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Scale dependence of diversity measures in a leaf-litter ant assemblage

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A reliable characterization of community diversity and composition, necessary to allow inter-site comparisons and to monitor changes, is especially difficult to reach in speciose invertebrate communities. Spatial components of the sampling design (sampling interval, extent and grain) as well as temporal variations of species density affect the measures of diversity (species richness S, Buzas and Gibson's evenness E and Shannon's heterogeneity H). Our aim was to document the small-scale spatial distribution of leaf litter ants in a subtropical dry forest of the Argentinian Chaco and analyze how the community characterization was best achieved with a minimal sampling effort. The work was based on the recent standardized protocol for collecting ants of the leaf litter ("A.L.L.": 20 samples at intervals of 10 m). To evaluate the consistency of the sampling method in time and space, the selected site was first subject to a preliminary transect, then submitted after a 9-month interval to an 8-fold oversampling campaign (160 samples at interval of 1.25 m). Leaf litter ants were extracted from elementary 1 m^2 quadrats with Winkler apparatus. An increase in the number of samples collected increased S and decreased E but did not affect much H. The sampling interval and extent did not affect S and H beyond a distance of 10 m between samples. An increase of the sampling grain had a similar effect on S than a corresponding increase of the number of samples collected, but caused a proportionaly greater increase of H. The density of species m^{-2} varied twofold after a 9-month interval; the effect on S could only be partially corrected by rarefaction. The measure of species numerical dominance was little affected by the season. A single standardized A.L.L. transect with Winkler samples collected $<45\%$ of the species present in the assemblage. All frequent species were included but their relative frequency was not always representative. A log series distribution of species occurrences was oberved. Fisher's α and Shannon's H were the most appropriate diversity indexes. The former was useful to rarefy or abundify S and the latter was robust against sample size effects. Both parametric and Soberón and Llorente extrapolation methods outperformed non-parametric methods and yielded a fair estimate of total species richness along the transect, a minimum value of S for the habitat sampled.

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Conservation biologists and environmental planners need reliable methods to evaluate the biological value of sites and to monitor changes over time. A major difficulty encountered when conducting diversity inventories is that species diversity cannot be recorded without reference to space, time and collection method. Components of species diversity include species richness (S, the number of species) and species evenness (E, equitability

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of the distribution of species abundance). Species diversity can be summarized into a single index of heterogeneity such as the Shannon's index H ($H = \ln S + \ln E$) (Hayek and Buzas 1997). To obtain the exact values of S, E, and H, complete diversity inventories should be conducted but are almost an unachievable goal for invertebrate taxa, especially under the tropics (Longino and Colwell 1997, Lawton et al. 1998, Longino et al. 2002). Alternatively, structured inventories based on limited but well-quantified sampling effort aim to reliably characterize communities (Longino and Colwell 1997) but depend on the spatial scale considered. The spatial components of the sampling scheme can be decomposed into sampling grain, interval and extent (Wiens 1989, Palmer and White 1994, Legendre and Legendre 1998). Sampling grain is the area concerned by each elementary sampling unit. Sampling interval is the distance between individual sampling units. Sampling extent is the total length, area or volume included in the study. In the case of a line-transect, the number of samples correspond to the extent divided by the interval. Adjacent sampling units are generally more similar in their fauna or flora than distant ones (Palmer 1995). In the case of social insects, if the sampling interval is too short one can expect to collect individuals from the same colony in contiguous samples. This should reduce the rate of species accumulation, in other terms the efficacy of the inventory and the shape of the species abundance distribution. On the other hand, increasing the sampling interval requires more field work and might also be unpractical when patches of habitat are small.

To circumvent the difficulty of comparing structured inventories with various spatial designs, an effort towards standardization of sampling protocols has been realized for a variety of taxa such as mammals (Wilson et al. 1996), amphibians (Heyer et al. 1993), termites (Eggleton et al. 1995, Jones and Eggleton 2000) and ants (Agosti and Alonso 2000).

