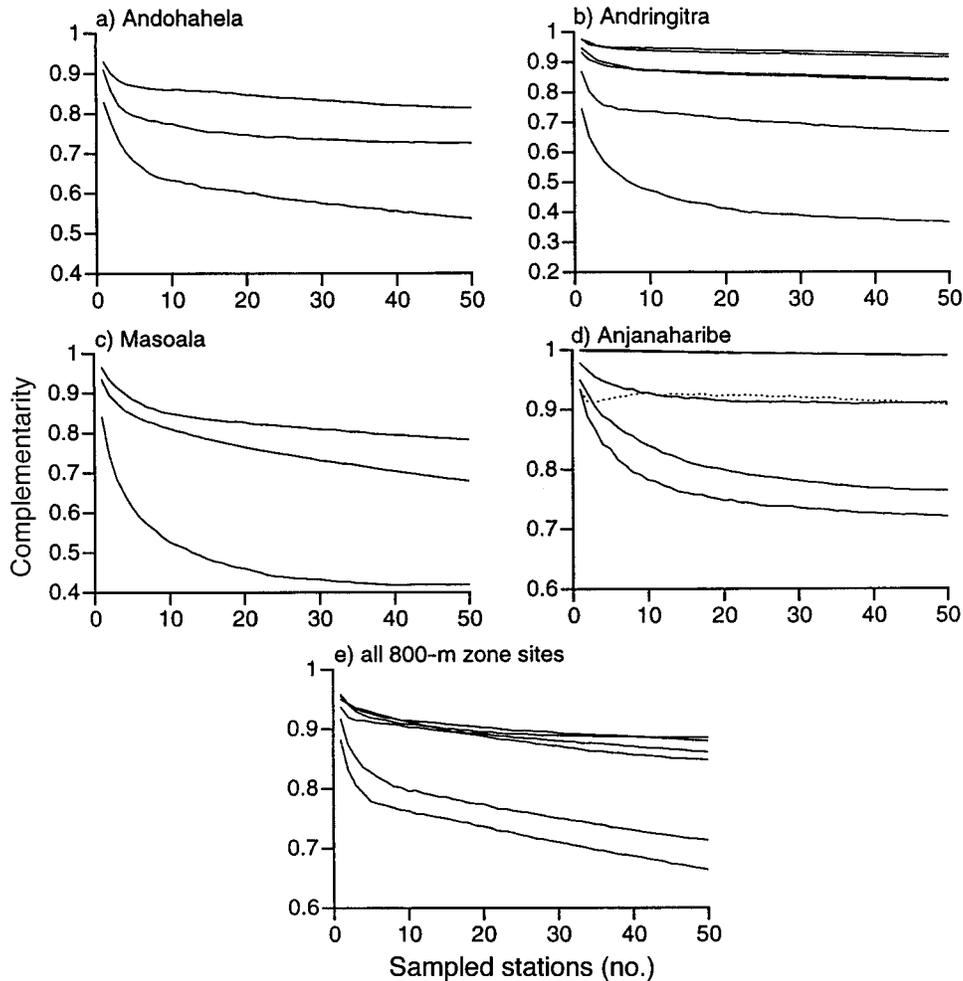


FIG. 8. Complementarity (M-S) accumulation curves for each between-site comparison within (a) the RNI d'Andohahela, (b) the RNI d'Andringitra, (c) the RS d'Anjanaharibe-Sud, and (d) the western Masoala Peninsula (dashed line is used to differentiate curves); and (e) between all 800-m zone sites in the four localities. For plot (e), data from the 785- and 825-m transects from the RNI d'Andringitra were combined. Each curve is plotted from the mean complementarity value of 100 randomizations of sample accumulation order. Note difference in scales.

a locality for each of the species-rich genera were significantly correlated to values calculated using all other species ($n = 15$; *Strumigenys*: Pearson $r = 0.895$, $P < 0.0001$; *Pheidole*: $r = 0.882$, $P < 0.0001$; *Tetramorium*: $r = 0.840$, $P < 0.0001$; *Hypoponera*: $r = 0.630$, $P < 0.01$). The relative ranking of complementarity values between elevations based on one of the four dominant genera was comparable to comparisons based on all other species, with a few discrepancies (e.g., *Hypoponera* and *Pheidole* at the RNI d'Andohahela; Table 5). The absolute value of complementarity for a given pair of sites was also comparable to analyses with all species, but with a few exceptions (e.g., *Strumigenys* vs. *Hypoponera* for 430/800 m Andohahela; Table 5). Each of the four genera also showed similar patterns of complementarity between localities compared to all other species (Table 6).

