

Evaluation of Sampling Methods and Species Richness Estimators for Ants in Upland Ecosystems in Florida

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ABSTRACT The growing emphasis on including invertebrates in global biodiversity conservation efforts has prompted an increase in the study of invertebrate assemblages. Invertebrate sampling designs and the bias of individual methods, nevertheless, remain poorly understood for a variety of habitats. We used a structured inventory approach to sampling ants in five upland ecosystems in Florida. We evaluated the efficiency of quantitative and nonquantitative methods for sampling ants. We also evaluated the performance of four species richness estimators. A total of 3,774 species occurrences were distributed among 1,732 samples that contained 94 species from 31 genera. Twenty unique species and 10 duplicate species were collected. Compared with a comprehensive species list for Florida, sampling captured $\approx 66\%$ of the regional fauna and $\approx 70\text{--}90\%$ of species within the ecosystems studied. Combinations of sampling methods were much more effective for assessing species richness. Individual methods were complementary and sampled only part of the entire assemblage. Nonparametric estimators (an incidence-based coverage estimator [ICE] and a jackknife estimator [Jack2]) performed better than lognormal fitting, and Michaelis-Menten curve extrapolation. However, none of the estimators was stable, and their estimates should be viewed with skepticism. The results of this study provide support for the use of the Ants of the Leaf Litter (ALL) protocol for thoroughly sampling ant assemblages in temperate and subtropical ecosystems. Furthermore, our results indicate that even in relatively species-poor (compared with the tropics) temperate and subtropical regions, a large sampling effort that includes multiple sampling methods is the most effective manner of thoroughly sampling an ant assemblage. Therefore, we suggest that structured inventory should be adopted for a wider variety of terrestrial invertebrate studies.

KEY WORDS Florida, Formicidae, rarefaction, species richness estimation, structured inventory

BIOLOGICAL INVENTORY IS A FUNDAMENTAL component of the life sciences. Inventories provide the foundation for improving the applied pursuits of sustainable resource management, conservation biology, and pest management (Price and Waldbauer 1994, New 1998). Appreciation of the importance of biological inventory and the value of biodiversity has steadily grown in the last two decades as the potential impact of the biodiversity crisis has been recognized (Wilson 1988, Raven and Wilson 1992). For many terrestrial vertebrates and some plants, intensive local or regional sampling can be expected to produce a comprehensive inventory when integrated with existing information, such as the taxon-based work of systematists (Eldredge 1992). However, for the vast majority of terrestrial organisms, particularly hyperdiverse groups such as arthropods, a comprehensive inventory is difficult to achieve except at very small scales or in

isolated regions with depauperate faunas (e.g., small oceanic islands; Disney 1986).

The goal of most arthropod inventories commonly falls into one of two categories: strict inventory or community characterization (Longino and Colwell 1997). Strict inventory generates a nearly comprehensive species list for a discrete spatiotemporal unit, which requires species-level identification of samples (Longino and Colwell 1997). Comparisons with other spatiotemporal units are not necessarily desirable. Traditionally, strict inventories have been carried out by systematists and museum collectors. In contrast, community characterization uses structured sampling (i.e., randomization and repetition) to permit statistical separation of different spatiotemporal units. This is done for the purposes of ranking units according to the goals of conservation or pest management (Cochran 1963, Longino and Colwell 1997). Unit ranking may not require sample identifications to the species level because the primary concern is the relative abundances of focal taxa and how they change across space or time (Colwell and Coddington 1994, Oliver and Beattie 1996). Normally, community characterization is carried out using one or a few sampling techniques and comprehensive species lists are neither necessary

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nor feasible (Disney 1986, Longino and Colwell 1997). Community characterization has most often been used by entomologists, ecologists, and conservation biologists.

Recently, analytical advances focused on examining arthropod ecology have converged with a growing emphasis on including arthropods in rapid biodiversity surveys for conservation purposes (Wilson 1988, Coddington et al. 1991, Kremen 1992, 1994, Kremen et al. 1993, Kim 1993, Colwell and Coddington 1994, Silva and Coddington 1996, Longino and Colwell 1997, New 1998, Fisher 1999a, Anderson and Ashe 2000, Gotelli and Colwell 2001, Sørensen et al. 2002). Accordingly, a number of taxon-specific, structured inventory techniques have been introduced that use a variety of sampling methods that combine the "species hunting" techniques of systematists with the more quantitative methods of ecologists (Coddington et al. 1991, Longino and Colwell 1997, Fisher 1999a). This approach serves as a practical, short-term alternative to long-term, comprehensive surveys (e.g., Deyrup and Trager 1986, Lawton et al. 1998) for assessing local arthropod diversity. By design, this methodology combines the quantitative approach of community characterization with the objectives of strict inventory. It permits analyses of inventory completeness and an assessment of the costs and benefits of methods when used individually and in combination (Longino and Colwell 1997, Fisher 1999a, Delabie et al. 2000).

To assess inventory methods, an account of species captured per sampling method (as well as per unit area or time) is necessary to evaluate effectiveness. Species accumulation curves are an effective method for evaluating the efficiency of various inventory techniques for sampling species richness (Clench 1979, Soberón and Llorente 1993, Colwell and Coddington 1994). A species accumulation curve is a plot of the cumulative number of species discovered within a defined area (and/or time) as a function of some measure of effort. Curves can be constructed to measure either species density (the number of species per unit area) or species richness (the number of species per individual; Gotelli and Colwell 2001). Species accumulation curves are similar to rarefaction curves (Gotelli and Colwell 2001), which are produced by randomly and repeatedly resampling a pool of individuals or samples and plotting the number of species represented by increasing numbers of individuals. In fact, rarefaction curves can be viewed as the statistical expectation of a corresponding species accumulation curve when samples are repeatedly reordered (Gotelli and Colwell 2001).

When the actual number of species in an area is unknown (as is typically the case for arthropods) the shape of a rarefaction curve can be used to estimate how completely an area has been sampled and how efficiently different methods have captured species in that area (Colwell and Coddington 1994, Longino and Colwell 1997, Fisher 1999a). A curve that approaches an asymptote after a large sampling effort is representative of a decrease in species accrual—a measure of sampling completeness (Colwell and Coddington

1994, Longino and Colwell 1997, Gotelli and Colwell 2001). Sampling completeness can be further evaluated by comparing curve asymptotes with values determined by species richness estimators or by observed species richness from well-sampled localities. When used in combination with a structured inventory, rarefaction curves are intended to permit quantitative analyses of species richness for comparison between methods or between sites. Additionally, subsamples can be evaluated within the context of the entire data set to determine the relative efficiency of method combinations and changes in design (e.g., the effect of increasing distance between samples; Fisher 1999a).