Among invertebrates, ants have numerous attributes that make them useful for biological evaluation and monitoring (Majer 1983, New 1995). They are ecologically important in most terrestrial ecosystems. In the Amazonian rainforest they constitute up to 15% of the total animal biomass (Fittkau and Klinge 1973). With 11 000 described species (Agosti 2003), it is not an hyperdiverse group and their taxonomy is fairly well known (Bolton 1994, 1995) and accessible to non-specialists (Oliver and Beattie 1996). They are good indicators of environmental changes (Majer 1983, Andersen 1997, Andersen and Sparling 1997, Peck et al. 1998, Vasconcelos 1999, Carvalho and Vasconcelos 1999, Whitford et al. 1999, Kaspari and Majer 2000, Kalif et al. 2001, Vasconcelos et al. 2001) and are useful for conservation planning (Alonso 2000, Alonso and Agosti 2000).

The standardized protocol for ground-dwelling ants, abbreviated "A.L.L." (Ants of the Leaf Litter), consists in a line-transect with an extent of 200 m^2 and a sampling interval of 10 m. The leaf litter fauna from 1 m^2 quadrats (= sampling grain) is extracted with a mini-Winkler apparatus (Fisher 1998, Bestelmeyer et al. 2000). Other fractions of the local ant fauna can be collected by complementary methods (pitfall activity traps, soil samples, wood samples and visual search) (Agosti et al. 2000). Data sets can be deposited in a database available on-line (Agosti 2003).

The use of the same sampling effort and methods should allow comparisons of inventories conducted by different research teams at different sites and lead to global analyses of species distribution. However, it may still be difficult to interpret the results of a single inventory since several questions remain open: which proportion of the local fauna is really collected, are all characteristic species (dominant species, functional groups, ...) of the assemblage included, are the measured species evenness and heterogeneity representative of the assemblage, would comparable results be obtained at another time of the year? The answers depend on the spatio-temporal distribution of individuals. Ants are social insects and most of them have sessile colonies so that one may expect a fair consistence between consecutive measures of species richness. In tropical forests the heterogeneity in species distribution may be high, for example Kaspari (2000) observed from 1 to 17 ant species nesting in patches of 1 m^2 of leaf litter. Behavioral traits of ants, such as competition or species associations, have also an effect on species spatial distribution and result in a patchy distribution of colonies, particularly marked in the canopy (arboreal ant mosaics) and to some extent at the ground level (Levings and Traniello 1981, Levings and Franks 1982, Majer 1993, Delabie et al. 2000a). Microenvironmental factors, such as nest site availability, are also known to affect species distribution (Byrne 1994, Kaspari 2000). Finally, despite the fact that most ants have sessile colonies, their abundance and foraging activity depends on temperature and humidity (Levings 1983, Bestelmeyer and Wiens 1996).

The aims of this paper were to study the effects of spatial components (number of samples, sampling interval, sampling extent, sampling grain) on diversity measures and to evaluate the performance of the standardized A.L.L. protocol at documenting local ant diversity. In particular, we addressed the following questions: is the sampling interval of 10 m optimal, are 20 samples enough to obtain a fair estimate of community diversity and to collect all numerically dominant species, what is the reproducibility of the diversity measures? To answer these questions the selected site was first subject to a preliminary transect, then submitted after a 9-month interval to an 8-fold oversam-

pling campaign. We focused on the most efficient collection method proposed in the A.L.L. protocol, the mini-Winkler extraction of leaf-litter ants (Fisher 1999, Delabie et al. 2000b).

Material and methods

Study site

The study site was located inside the Rio Pilcomayo National Park in northern Argentina (25°04′06″S, 58°05′36″W). The habitat, called "monte fuerte" is a subtropical mesoxerophile oligarchic forest (Pujalte et al. 1995, PHYSIS habitat unit 48.2412 of Devillers and Devillers-Terschuren 1996).

Sampling protocol, environmental measures

A preliminary transect, following the A.L.L. protocol (Agosti et al. 2000) was conducted on 8 October 1999. A 200 m long line transect was traced and at intervals of 10 m the leaf litter present inside a 1 m^2 quadrat was collected, sifted and put in a bag. The sifted material was brought back to the field laboratory and its fauna was extracted with a mini-Winkler apparatus (Fisher 1998) for 24 h. Temperature variations during the sampling period were recorded with a datalogger. A calibration transect was conducted 9 months later, between 23 and 31 July 2000, 2 m aside the preliminary transect. The calibration transect followed the same protocol as the preliminary transect except that samples were collected at an 8-fold increased density: central points of successive quadrats were at intervals of 1.25 m instead of the 10 m used in the preliminary transect. Temperature during that period fluctuated between 3.6°C (at night) and 27.6°C with an average of 14.1 ± 4.1°C and was colder than during the preliminary sampling of October 1999 (values of 18.0–24.4°C and 22.2 ± 1.5°C for the same parameters).