DISCUSSION

Invertebrates, the bulk of terrestrial diversity, are often excluded from inventories of natural areas despite their importance in ecosystem functioning because, it is argued, they (1) are protected by umbrella species; (2) are too numerous to survey; (3) lack appropriate methods for rapid assessment; and (4) are in such a state of taxonomic chaos that identification tools cannot be developed for use in biodiversity assessment. This study is part of a growing literature that clearly shows that these first three assumptions are false, and that effective and practical methods to inventory hyperdiverse groups like ants are possible and that the results can make important contributions towards understanding landscape-level patterns of invertebrate biodiversity (Majer 1983, Hammond 1990, Pearson and Cassola 1992, Olson 1994, Fisher 1996, Ingham and Samways

TABLE 3. Number of species of the four richest ant genera collected in the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula in Madagascar.

Locality	Elevation	<i>Pheidole</i>	<i>Tetramorium</i>	<i>Strumigenys</i>	<i>Hypoponera</i>
Andohahela	430	16	6	5	2
	800	13	11	7	9
	1250	10	7	6	7
	All elevations	22	14	10	13
Andringitra	785	13	12	10	11
	825	10	13	6	8
	1275	6	5	7	7
	1680	4	4	4	4
	All elevations	18	17	18	13
Masoala	25	14	13	10	9
	425	14	18	13	11
	825	16	13	14	11
	All elevations	28	24	18	19
Anjanaharibe	875	16	10	11	14
	1200	14	12	10	10
	1280	9	10	7	8
	1565	6	7	8	7
	1985	1	1	1	1
	All elevations	29	21	24	28

1996, Oliver and Beattie 1996, Olson and Andriamiana-dana 1996, Fisher 1998; Fisher, *in press*). The challenge remains for systematists to develop products that address the taxonomic tools needed in conservation.

Species and complementarity accumulation curves were used to evaluate the efficiency of inventory methods developed for leaf-litter ants in tropical rain forest in eastern Madagascar. The major findings were: (1) mini-Winkler methods were more efficient than pitfall traps; (2) 5 m was an appropriate distance between samples; (3) 25 samples were sufficient for comparing species richness and complementarity values between sites; (4) the percentage increase in species richness from a doubling of sampling effort served as an index of completeness; and (5) species-rich genera such as *Strumigenys* function as a surrogate taxon for all leaf-litter ant diversity.

The efficiencies of pitfall and mini-Winkler sifting methods to collect ants foraging or nesting in the leaf litter were not equal (Fig. 3). It was more cost effective to use mini-Winklers alone in the rain forest of eastern Madagascar. Pitfall traps were redundant; they collected fewer individuals of the same species sampled by litter sifting. In Costa Rica, Olson (1991) found that the same type of pitfall traps used in this study collected a greater proportion of larger, generalist scavenger species than did litter sifting. In the wet rain forest in eastern Madagascar, fewer large, generalist or scavenger species may exist. For example, the Neotropical ponerine genera, *Ectatomma*, *Odontomachus*, *Paraponera*, *Pachycondyla*, which include large generalist species that forage on the forest floor, are either absent or smaller in body size in Madagascar. Pitfall traps, however, may be an efficient method for collecting species in dry forest and spiny bush habitats in Madagascar. In a dry forest site in Madagascar, where there were areas of open bare ground, pitfall traps collected

a greater proportion of species and individuals than in eastern rain forests (Fisher and Razafimandimby 1997). Studies in dry forest sites are needed to evaluate whether it is cost effective to include pitfalls in these habitats.

Species richness based on pitfall trap samples, however, was positively correlated to richness from leaf litter samples. In the eastern rain forest of Madagascar, pitfall samples as indicators of ant diversity should be used with caution. Pitfall-based species richness did not always reflect the same relative ranking or magnitude of difference between elevations (e.g., Masoala, Table 1).