Among arthropods, ants (Hymenoptera: Formicidae) have been a focal group for development of structured inventory protocols and novel techniques for analyzing data generated from structured inventory. Ants are an appropriate group for testing the effectiveness of new methods. They are diverse, abundant, and nearly ubiquitous. They influence the biotic and abiotic processes of the ecosystems where they occur. A majority of species nest in fixed positions, largely ensuring that species dwell where they are sampled. They are among the most studied terrestrial invertebrate taxa and have been used to monitor environmental impact and ecosystem recovery (Andersen 1990, 1993, Hölldobler and Wilson 1990, Folgarait 1998). Numerous, established sampling techniques are available, representing a range of costs and yields (Bestelmeyer et al. 2000). Furthermore, structured inventory techniques and biodiversity data analyses have been established for inventorying and estimating ant species richness in tropical rainforest ecosystems (Fisher 1996, 1998, 1999a, b, 202, Longino and Colwell 1997, Agosti et al. 2000a, b, Longino et al. 2002). Much less is known about the performance of structured inventory methods to capture ants in subtropical and temperate ecosystems. Similarly, the performance of species richness estimators remains largely untested on data drawn from temperate or subtropical ant communities. The biodiversity crisis is not confined to the tropics (Platnick 1992) and neither are the goals of conservation biology, entomology, and ecology. Accordingly, improving structured inventory methods and species richness estimation for ants and arthropods in a variety of ecosystems is warranted.

In this study, we evaluated the efficiency of a structured inventory of ants in northern and central Florida. In so doing, we compared the efficiency of four individual sampling methods and the performance of three species richness estimation techniques. The ant fauna of Florida has been thoroughly surveyed in the past 50 yr throughout the state (Van Pelt 1956, 1958, Deyrup and Trager 1986, Deyrup et al. 2000, Lubertazzi and Tschinkel 2003, M. Deyrup, L. Davis, Z. Prusak, S. Cover, and J. R. King, unpublished data). As a result, there is a clear record of distribution and habitat association for a majority of species (Deyrup 2003). Consequently, this study presented a unique opportunity to compare inventory results and species richness estimations with approximate species rich-

ness values expected at local and regional scales. In evaluating sampling methods our objectives were (1) to compare the number of ant species captured by baits, pitfalls, litter extraction, and hand-collecting methods (and combinations thereof) in five different ecosystems, (2) to compare the complementarity of sampling methods, and (3) to determine the relative costs (in time) of sampling methods. These objectives permit an analysis of the efficiency of sampling methods in the context of facilitating conservation or land-planning decisions that require comparable estimates of species richness and endemism (Coddington et al. 1991, Platnick 1992).

Materials and Methods

Study Area. A detailed description of the ecosystems sampled and the methods used in this study can be found in King (2004). Briefly, this study was carried out in 3 sites in each of five different ecosystems (a total of 15 study sites) in north and central Florida. Sampling was performed in temperate hardwood forests in the San Felasco Hammock State Park, pine flatwoods in the Osceola National Forest, high pine in the Katherine Ordway Biological Preserve, and Florida scrub forest in the Archbold Biological Station. The plant community descriptions of Myers and Ewel (1990) were used as a basis for ecosystem selection. These sites were selected a priori because they contain some of the remaining nearly undisturbed native upland ecosystems in Florida. We also sampled a non-native ecosystem, consisting of converted (previously cleared) fields, to represent moderately disturbed habitat. A field was sampled in an area adjacent to natural areas at San Felasco Hammock State Park, the Katherine Ordway Biological Preserve, and the Archbold Biological Station. The ecosystems sampled represent a gradient of upland plant communities that include closed-canopy, hardwood forests, open-canopy pine and oak woodland, and completely open, herbaceous savannah.

Sampling. Ants were sampled from June through September 2001 using baits, pitfall traps, leaf litter extraction with Berlese funnels, and hand collecting. A total of 36 pitfall and 36 litter samples were taken separately at 5-m intervals (180 m total) in two parallel lines separated by 10 m (Fisher 1996, 1998, 1999b, 2002). A transect of 36 baits was placed between the pitfall and litter extraction lines, with each bait corresponding to pitfall and litter extraction samples. Pitfall traps were 85-mm-long plastic vials with a 30-mm internal diameter partially filled with ≈ 15 mm of non-toxic, propylene glycol antifreeze. Traps were buried with the open end flush with the surface of the ground and operated for 3 d. Two 0.25-m² litter samples were taken after setting pitfall traps at each litter sample point. Litter samples were obtained by collecting all surface material and the first ≈ 1 cm of soil within quadrats. The two samples were pooled; larger objects (e.g., logs) were macerated with a machete and sifted through a sieve with 1-cm grid size. Sifted litter was placed in covered metal 32-cm-diameter Berlese fun-

nels under 40-W light bulbs. The funnels were operated until the samples were dry (≈ 48 –72 h). Baits were 12 by 75-mm test tubes with a piece (≈ 2 g) of hot dog (Oscar Meyer, Northfield, IL) inserted ≈ 2 cm into the tube. At each sampling point, a small spot was cleared of any litter, and the bait tube was placed directly on the ground (to speed discovery and access) and shaded with one half of a Styrofoam plate. The baits were left for 0.5 h and collected, and the ends were plugged with small cotton balls to prevent the ants from escaping. Hand collecting consisted of systematically searching vegetation, tree trunks, logs, and small twigs for 2 h per site. Hand collecting was performed within and immediately adjacent to (≈ 5 –10 m) sites. Time records were kept for each step of the sampling and sorting process to estimate costs. Time costs included installation, operation, and collecting of samples, traps, and baits, and time spent processing and identifying specimens. For the sake of technical consistency, and with the exception of one high pine site, all sampling was performed by J. R. King. Similarly, all ants, from all samples, were sorted, counted, and identified to species by J. R. King.

Analysis. All records used in this study were based on the worker caste as their presence provides evidence of an established colony (Fisher 1999a, Longino et al. 2002). The purpose of the sampling design was to produce a representative, nearly complete species list for each ecosystem type. The relative abundance of individuals is an important measure when considering species richness (Gotelli and Colwell 2001). For ants, however, the sampled abundance of foraging workers is not comparable with individuals of other animals. The sociality of ants can often lead to extreme clumping of individuals within samples (particularly litter samples, which may include entire colonies), which may skew species richness comparisons and species/abundance relationships (Gotelli and Colwell 2001). To partially remedy this, species occurrences (incidence data) were used in place of the abundance of individuals when evaluating species-based abundance measures (Longino 2000, Fisher and Robertson 2002, Longino et al. 2002). Therefore, data for the three sites sampled within each ecosystem type were pooled and converted to a species \times sample incidence (presence-absence) matrix (Longino 2000, Longino et al. 2002). A regional data set was also generated by pooling all of the data into a single species \times sample incidence matrix.