Data analysis

All ants were identified to species or alternatively to morphospecies. The data concerning both specimens and stations was input into a database (SIDbase, Leponce and Vander Linden 1999) which allowed to retrieve the data and perform all the subsequent diversity analyses. Species occurrence in samples (absence/presence data) was used as a surrogate of species abundance because ants are social insects, which implies that a single sample may contain an extreme abundance of a rare species (Longino 2000). Occurrences provide reliable information on species proportions and the statistical distributions that are used to fit species abundance observations can also be used for fitting species occurrences (Hayek and Buzas 1997).

Species richness (S), Shannon's index of diversity (H) and Buzas and Gibson's evenness E were calculated for an increasing number of samples taken in natural order to keep the sampling interval to a constant value of 1.25 m. H was obtained from the equation: $H = -\Sigma p_i . \ln(p_i)$ where p_i is the proportion of the ith species (Shannon and Weaver 1949). Evenness (i.e. equitability or dominance), E, was calculated with the equation: $E = e^H / S (0 < E \leq 1)$. H was decomposed into $H = \ln S + \ln E$ by Hayek and Buzas (1997) and these two latter values were calculated as well because the pattern of H, ln S, ln E, and ln E/ln S during the accumulation of individuals are characteristic of the underlying distribution of species abundance. For a broken stick distribution ln E remains constant, for a log normal distribution ln E/ln S remains constant, and for a log series H remains constant. The evaluation of these patterns has been named "SHE analysis" by Hayek and Buzas (1997).

The effects of sampling interval and sampling extent, for fixed sample sizes (5, 10, 20, 40, 80, 160 quadrats) and for a sampling grain of 1 m^2 corresponding to the size of the elementary quadrats, on SHE values were explored by subsampling the pool of 160 quadrats. For each sample size and sampling interval (ranging from 1.25 to 40 m), all possible groups of quadrats were drawn from the pool of 160 quadrats. The effect of sampling grain was investigated by pooling 2, 4 or 8 contiguous quadrats yielding elongated sampling units. SHE values were then calculated according to a similar procedure as for the analysis of the effect of interval and extent. No attempt were made to test statistical hypotheses when comparing groups of different interval, extent or grain because of the non-independence of data (nearby quadrats more similar than distant ones, data present in one grain contribute to the data of the next highest grain, etc.

The predictive performance, in terms of estimation of local species richness, of a single A.L.L. transect was tested by decomposing the calibration transect (160 quadrats at intervals of 1.25 m) into eight A.L.L. transects (20 quadrats at intervals of 10 m). Each data set was then extrapolated by three different approaches (Chazdon et al. 1998): 1) parametric methods; 2) non-parametric methods; 3) curve-fitting extrapolation. We tried one or several estimators among the more commonly used in each category since at this stage of knowledge it is very difficult to guess a priori which estimator will work best for a given data set.

For parametric methods the observed relative abundance species distribution was first compared to several theoretical data distributions (log-normal, log series, broken-stick) (Preston 1948, Magurran 1988, Miller and Wiegert 1989, Hayek and Buzas 1997, Krebs

1999). Our data fitted well a log series distribution (Fig. 4). For the logarithmic series the total number of species is given by: $S = -\alpha \cdot \ln(1-x)$ (eq. 9.12 in Hayek and Buzas 1997) where α is a constant and x a number ($0 < x \leq 1$) can be calculated with $x = I/(I+\alpha)$ where I is the number of species occurrences (eq. 9.14 in Hayek and Buzas 1997). Log series parameter α was calculated with the computer program EstimateS (Colwell 1997). The relationship between species occurrences (I) and sample size (A) was calculated by fitting a linear function to the points with Statistica 5.5 (Anon. 2000). To estimate S for 160 samples, the α value obtained with 20 samples was used and the number of species occurrences was extrapolated with the linear function linking I with A.