Spatial dependence among subsamples suggests that capture rates might be improved by increasing the distance between subsamples (Fig. 4). Samples 30 m apart were on average 13% less similar than samples 5 m apart. The rate new species were captured, however, could not be generally improved by increasing the spacing (distance apart) of subsamples from 5 to 10 or 15 m (Fig. 5). Because of the small size of the subsample and the low similarity between samples 5 m apart, tests for improvements in the rate of species accrual might require much greater distances between samples. For the habitats and scale of this survey, a distance of 5 m between samples can be recommended for inventory design. Sample distances >5 m are also supported by the data and may be appropriate for inventories at a larger scale, but may require greater effort in establishing the transect in the field.

For each elevation sampled, species accumulation curves showed decreased rates of new species accrual, and thus reflect the actual number of species present that could be captured using pitfall and Winkler methods in the area sampled along the 250-m transect (Fig. 2). Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely collect additional species. For example,

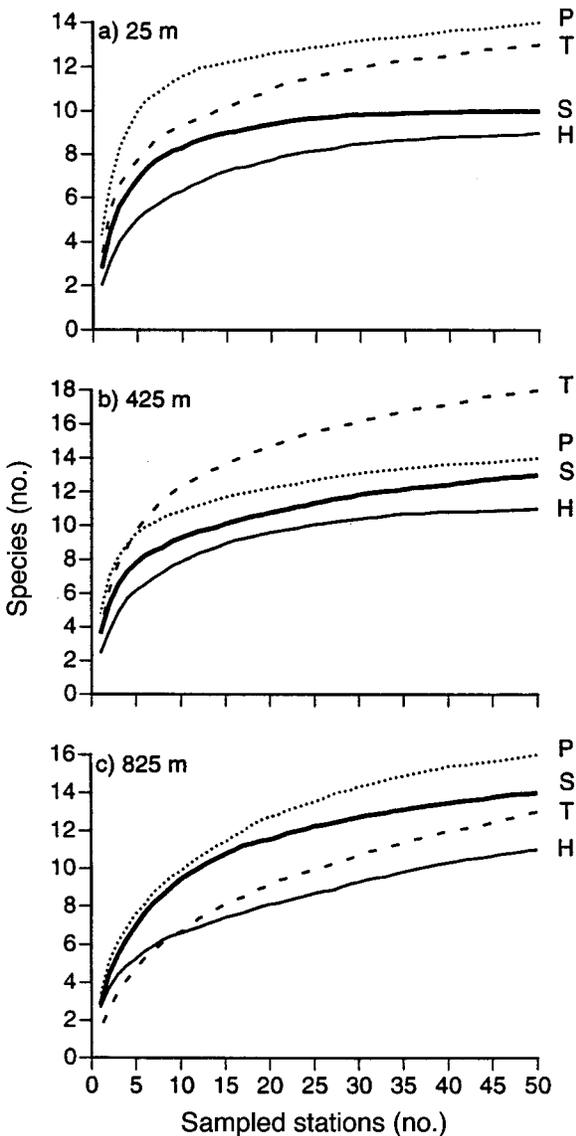


FIG. 9. Species accumulation curves for the four richest genera: *Strumigenys* (S), *Hypoponera* (H), *Tetramorium* (T), and *Pheidole* (P). Data from (a) 25 m, (b) 425 m and (c) 825 m on the western Masoala Peninsula.

general collecting methods conducted adjacent to each transect at each elevation site, which included searching in arboreal microhabitats, revealed an additional 90 species and 6 genera (Fisher 1996, 1998; Fisher, *in press*).

The examination of smoothed species and complementarity accumulation curves proved a useful technique for examining the effect of sample size on species richness and complementarity (Figs. 2, 8). Comparing the relative ranking of richness in species accumulation curves makes the important assumption that the underlying order of community structure is similar among sites. A more robust comparison would require repli-

cate transects at each site, greatly increasing the efforts in this study.

In this study, 25 samples were sufficient for comparing the relative ranking of complementarity and species richness between sites and localities. Additional collecting beyond 25 samples provided important taxonomic information, but did not change the ranking of sites based on complementarity or species richness. Different criteria for sufficient sampling would apply for evaluating inventories, depending on the importance of knowing the identity of species at a site and the general aims of the project.