Sample-based rarefaction curves were used to compare total species richness within ecosystems and for the regional data set. Total species richness captured by each method in each ecosystem was similarly evaluated. Rarefaction curves were generated by random reorderings (50 times) of samples using the program EstimateS (Colwell 2000). We compared these sample-based rarefaction curves with the observed number of species plotted on the y-axis (ordinate) against species occurrences (incidence data) plotted on the x-axis (abscissa) to assess differences in species richness between and among curves representing ecosys-

tems and methods (Colwell and Coddington 1994, Gotelli and Colwell 2001).

Species richness was estimated in three ways for each ecosystem and for the regional data set: (1) by fitting a lognormal distribution, (2) by extrapolating rarefaction curves, and (3) by using nonparametric estimators. For the parametric model fitting, the sample data from each site were fitted to the lognormal distribution using the method of Preston (1948). In this method, the sample data were fitted to the lognormal distribution, $S(R) = S_0 e^{(-a^2 R^2)}$, where $S(R)$ is the number of species in the R th octave, S_0 is the number of species in the modal octave, and a is a parameter related to the width of the distribution. Parameters of the lognormal were estimated using a modified version of the method of Ludwig and Reynolds (1988). Octaves were assigned to abundance classes (observed), and parameters S_0 and a were estimated using nonlinear curve fitting (proc nlin, Newton's estimation method and least squares fitting, SAS release 8.02; Longino et al. 2002). Species richness was estimated by calculating the total area under the fitted curve, including the portion of the curve hidden behind the "veil line" (Magurran 1988).

Projection of the rarefaction curves for the regional data set was accomplished using sample-based rarefaction plots (Soberón and Llorente 1993, Gotelli and Colwell 2001). Patterns observed in the rarefaction curves generated for individual ecosystems were similar to those of the regional data set and were not displayed. The smoothed curves were created by averaging repeated, random reorderings (50 times) of the samples with the mean number of species occurrences from each sample computed in succession (Colwell and Coddington 1994, Gotelli and Colwell 2001). The smoothed curves were projected by fitting the asymptotic Michaelis-Menten equation,

$$S(n) = \frac{S_{\max} n}{B + n},$$

where $S(n)$ is the number of species, n is the number of samples, and S_{\max} and B are fitted constants (Colwell and Coddington 1994). Following Raaijmakers (1987), maximum likelihood estimators for parameters (S_{\max} and B) were determined for the Eadie-Hofstee transformation of the equation (Colwell and Coddington 1994, Longino et al. 2002).

We also used two nonparametric methods to estimate species richness for comparison with the rarefaction curves. A jackknife (henceforth Jack2) estimator,

$$S = S_{\text{obs}} + \left[\frac{L(2n - 3)}{n} - \frac{M(n - 2)^2}{n(n - 1)} \right],$$

was used, where L = the number of species in one sample, M = the number of species that occur in two samples, and n = the number of samples (Burnham and Overton 1978, 1979). An incidence-based coverage estimator (ICE),

$$S_{\text{ice}} = S_{\text{freq}} + \frac{S_{\text{infr}}}{C_{\text{ice}}} + \frac{Q_1}{C_{\text{ice}}} \gamma_{\text{ice}}^2,$$

was also used, where S_{freq} = number of frequent species (found in >10 samples), S_{infr} = number infrequent species (found in <10 samples), C_{ice} = sample incidence coverage estimator, Q_1 = frequency of uniques (the number of species known from only one sample), and γ_{ice}^2 = estimated coefficient of variation of the Q_1 for infrequent species (Lee and Chao 1994). These estimators were chosen because they have been shown to reliably provide intermediate (ICE) and upper (Jack2) level species richness estimates relative to observed species richness and other nonparametric estimators in biological inventories (Colwell and Coddington 1994, Chazdon et al. 1998, Sørensen et al. 2002).

All species richness estimates were compared with total species richness values generated for each ecosystem and the region from previous collection records. These records included published (Van Pelt 1956, 1958, Deyrup and Trager 1986, Lubertazzi and Tschinkel 2003) and unpublished inventories (Van Pelt 1947, Prusack 1997) and personal collection data sets (J. R. King, L. Davis, M. Deyrup). Amassed over >50 yr, these collections represent a comprehensive species occurrence data set for several localities and the region as a whole. Using these data, a potential upper limit of species richness was determined for the regional data set by including all of the species with collection records coinciding with the study area (north Florida in the region stretching from Columbia and Baker Counties southward along the central ridge of the peninsula to the end of the Lake Wales Ridge in Highlands County).

At the scale of the ecosystem, the potential species richness value was also established using collection records. The potential species richness values were determined using the highest number of species previously captured by an approximately similar sampling effort (many samples taken using multiple methods) within a study area of similar size to those sampled in our study (e.g., the hardwood hammock within San Felasco Hammock State Park). The potential species richness values are approximations and represent a generous upper limit estimate of the potential of species that may occur at the regional scale and within ecosystems. Similarly, collection records were used to assess the observed rarity of species collected in this study. Species that were unique to either the study as a whole (uniques: the number of species known from only one sample) or to individual sampling methods were compared with collection records to determine whether the rarity of these species was a product of insufficient (or inappropriate) sampling or if they were truly rare.

To assess complementarity among methods, we used a measure that describes the proportion of all species in two sites that occurs in only one or the other site (Colwell and Coddington 1994). Pairwise complementarity or distinctness values were calculated using the Marczewski-Steinhaus (M-S) distance:

Table 1. Species richness estimates and measures of inventory completeness for each ecosystem and for the regional data set

	Hardwood hammock	Pine flatwoods	Florida scrub	High pine	Field	Regional
Potential species richness	41	46	48	58	45	142
Observed species richness (% of potential)	29 (71%)	39 (85%)	43 (90%)	48 (83%)	35 (78%)	94 (66%)
Richness estimators						
Lognormal	29	39	43	48	35	96
MMMean	26	38	42	50	37	87
ICE	35	49	50	53	41	113
Jack2	41	52	56	57	47	124
Singletons	7	9	9	8	7	20

Potential species richness values represent known species richness values determined from previous inventories. Richness estimator (MMMean, ICE, and Jack2) values represent the mean of 50 randomizations of sample order. Singleton values represent the no. of species with only one individual in samples. All values were rounded to the nearest whole no.

$$C_{MS} = \frac{a + b - 2j}{a + b - j},$$

where a = the number of species at site A, b = the number of species at site B, and j = the number of species common to both. Methods were compared within ecosystems and for the regional data set. To further analyze the sampling efficiency of quantitative methods, litter and pitfall data were examined within sites to determine the impact of spatial separation among sample points on the similarity of species sampled. Within sites, faunal similarity among samples along each transect was determined using the Jaccard index:

$$S_j = \frac{j}{a + b - j}$$

(the complement of the M-S distance). The similarity of samples for all pairwise combinations of sample points (5–175 m apart) along each transect was plotted against increasingly larger distances along each site transect to determine the homogeneity of samples (Fisher 1999a). These were averaged among sites within each ecosystem. Comparisons beyond 150 m were excluded from the analysis because there were increasingly fewer replicates to generate means (e.g., there is only one pairwise comparison of samples 175 m apart).