Among non-parametric estimators of species richness, five common incidence-based estimators were compared (see Colwell 1997, EstimateS user guide for their description): Jackknife 1 and 2 (Heltsche and Forrester 1983, Palmer 1991), Chao 2 (Chao 1987), bootstrap (Smith and van Belle 1984), and ICE (Lee and Chao 1994). These estimators were calculated with EstimateS 5 (Colwell 1997).

Among curve-fitting extrapolation methods two non-asymptotic models were chosen because the species accumulation curve failed to reach a plateau (Fig. 2): a) the Arrhenius species-area model: $S = c.A^{-z}$ where z and c are curve-fitting parameters (Arrhenius 1921, Preston 1962a, b); b) the Soberón and Llorente model (Soberón and Llorente 1993, Fisher 1999): $S(t) = \ln(1 + z.a.t)/z$ which assumes that the probability of adding a new species depends on the current size of the species list. The parameter t represents the sampling effort (i.e. sampling time, number of samples, number of individuals), other parameters (z, a) are curve-fitting parameters. Species accumulation curves for each of the 8 data sets were smoothed (sample-based rarefaction sensu Gotelli and Colwell 2001) by 500 random ordering of samples using EstimateS 5 (Colwell 1997). Models were fit to the curves by the quasi-Newton method provided in Statistica 5.5 (Anon. 2000).

The reproducibility of diversity measures obtained with a single A.L.L. transect and the mini-Winkler method was evaluated by comparing the values obtained with the 8 A.L.L. transects constituting the calibration transect to those obtained with the preliminary transect. Species richness was compared among transects by adjusting the series of samples to a common number of occurrences, a procedure called rarefaction (Sanders 1968, Krebs 1999, Gotelli and Colwell 2001). Rarefaction curves were calculated with the Coleman method of EstimateS 5 (Colwell 1997). In addition, the rarefied species richness for an equivalent α diversity was calculated with the formula: $S_1 = \alpha_2.\ln(1+(I_1/\alpha_2))$ where α_2 represents the parameter of the log series for I_2 occurrences and S_2 species and where S_1 is the expected species richness for an equivalent diversity with a lower number of occurrences I_1 ($I_1 < I_2$) (eq. 12.12 in Hayek and Buzas 1997).

Results

Species spatial distribution

Sixty-six species corresponding to 720 occurrences and 10 554 individuals were found in the 160 quadrats of the calibration transect. A single quadrat contained between 0 and 13 species (median value = 4.0, n = 160) and the Jaccard index of faunal similarity between quadrats was 0.18 ± 0.16 (avg $\pm$ SD, n = 12 654). Species present in only one ("uniques") or two ("duplicates") quadrats represented 44% of the 66 species collected. Only 11 species were found in at least 10% of the quadrats, and will hereafter be referred as "frequent species". An interval of 1.25 m revealed that for most of them, except the arboreal *Crematogaster* sp.2 and the *Pheidole* sp.1 (species #6 and #7 on Fig. 1), occurrences are non-randomly clumped in adjacent quadrats (Runs tests, $p \leq 0.05$). By contrast, less frequent species that occurred in at least 4 quadrats were generally randomly distributed (14 of the 21 Runs tests performed on these species yielded a $p > 0.05$). The randomness of the distribution of the 34 remaining species was not tested due to insufficient data.

S, H, E vs number of samples

The mean number of species collected in the calibration transect, with a sampling interval of 1.25 m, could be approximated by a logarithmic function of the number of quadrats and of species occurrences (Fig. 2). After 160 quadrats no plateau was reached. The number of uniques reached 20 and was still increasing. The number of duplicates tended to level off to 9 species beyond 110 quadrats. Values of S, E, H for an increasing number of quadrats, taken in natural order to keep a fixed sampling interval of 1.25 m, are plotted in Fig. 3. Evenness values decreased as quadrats accumulated; ln(E) decreased by the same amount as ln(S) so that H ($H = \ln S + \ln E$) changed little beyond 22 samples (around 70 species occurrences). This pattern resembles the typical pattern obtained for a log series distribution of abundance (see Fig. 14.1 in Hayek and Buzas 1997). The species abundance distribution of the calibration transect indeed conformed well to a log series distribution (goodness of fit test, $\chi^2 = 6.46$, DF = 6, ns) (Fig. 4). The corresponding log series Fisher's α parameter was 17.7.