I evaluated two methods for defining the level of completeness for a quantitative inventory. First, I tried defining completeness as the percentage collected of the ICE-estimated species richness at the site. The precision of an ICE (or other estimator) estimated species richness would be difficult to determine since a site would need to be exhaustively surveyed to produce a complete species list. More important than precision, however, is a strong and consistent (in magnitude) relationship to true species richness that is not strongly affected by sample size. The ICE nonparametric estimate of species richness was not practical as an index of completeness because of the strong relationship between sample size and estimated species richness (Fig. 5). A relationship between sample size and the first-order jackknife nonparametric estimate of species richness has also been documented (Fisher 1996, 1998; Fisher, *in press*). These estimators may have performed poorly because the number of rare species did not decrease with increased sampling (Fig. 6). Even over a larger scale, rare ants do not always decrease with increased sampling. After collecting 500 Winkler samples from one square hectare of abandoned cocoa plantation in eastern Brazil, the number of doubletons did not decrease, even though singletons did decrease to 10 species from a maximum of 20 (J. Delabie, *unpublished data*). An alternative approach to estimating species richness that is not based on the assumption that rare species (e.g., singletons and doubletons) decrease in number with increased sampling may show increased performance as an index of completeness for hyperdiverse taxa.

Second, I tried defining the level of completeness of

TABLE 4. Pearson correlation values of species richness of the four richest ant genera compared to the richness of all other species found at each elevational site. The two most highly correlated two-genus combinations are also given ($n = 15$; $P < 0.0005$).

Genus	Pearson r
<i>Strumigenys</i>	0.915
<i>Hypoponera</i>	0.852
<i>Tetramorium</i>	0.836
<i>Pheidole</i>	0.810
<i>Strumigenys</i> + <i>Pheidole</i>	0.928
<i>Hypoponera</i> + <i>Pheidole</i>	0.928

TABLE 5. Complementarity values for between-elevation comparisons within each locality, using each of the four most species-rich genera, for all species minus each dominant genus, and for all species. Higher values represent greater distinctness.

a) The RNI d'Andohahela			
Taxa	430 m/800 m	800 m/1250 m	430 m/1250 m
<i>Strumigenys</i>	0.286	0.700	0.778
All – <i>Strumigenys</i>	0.560	0.728	0.817
<i>Hypoponera</i>	0.900	0.667	1.000
All – <i>Hypoponera</i>	0.486	0.733	0.793
<i>Tetramorium</i>	0.583	0.615	0.917
All – <i>Tetramorium</i>	0.529	0.742	0.797
<i>Pheidole</i>	0.474	0.722	0.700
All – <i>Pheidole</i>	0.556	0.726	0.845
All species	0.536	0.725	0.813

b) The RNI d'Andringitra						
Taxa	785 m/825 m	825 m/1275 m	1275 m/1680 m	785 m/1275 m	825 m/1680 m	785 m/1680 m
<i>Strumigenys</i>	0.333	0.800	0.714	0.692	0.867	0.933
All – <i>Strumigenys</i>	0.338	0.838	0.622	0.835	0.904	0.911
<i>Hypoponera</i>	0.273	0.636	0.429	0.615	0.800	0.750
All – <i>Hypoponera</i>	0.355	0.863	0.725	0.874	0.932	0.951
<i>Tetramorium</i>	0.400	0.818	0.900	0.867	1.000	1.000
All – <i>Tetramorium</i>	0.3347	0.842	0.675	0.862	0.926	0.923
<i>Pheidole</i>	0.231	0.929	0.714	0.941	0.923	0.938
All – <i>Pheidole</i>	0.365	0.818	0.675	0.819	0.914	0.922
All species	0.345	0.835	0.681	0.840	0.916	0.925

c) The western Masoala Peninsula			
Taxa	25 m/425 m	425 m/825 m	25 m/825 m
<i>Strumigenys</i>	0.231	0.500	0.588
All – <i>Strumigenys</i>	0.444	0.702	0.807
<i>Hypoponera</i>	0.333	0.778	0.889
All – <i>Hypoponera</i>	0.430	0.667	0.769
<i>Tetramorium</i>	0.450	0.652	0.762
All – <i>Tetramorium</i>	0.413	0.684	0.786
<i>Pheidole</i>	0.250	0.846	0.889
All – <i>Pheidole</i>	0.448	0.647	0.760
All species	0.420	0.679	0.783