We examined the time costs of individual methods. Time costs included time spent in the field collecting samples and in the laboratory sorting and identifying specimens. Laboratory hours were spent on tasks that required previous, rigorous scientific training (e.g., sorting and identifying specimens to the species level). Field hours were an account of time spent on tasks that did not require specialized training (e.g., laying out pitfalls, sifting litter). Although the time required to accomplish these tasks would undoubtedly vary among different workers, a comprehensive account of time costs per method provides an estimate of the amount of time required to reproduce similar results under similar conditions. The time cost per method would remain consistent relative to the time costs for the other methods even if, for example, multiple workers were using the same methods.

Finally, the effectiveness of quantitative methods for predicting total site species richness was deter-

mined. Ordinary least-squared regressions were used to determine the relationship between total species richness and species richness per method for baits, pitfalls, and litter samples within sites.

Results

The inventory captured 37,961 individual ants representing 94 species from 31 genera. A total of 3,774 species occurrences were distributed among 1,732 samples. Seventy-four ground-dwelling species, 12 arboreal species, and 8 subterranean species were captured. A species list and detailed discussion of the relative abundance, body size, and ecology of individual species captured in this study can be found in King (2004).

Observed and Estimated Species Richness. Observed species richness varied among ecosystems. The most species were captured in high pine and Florida scrub ecosystems, whereas fewer species were captured in pine flatwoods, field, and hardwood hammock ecosystems, respectively (Table 1, observed species). At the regional scale, the 94 species sampled included 20 uniques (the number of species known from only one sample) and 10 duplicates (the number of species known from two samples; Fig. 1). Two-thirds of the species were captured within the first ≈ 750 species occurrences. Beyond 750 species occurrences, the addition of species was considerably diminished.

Species richness estimates performed poorly at the regional scale (Fig. 1). At the local scale, nonparametric estimators performed better than projecting the Michaelis-Menten curve or lognormal curve fitting (Table 1). The method of lognormal curve fitting to estimate species richness consistently predicted species richness levels at or only slightly above the observed richness (Fig. 1; Table 1). All other richness estimators generally did not stabilize with increasing sampling effort. As sample size increased, so too did the estimates (Fig. 1). Estimators also consistently predicted widely separated results relative to each other. Projecting the Michaelis-Menten curve produced estimates at or, most frequently, below observed species richness. The MMeans estimate also increased steadily with sample size with no evidence of leveling off (Fig. 1). The ICE consistently predicted species richness greater than the observed species

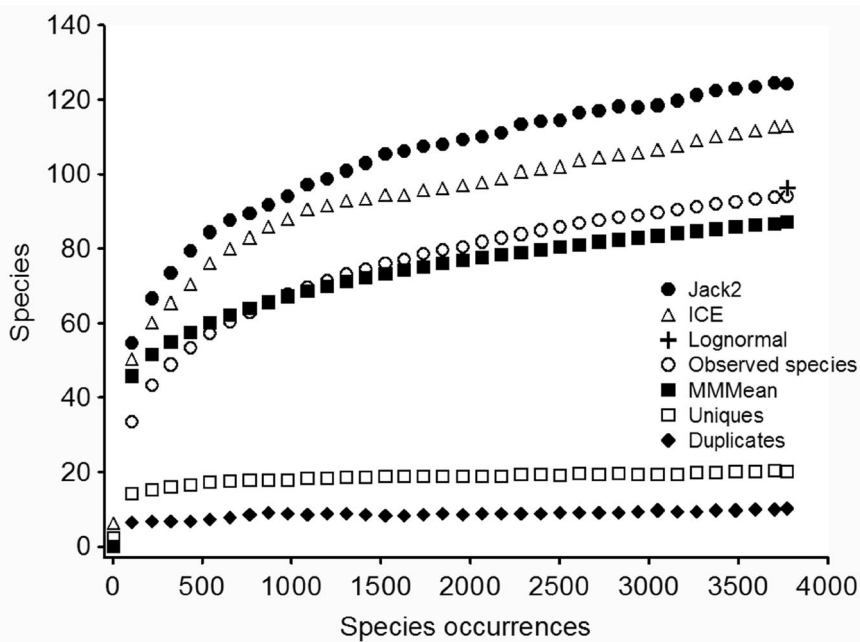


Fig. 1. Observed species richness, uniques (the number of species known from only one sample), duplicates (the number of species known from two samples), and estimated species richness for the jackknife (Jack2), incidence-based coverage (ICE), lognormal, and Michaelis-Mentin curve (MMMean) estimators for the regional (all samples pooled) data set (see text for estimator formulas). Curves are sample based rarefaction curves generated from 50 randomizations of sample order. The lognormal estimate is a single value determined by fitting a lognormal curve to the full species abundance distribution.

richness but less than Jack2 estimates. Both ICE and Jack2 showed some evidence of leveling off between 1,500 and 2,200 species occurrences; however, they both became unstable beyond 2,200 occurrences, rising steadily with increasing sample size. Neither uniques (the number of species known from only one sample) nor duplicates (the number of species known from two samples) showed any sign of decreasing. Rather, they remained at nearly the same level throughout the majority of the sampling effort.

The estimates for the completeness of the inventory ranged from 71 to 90% of the potential species richness estimates within ecosystems (Table 1). Similarly, an estimated 66% of the total regional fauna was sampled during this study. Within ecosystems, the ICE and Jack2 estimators were very near the potential site estimates predicted from previous survey work. In contrast, MMeans and lognormal estimates were little different from observed species richness values. For the regional data set, Jack2 was nearest to the potential site estimate while all other estimators produced considerably lower species richness estimates.