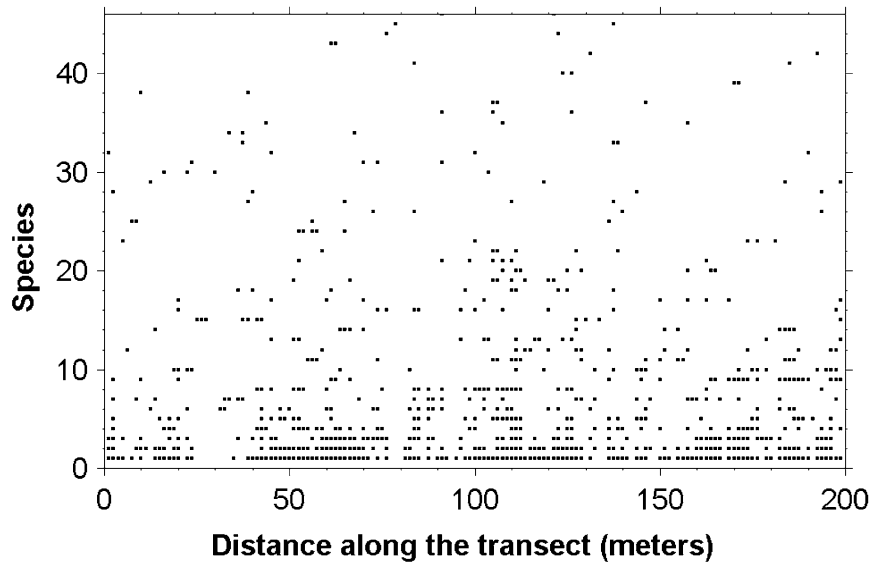

Fig. 1. Spatial distribution of the 46 ant species present in at least two samples along the 200 m calibration transect. Each square represent the species presence in a 1 m^2 quadrat. Quadrats were separated by 0.25 m. Each row represents a different species. Species were sorted by decreasing occurrence in samples.

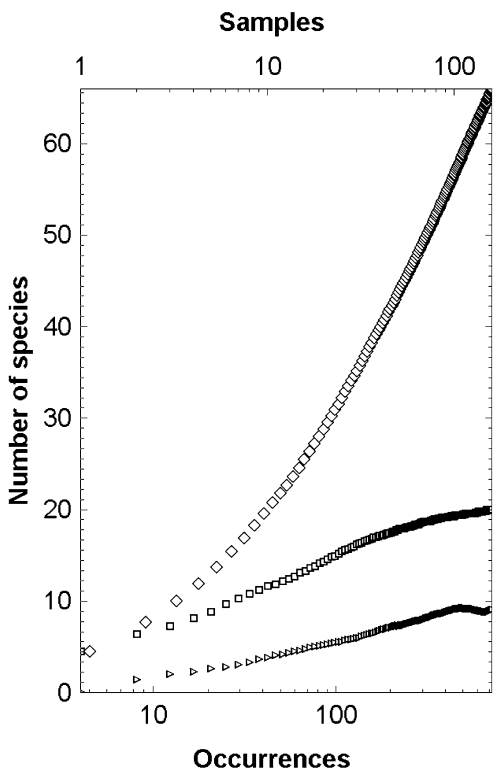

Fig. 2. Rarefaction curve representing the average number of species expected for a given number of quadrats (diamonds, sample-based rarefaction sensu Gotelli and Colwell 2001) or species occurrence (occurrence-based rarefaction, superimposed to the previous curve) and for a given number of species present in only one ("uniques", squares) or two quadrats ("duplicates", triangles). The abscissa is scaled logarithmically to reveal more clearly the logarithmic nature of curves.