d) The RS d'Anjanaharibe-Sud						
Taxa	875 m/1200 m	1200 m/1565 m	1565 m/1985 m	875 m/1565 m	1200 m/1985 m	875 m/1985 m
<i>Strumigenys</i>	0.688	0.875	0.944	1.000	1.000	1.000
All – <i>Strumigenys</i>	0.724	0.745	0.913	0.906	0.988	0.989
<i>Hypoponera</i>	0.957	0.692	1.000	1.000	1.000	1.000
All – <i>Hypoponera</i>	0.675	0.773	0.891	0.895	0.988	0.989
<i>Tetramorium</i>	0.625	0.643	1.000	0.692	1.000	1.000
All – <i>Tetramorium</i>	0.732	0.781	0.891	0.934	0.988	0.989
<i>Pheidole</i>	0.636	0.947	0.833	0.952	1.000	1.000
All – <i>Pheidole</i>	0.736	0.725	0.917	0.904	0.987	0.989
All species	0.720	0.764	0.907	0.911	0.989	0.990

Note: All – [genus] = all species in both elevations minus the genus in question.

an inventory as the percentage increase in species richness for a doubling of sampling effort. Combined with extrapolation, this technique provides a general approach for relating sampling to completeness. For example, inventories can be standardized to sample until additional collection efforts achieve a defined increase

in the number of species sampled based on the collection methods employed. Extrapolation also serves to define the effort required for the collection of additional species and for evaluating the effect of additional sampling on between-site patterns of species richness.

The four richest genera collected, *Strumigenys*, *Hy-*

TABLE 6. Complementarity values for between-locality comparisons using each of the four most species-rich genera, for all species minus each dominant genus, and for all species. Higher values represent greater distinctness.

Taxa	Ando/Andri	Mas/Anj	Ando/Mas	Ando/Anj	Andri/Mas	Andri/Anj
<i>Strumigenys</i>	0.682	0.727	0.833	0.903	0.879	0.925
All – <i>Strumigenys</i>	0.641	0.718	0.850	0.842	0.871	0.865
<i>Hypoponera</i>	0.471	0.763	0.968	0.861	0.968	0.861
All – <i>Hypoponera</i>	0.667	0.712	0.829	0.848	0.858	0.876
<i>Tetramorium</i>	0.760	0.714	0.848	0.871	0.829	0.914
All – <i>Tetramorium</i>	0.627	0.720	0.846	0.847	0.879	0.868
<i>Pheidole</i>	0.710	0.674	0.936	0.891	0.955	0.956
All – <i>Pheidole</i>	0.632	0.728	0.825	0.841	0.854	0.857
All species	0.647	0.720	0.846	0.850	0.872	0.874

Note: All – [genus] = all species in both localities minus the genus in question; Ando = the RNI d'Andohahela, Andri = the RNI d'Andringitra, Mas = the eastern Masoala Peninsula, and Anj = the RS d'Anjanaharibe-Sud.

ponera, *Tetramorium*, and *Pheidole*, were effectively surveyed at each elevation (Table 3, Fig. 9). Each was significantly correlated with species richness and complementarity values based on all other ant species (Tables 4, 5). *Strumigenys* was most correlated with species richness and complementarity. These results support the use of *Strumigenys* as a surrogate taxon in eastern Madagascar when collected using these methods. Its use as an indicator taxon by nonspecialists would be aided by the development of user-friendly identification keys. Like most of the ant fauna of Madagascar, unfortunately, the taxonomy is incompletely known: of the 51 species of *Strumigenys* collected in the four localities, 50 were undescribed (Fisher 1997a).

In summary, the evaluation of the efficacy of the transect methods suggests that even though increased sampling would collect new species, the results on relative species richness and complementarity values between sites and localities would change little after 22 samples. Therefore, 25 samples is suggested as sufficient in these communities. At 25 samples, a doubling of sampling effort would result in an 11–20% increase in species richness.

To better understand the effect of scale and habitat on these results, a variety of real and simulated data sets should be explored. Replicate transects at various distances apart in the same habitat, would provide information on the scale of species turnover within a habitat and would indicate the extent to which patterns of species richness and complementarity are scale- and site-specific. Work on other taxa would test the generality of the results on diversity patterns of ants in Madagascar and the robustness of methods used in this study for improving inventory efficiency.

Inventories provide baseline information for understanding geographic variation in biotic assemblages and can effectively and efficiently include invertebrates. They are the first step to defining areas of endemism or areas of high species richness. In addition, they provide the necessary material for improving our understanding of taxonomic and phylogenetic diversity. For most insects, this work has just begun.

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