Rarity. Uniques (the number of species known from only one sample) accounted for $\approx 21\%$ of the total species richness. The 20 uniques captured in this study included five arboreal species. All of the arboreal species captured are common, although not abundant throughout the range of the study and were poorly sampled by the methods used. Similarly, two of the uniques were subterranean species that are rarely captured, although an alternative sampling method (sub-

terranean baiting; J. R. King, unpublished data) has revealed that one of these species is common. Five ground-dwelling species among the uniques are frequently encountered within peninsular Florida, although their low abundance here suggests that they are uncommon in the upland habitats sampled. The remaining eight ground-dwelling species have not been commonly collected previously, suggesting that these species are truly uncommon or rare. For a list of the unique species, see King (2004).

Complementarity of Ecosystems. Comparing the fauna of different sites revealed that, on average, species composition was much more similar among sites in the same ecosystem type than among different ecosystems (Table 2). Between different ecosystems, the complementarity of species lists was similar. A

Table 2. Mean percent faunal complementarity \pm SD between ecosystems

	Hardwood hammock	Pine flatwoods	High pine	Florida scrub	Field
Hardwood hammock	40 \pm 5	76 \pm 4	78 \pm 2	69 \pm 8	79 \pm 5
Pine flatwoods		47 \pm 3	73 \pm 8	65 \pm 5	81 \pm 8
High pine			43 \pm 9	71 \pm 5	72 \pm 9
Florida scrub				45 \pm 15	76 \pm 5
Field					64 \pm 2

Complementarity values are M-S distances between species lists for each ecosystem. Bold values represent comparisons among sites within the same ecosystem. Higher values indicate that sites have increasingly dissimilar fauna.

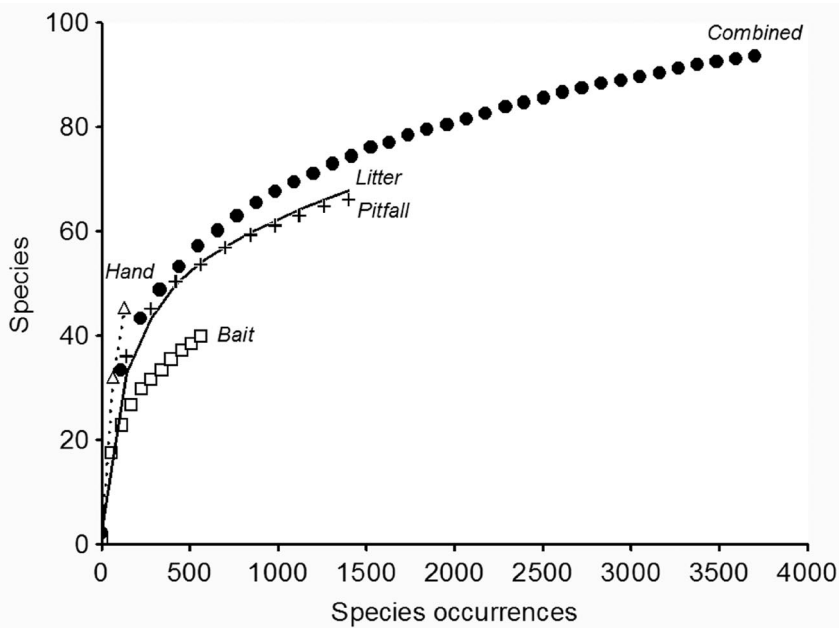


Fig. 2. Effectiveness of individual and combined sample methods. Curves are sample-based rarefaction curves based on 50 randomizations of sample order. Curves correspond to individual methods (H, hand collected; P, pitfall; L, litter extraction; B, bait) and a combination of methods (P + L + B, combined pitfall, litter extraction, and baits).

similar pattern was also seen among sites of the same ecosystem with the exception of field sites. Field sites were less similar to one another than other ecosystems, probably as a result of their geographic separation. The greatest difference in species composition occurred between pine flatwoods and field sites, whereas the least difference was seen between Florida scrub and pine flatwoods sites.

Effectiveness of Sampling Methods. Sample-based rarefaction curves for individual methods (Fig. 2) revealed that pitfall and litter samples were nearly identical in the number of species each captured and both methods captured more species than hand collecting and baiting. This pattern was consistent within individual ecosystems as well, except for hardwood hammocks (data not shown). In hardwood hammocks, litter sampling captured a much greater number of species (26) than pitfalls (17). Baiting was the least productive method for capturing species richness. The combination of quantitative methods (pitfall, litter, and bait samples) was the most thorough approach for capturing species richness. The hand collecting curve shows little evidence for an asymptote at all, indicating a very rapid increase in species per individual collected and no evidence of an asymptote. The rapid accrual of species by hand collecting and the lack of an asymptote suggest that collecting in this manner is the most efficient method for maximizing species richness. The lack of an asymptote suggests that too little time was spent hand-collecting per site. However, this is a methodological artifact, because duplicate collections were generally avoided. Consequently, time, rather than species, occurrences are a better ordinate for assessing the effectiveness of this method.

Litter and pitfall samples were the most similar in species composition among all sampling methods (Table 3). Baits and litter samples were the least similar in species composition. Overall, the fauna captured by hand collecting was the least similar in species composition to any of the other collecting methods. Litter extraction sampling was particularly useful for capturing cryptic species living in rotting wood and in leaf litter. Pitfall samples were most effective at capturing highly active, surface foraging species. Hand collecting captured a number of arboreal species that were not captured by other methods.

Within ecosystems, the similarity of species in samples along 180-m linear transects generally varied only slightly between nearby and distant samples (Fig. 3A and B). Field sites, however, exhibited the most dissimilarity between nearby and distant sites with a steady decrease in the similarity of species composition per sample as a function of increasing distance (Fig. 3A and B). Sample autocorrelation differed among ecosystems and methods. Hardwood hammock samples exhibited greater similarity among samples,

Table 3. Percent faunal complementarity of sample methods for the regional data set

	Pitfall	Litter	Bait	Hand
Pitfall	—	38	47	55
Litter		—	60	57
Bait			—	56
Hand				—

Values are M-S distances generated from the regional (all sites pooled) species list. Higher values indicate that methods are more dissimilar in the species captured.