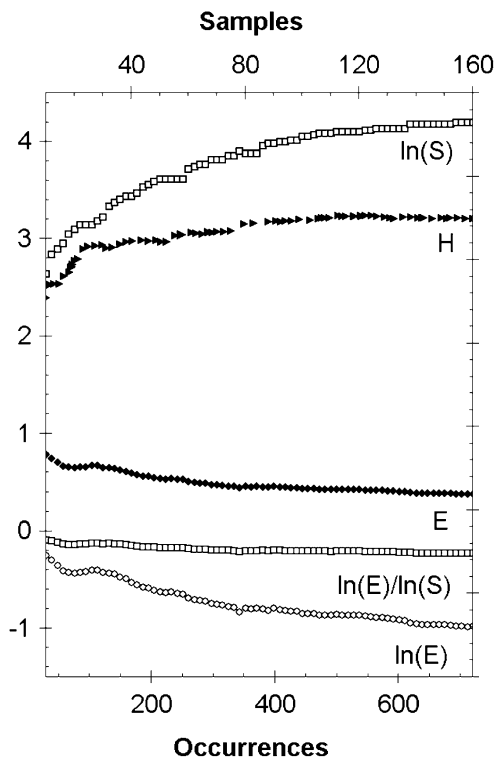

Fig. 3. SHE analysis of the calibration transect. Values for species richness S, Shannon H, and Hayek and Gibson's evenness E are calculated for an increasing number of quadrats taken in natural order of accumulation along the transect. $H = \ln S + \ln E$.

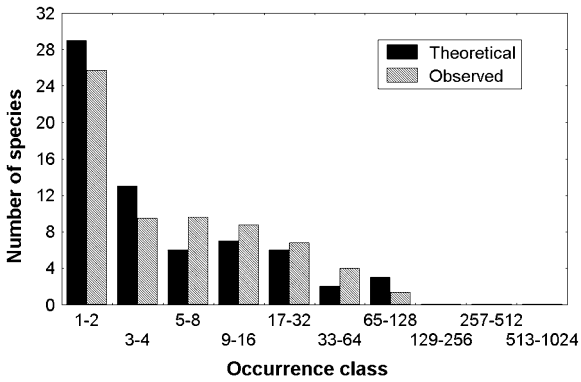

Fig. 4. Species occurrence distribution (hatched) and predicted values for a log series distribution with $\alpha = 17.7$ (solid).

S, H, E vs sampling interval and extent

As Fig. 5 shows, with a sampling grain of 1 m^2, the number of samples had a stronger influence than sampling interval and extent on values of S, H and E. This is particularly true for evenness E, which was almost constant for a given sample size but ranged from 0.87, with 5 samples, to 0.37, with 160 samples. S and H initially increased with the sampling interval and extent but reached a plateau for intervals over 10 m and extents over 100 m^2. Shannon's H varied between 2.3 (5 samples at intervals of 1.25 m) to 3.2 (160 samples).

S, H, E vs sampling grain

Contiguous quadrats were pooled to investigate the effect on diversity measures of a doubling of the sampling grain to 2, 4 and 8 m^2. To avoid the depressing effect caused by small intervals, sampling intervals considered were equal or at least 10 m. Mean values of SHE for 5, 10 and 20 sampling units are presented in Fig. 6. For a given sampling effort, doubling the grain or doubling the number of samples yielded similar results in term of species richness but caused a proportionally greater increase of heterogeneity (H). Evenness values decreased much more when the number of samples was doubled than when the grain was doubled.

Performance of the standardized A.L.L. protocol

Inside the area sampled of 200 m^2 it appeared that, with 20 samples at intervals of 10 m, a substantial variation of the diversity measures was observed among the 8 A.L.L. transects constituting the calibration transect (Fig. 5). The variation range was 27–32 (average = 30 ± 2) for the species richness S, 910–1865 (average = 1320 ± 369) for the number of individuals N, 77–104 (average = 90 ± 9) for the number of occurrences I, 0.59–0.69 (average = 0.64 ± 0.03) for the evenness E, 2.87–3.03 for Shannon's H (average = 2.94 ± 0.07), and 13.3–17.9 for Fisher's α (average = 15.7 ± 1.8). Therefore, on the average, a single A.L.L. transect collected $< 45\%$ (30/66) of the species really present in the habitat. The average faunal similarity between the 8 A.L.L. transects, measured with the Jaccard index, was 0.48 ± 0.06.