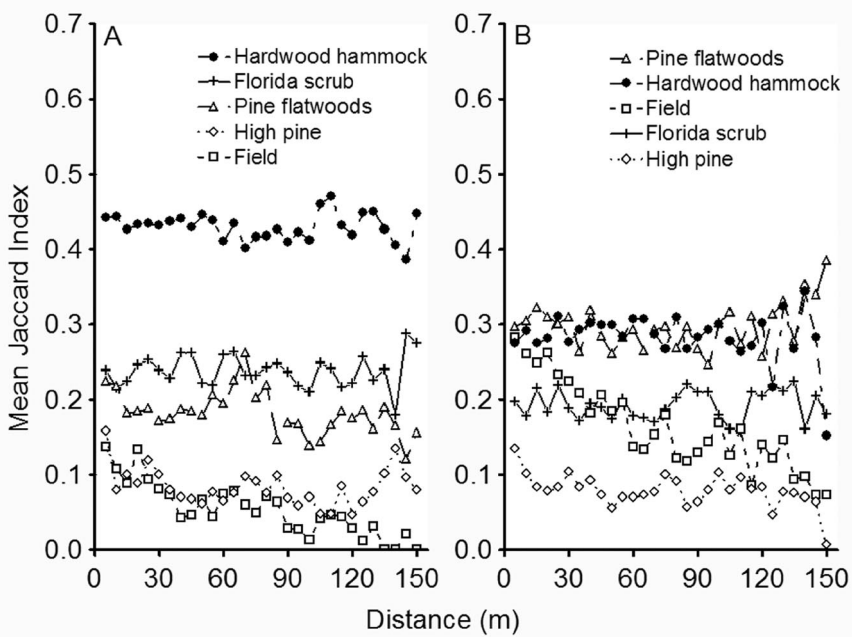


Fig. 3. Similarity of ant species in (A) litter and (B) pitfall samples as a function of distance. Curves represent Jaccard index values of pairwise comparisons of pitfall and litter data at increasing distances between samples. Jaccard index values were averaged across (3) replicate sites for each ecosystem, where higher values indicate greater similarity among samples.

on average, than other ecosystems—particularly among litter samples (Fig. 3A). Pine flatwoods and Florida scrub ecosystems were most similar in the degree of sample autocorrelation, whereas hardwood hammock and high pine were the least similar (Fig. 3A and B). With the possible exception of fields, the impact of ecosystem type seems to be a greater determinant of sample autocorrelation than distance between samples.

Litter samples required the most time to collect, sort, and process, followed by pitfalls, baits, and hand collected samples, respectively (Fig. 4A). Baits commonly produced very large numbers of individuals of the same species, particularly mass recruiting species such as *Pheidole dentata* Mayr and *Solenopsis invicta* Buren (Fig. 4B). Litter sampling often captured entire colonies or colony fragments of multiple species, also resulting in large numbers of individuals. Pitfall samples and hand collecting tended to produce more species per individual sampled. There were 8 species captured only in pitfall samples, 13 species captured only in litter samples, 8 species captured only by hand collecting, and 1 species captured only by baiting (Fig. 4A).

Pitfall species richness predicted 69% of total site species richness (Fig. 5; total = 3.58 + 1.29pitfall, $R^2 = 0.69$, $P < 0.01$). Litter species richness accounted for slightly less (61%) of the variability in total species richness (total = 7.47 + 1.04litter, $R^2 = 0.61$, $P < 0.01$), whereas bait species richness predicted 46% of total site species richness (total = 15.98 + 1.29bait, $R^2 = 0.46$, $P = 0.01$) across all sites.

Discussion

Inventory Completeness. There are 218 ant species currently known from the entire state of Florida, 142 of which are known to occur within the region of this study (Deyrup 2003). It is less clear how many species might dwell within a given upland ecosystem in the state, although previous inventories provide reasonable estimates (Table 1). At the regional scale, $\approx 66\%$ of the ant fauna was captured. Within the ecosystems sampled, $\approx 70\text{--}90\%$ of the ant fauna was captured. Because our estimates of the upper limit of species richness were conservative (see Materials and Methods), it is quite possible that we actually captured a higher percentage of the ant species present, particularly at the local scale. At the local (ecosystem) scale, this level of inventory completeness is equal to or better than similar studies conducted in tropical rainforests (Longino and Colwell 1997, Fisher 1999a, Agosti et al. 2000a, b). There are no comparable studies of structured inventory for capturing the ant species richness of a regional fauna, although intensive sampling in temperate and subtropical localities has captured similar levels of species richness (Talbot 1975, Deyrup and Trager 1986). Among similar, thorough inventories of ant species richness, regardless of scale, the sampling effort put forth in this study was comparable in the total number of samples taken (Talbot 1975, Deyrup and Trager 1986, Fisher 1996, 1998, 1999a, b, 2002, Longino and Colwell 1997).

Although our sampling design captured a large portion of the species present, it still cannot be described

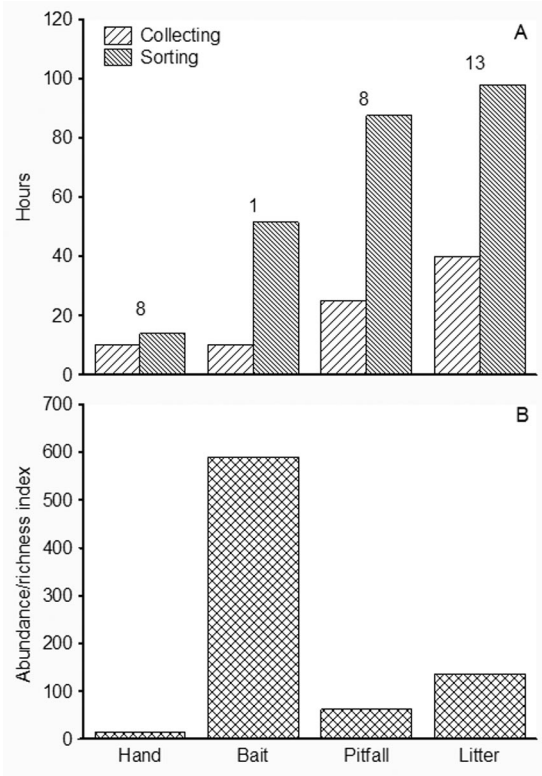


Fig. 4. The efficiency of methods as measured by (A) the total time required and the number of unique species (number of species captured only by that method; represented by the values above the bars) sampled by different collecting methods and (B) the abundance/richness index. Sorting (in hours) represents the total amount of time required to sort and identify specimens per method. Collecting (in hours) represents the total amount of time required to collect samples per method. It does not include the time required to operate pitfall traps (3 d). The abundance/richness index is the ratio of total number of ants captured divided by the total number of species captured per method. Higher numbers represent fewer species per individual captured.

as comprehensive—undoubtedly species were missed at local and regional scales. At both scales, the shortcomings of the sampling methods and the spatial limitations of the sample design were probably largely responsible for the underestimates, rather than the sampling effort (the number of samples; Longino and Colwell 1997). Sampling additional sites or using different methods would capture more species much more readily than additional sampling within sites. Nevertheless, the structured inventory protocol used here provided a sufficiently thorough sample of local and regional ant species to permit an accurate comparison of the complementarity and total species richness of different areas. Traditionally, invertebrates have been excluded from natural area inventories because of the difficulty of obtaining accurate estimates of local and regional species richness. This approach has been adopted despite their importance in ecosystem functioning and their contribution to total local

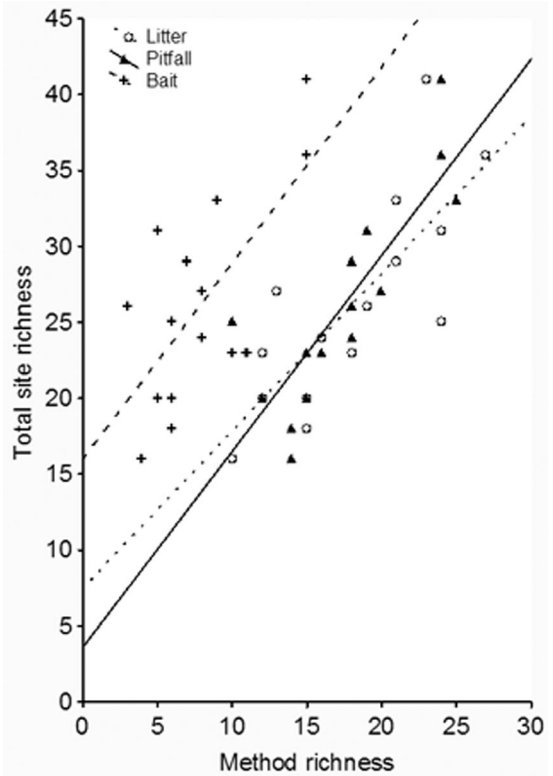


Fig. 5. The relationship between total site species richness and total method species richness for bait, pitfall, and litter samples. All regressions were significant ($P < 0.01$). Pitfall site species richness accounted for the most variability in total site species richness ($R^2 = 0.69$) followed by litter ($R^2 = 0.61$) and baits ($R^2 = 0.46$).

and regional biodiversity. The results presented here and for tropical ant inventories (Fisher 1996, 1998, 1999a, b, 2002, Longino and Colwell 1997) suggest that structured inventory can provide sufficiently accurate measures of ant diversity to include them in natural area inventories in temperate, subtropical, and tropical regions. Similar results have been obtained using structured inventory to capture spiders (Coddington et al. 1991, Silva and Coddington 1996, Dobyns 1997, Toti et al. 2000, Sørensen et al. 2002). Accordingly, structured inventory of arthropods should be adopted as a primary component of future natural area inventories.

Performance of Species Richness Estimators. Whether evaluated for individual ecosystems or for the regional (combined) data set, the four species richness estimators differed considerably among each other. They produced a wide range of estimates and generally did not stabilize as sample numbers increased (Fig. 1). Instability of coverage-based estimators, curve extrapolation, and the lognormal model generally seems to be the rule rather than the exception, regardless of the origin of the data set (Chazdon et al. 1998, Toti et al. 2000, Longino et al. 2002, Sørensen et al. 2002). This trend suggests that species

richness estimates calculated with these estimators should be very cautiously interpreted as approximations of potential species richness. If used at larger scales, they are probably even less reliable. Lognormal and MMMeans estimates were at or slightly below observed species richness. The ICE estimator predicted higher numbers of species than either lognormal or MMMeans, and Jack2 consistently predicted the highest number of species. Only ICE estimates showed any evidence of stability for the regional data set (Fig. 1). However, the curve stabilized only between $\approx 1,000$ and $2,000$ species occurrences and showed no evidence of stabilization above or below these values (Fig. 1). Within ecosystems, both ICE and Jack2 estimates were very near to potential species estimates (Table 1). However, because the estimators were unstable and were proportional to sample size, the values of species richness they predict should also be viewed with skepticism. It has been suggested that using nonparametric estimators in combination may predict upper and lower boundaries of local species richness (Toti et al. 2000). We would suggest that it has not yet been clearly shown that such an approach is valid.

The poor performance of the lognormal and MMMeans estimators for our data set contrasts with their performance in other intensive inventories (Toti et al. 2000, Longino et al. 2002). Our data were poorly fit by lognormal and asymptotic functions (King 2004), and as such, the estimators were inappropriate for the data set. The use of these estimators should be closely evaluated based on their fit to data and the number of rare species in the data set (Longino et al. 2002). The lognormal in particular may be problematic because of the necessity of fitting a continuous distribution to discrete data, the variability of estimates resulting from the selection of different intervals of abundance categories, and the lack of fit to some data sets (Colwell and Coddington 1994). The lognormal model should not be assumed to fit the abundance distribution of species (Lambhead and Platt 1985, Hughes 1986), particularly for temperate and subtropical invertebrate assemblages (Siemann et al. 1999).

Rarity. In contrast to many tropical insect (e.g., Hemiptera, Lepidoptera) inventories, rare species did not account for a majority of the species captured (King 2004). Among unique species, a majority were rare because of methodological edge effects (Longino et al. 2002), range limitations, or small populations within the sampled area (i.e., they are known to be common elsewhere within the region). Arboreal species and some of the subterranean species were undersampled because of the limitations of the sampling design. Of 20 unique species, only 8 species ($\approx 8\%$ of the total number of species) could be considered truly rare compared with their known distributions. These results are similar to other comprehensive temperate, subtropical, and tropical ant inventories, where truly rare species comprise a minority of species (Van Pelt 1956, 1958, Talbot 1975, Deyrup and Trager 1986, Longino et al. 2002). The occurrence of only a small

number of truly rare species (apparently range restricted and numerically uncommon) within a given region seems to be a persistent pattern among ants as revealed by intensive inventory efforts (Longino et al. 2002). This pattern of rarity in ants contributes to the stability and accuracy of species richness estimators, particularly nonparametric estimators, because their calculation is dependent on the number of rare species (Colwell and Coddington 1994, Chazdon et al. 1998, Longino et al. 2002). It is unclear, however, how changes in the relative proportion of rare species from data set to data set are ultimately expressed in the stability and success of the estimators.