Extrapolations of S from 20 samples

The performance of various extrapolation methods in estimating species richness from the 8 A.L.L. subtran-

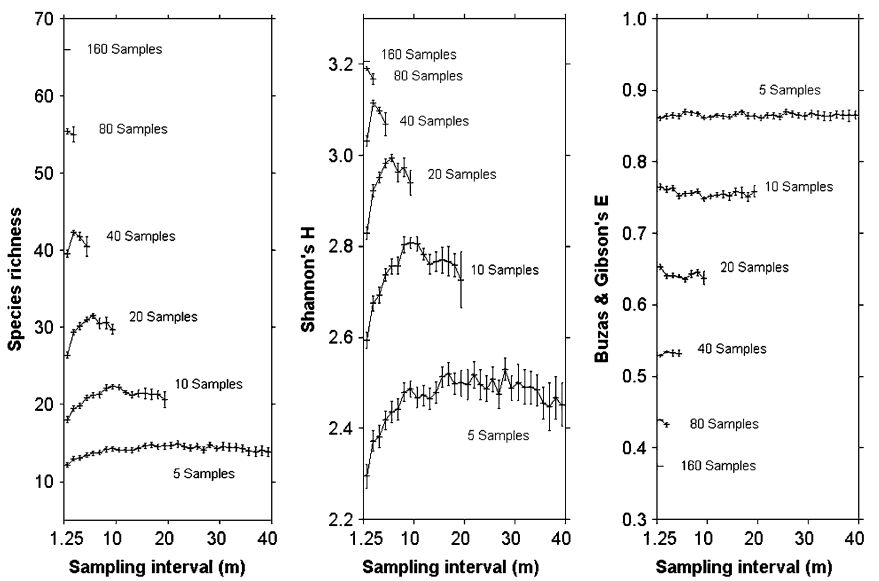

Fig. 5. Effect of sampling interval on mean values of species richness (S), evenness (E) and heterogeneity (H). Vertical bars indicate the standard error on the mean. The effect is presented by classes of sample sizes because of the predominent effect of this latter factor on S, H, E values. The sampling extent corresponding to each mean can be easily calculated by multiplying the sampling interval by the number of samples (on the x-axis, an extent of 200 m^2 corresponds to an interval of 40, 20, 10, 5, 2.5, 1.25 m for 5, 10, 20, 40, 80, 160 samples respectively). The sampling grain was kept constant to 1 m^2.

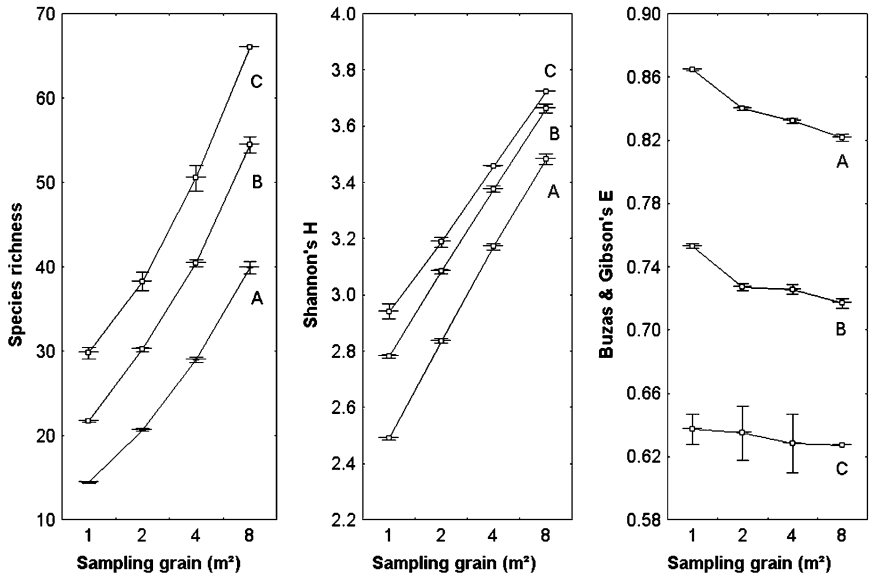

Fig. 6. Effect of sampling grain on mean values of species richness (S), heterogeneity (H) and evenness (E). Means were calculated for sampling intervals equal to or over 10 m to reduce the influence of this factor on S, H, E. Vertical bars indicate the standard error on the mean. Curves A, B, C correspond to 5, 10 and 20 sampling units respectively. A sampling unit comprises 2, 4 or 8 contiguous 1 m^2 sampling quadrats that were pooled to increase the sampling grain over 1 m^2.