Effectiveness of Sampling Methods. The completeness of the structured inventory shows the effectiveness of the combined methods for accurately sampling the species richness and relative abundance of ants in upland ecosystems in Florida. Individual methods were much less effective than combined methods at capturing total species richness (Fig. 2). The combined quantitative methods (pitfalls, litter samples, baits) also provided an accurate measure of the relative abundance of ground-dwelling species (King 2004). Both measures are crucial components for accurately measuring and comparing biodiversity among different areas or times (Gotelli and Colwell 2001). Relative to other thorough sampling projects, such as long-term, strict inventories (e.g., Talbot 1975, Deyrup and Trager 1986), a structured inventory is a faster approach to capturing a large majority of local species richness. However, we do not suggest that structured inventory is a replacement for long-term taxonomic inventories, if time allows. These results and those of other structured inventories reveal that, regardless of where the sampling occurs, the fastest way to thoroughly sample a given area is to use a variety of sampling methods and take a large number of samples (and in so doing, capture a large number of individuals; Longino and Colwell 1997, Majer 1997, Fisher 1999a, Longino et al. 2002). This is not new information, but the increasing number of rapidly generated, thorough inventories from a variety of regions and habitats serve as an important reminder of a simple truth of invertebrate sampling that bears repeating: a large sampling effort is required to accurately measure the biodiversity of invertebrates. Some caveats are that the application of individual methods may be adequate in certain habitats, for use in sampling projects that do not require thorough inventories, or perhaps if an extremely large number of samples are applied.

Different ecosystems and individual methods generated complementary species lists (Tables 2 and 3). Additionally, the spacing of samples at or above 5 m had little or no effect on the similarity of samples (Fig. 3A and B) within ecosystems. These results suggest that samples spaced 5 m or further apart may be considered independent. Similarity among samples was more dependent on the ecosystem where sampling occurred. These results emphasize the differences among ecosystems and the sampling bias of individual sampling methods. Hardwood hammock

and Florida scrub ecosystems have closed canopies and a deep layer of litter. Pine flatwoods, high pine, and field ecosystems are increasingly open with a decreasing amount of litter. Accordingly, the ant fauna of hardwood hammocks is, for example, rich in cryptic species that nest in rotten wood and leaf litter relative to high pine ecosystems that have much less litter. Pitfalls and litter samples produced species lists that were the most similar among sampling methods (Table 3). The underlying reason for the difference seen between the two methods was the number of unique species captured by litter sampling in hardwood hammock. In all of the other ecosystems, pitfalls were equal to or better than litter sampling. In combination with studies conducted in tropical forests where litter sampling was superior to pitfall sampling (Fisher 1999a), these results provide further support for the application of the Ants of the Leaf Litter (ALL) protocol in a wide variety of ecosystems for generating estimates of species richness (Agosti et al. 2000a). The standardized ALL protocol emphasizes pitfall and litter sampling in addition to hand collecting to generate accurate estimates of local ant biodiversity. The protocol is quantitative and flexible enough to permit its application in a variety of habitats. The deficiencies of individual methods in a given habitat are compensated for by the performance of other methods. For example, in habitats with a well-developed leaf litter, the inadequacy of pitfalls will be overcome by the superiority of litter sampling techniques and the flexibility of hand collecting (Melbourne 1999).

Despite the obvious advantages of applying multiple sampling methods to generate a structured inventory, the expertise and time required to execute an inventory often precludes this approach to sampling invertebrates (Burbidge 1991). Individual sampling methods are, therefore, often applied to generate a community characterization (Longino and Colwell 1997). The inadequacies of individual sampling methods suggest that their unaccompanied application requires additional consideration. Among the methods applied in this study, baits were the least effective at producing estimates of biodiversity and unique species (Figs. 4A and 5). Despite the small amount of time required to sort and identify species collected in baits, the limited amount of information they produced diminished their value as a biodiversity sampling technique (Fig. 4B). In contrast, hand collecting was the most efficient method for capturing species richness and was an effective method for producing unique species (Fig. 4A and B). The rarefaction curve suggested a much greater potential for capturing species richness if more time were spent hand collecting in each site (Fig. 2). However, the success of hand collecting is dependent primarily on the experience of the collector (Longino et al. 2002, Sørensen et al. 2002)—experienced collectors will collect more species more quickly than inexperienced collectors. Hand collecting is also not quantitative, so relative abundance cannot be reliably estimated.

Both pitfall and litter extraction sampling were most closely correlated with total site species richness

(Fig. 5) and provided relative abundance data. There were also a number of species unique to each method (Fig. 4A). However, pitfall sampling and leaf litter extraction were costly, requiring the most time to sort and identify specimens and the use of specialized equipment (i.e., Berlese funnels). Pitfall samples required less time ($\approx 18\%$) to sort and identify specimens and, with the exception of hardwood hammock sites, were equal or better than litter sampling for upland ecosystems in Florida. Although pitfall samples tend to undersample cryptic species and arboreal species (Majer 1997) and do not perform as well as litter extraction sampling in ecosystems with a well-developed litter layer (Fisher 1999a, Melbourne 1999), their greater efficiency suggests that pitfalls are the best choice for an individual sampling method in a majority of warm temperate and subtropical upland ecosystems (i.e., those without a deep layer of litter). Pitfall traps can be made even more effective if they are operated for longer periods, and more traps of larger diameter are used (Abensperg-Traun and Steven 1995, Majer 1997).

Although it is a central tenet of ecological methodology (Southwood and Henderson 2000), the impact of methodological bias on experimental and sampling design in the study of invertebrate assemblages is often a neglected point of discussion. Before a design that uses a single sampling method is initiated, it should be considered that the effect of treatments may be either obscured or falsified by sampling bias if species richness and relative abundance are the variables of interest (Melbourne 1999). Sampling bias should be of particular concern in studies where community-level effects are assessed by sampling assemblages of invertebrates at local scales. More specifically, hypothesis-testing studies designed to explore complex ecological processes, such as the factors determining assembly rules, require accurate measurement of species richness and relative abundance and must account for sampling bias. Ideally, this accounting should be done a posteriori and should consider the results of previous inventories whenever possible.

A structured inventory approach should also be adopted for larger-scale invertebrate studies, despite the cost savings of using sampling methods individually. Structured inventories are often contrasted with single-species time-series population studies, land management programs, or regional and geographic scale biodiversity assessment. In these types of studies, costly sampling protocols are considered unnecessary, intractable, and undesirable (Andersen 1997, Andersen et al. 2002). Nevertheless, even these studies would likely benefit from incorporating some of the methods of structured inventory, such as using multiple (more than one or two) sampling techniques. The shown effectiveness of using a structured inventory approach to sampling ants (Longino and Colwell 1997, Fisher 1999a, Agosti et al. 2000a, Longino et al. 2002) and spiders (Coddington et al. 1991, Silva and Coddington 1996, Dobyns 1997, Toti et al. 2000, Sørensen et al. 2002) also supports its broader use in taxonomic studies. For these studies, accurate assess-

ments of species richness and the time savings relative to traditional taxonomic studies will be particularly valuable. Finally, an increase in the use of structured inventory to study invertebrates in a variety of habitats (regardless of the type of study) will make a significant contribution toward cataloging, conserving, and understanding biodiversity.

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