sects was compared in Fig. 7. Parametric and curve-fitting extrapolation methods allow to calculate an estimate for a given number of samples. Since the species richness for 160 samples was known (66 species), extrapolations were performed for 160 samples with the parametric log series model and the curve-fitting species-area and Soberón and Llorente models (Fig. 7A). The log series and the Soberón and Llorente models yielded both the closest estimates although they tended to underestimate the true value by 10% on average. The species-area model of Arrhenius tended to largely overestimate the true value. All non-parametric estimators for incidence data (i.e. based on species occurrence) which were tested (Jackknife 1 and 2, Chao 2, Bootstrap, ICE) tended to underestimate the total species richness which was at least 66 species (Fig. 7B). These five non-

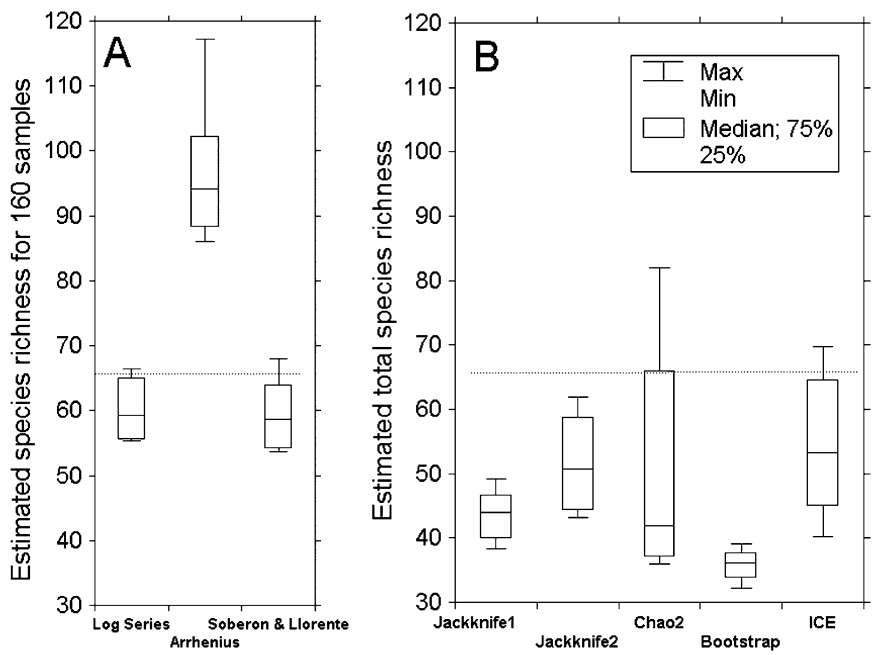

Fig. 7. Extrapolation of species richness from the 8 standardized A.L.L. transects (20 samples at intervals of 10 m) composing the calibration transect. Comparison of the performance of (A) parametric, curve-fitting and (B) non-parametric extrapolation methods. Observed species richness for 160 samples, a minimum value for the true total species richness, was 66 species (dotted line). All estimations were based on occurrence data.

parametric estimators still steadily increased with sample size so that the value obtained with 20 samples cannot be considered as a stable estimate of total species richness. Even with 160 samples all non-parametric estimators failed to reach a stable value of total species richness.

Species proportions

In seven out of the eight A.L.L. transects extracted from the calibration transect, all locally frequent species were collected (Fig. 8). In one case, the frequent species *Crematogaster* sp.2 was missed.

Temporal variation of S, H, E

A preliminary A.L.L. transect was performed 9 months earlier 2 m aside the calibration transect. Diversity values obtained with this preliminary transect were $S = 45$ species, $E = 0.66$, $H = 3.39$, $I = 161$ occurrences, $N = 2316$ individuals, Fisher's $\alpha = 20.7$. Its average faunal similarity with the 8 A.L.L. transects was 0.44 ± 0.04 (Jaccard index). The density of individuals collected and the number of species occurrences m^{-2} were significantly higher in the preliminary transect than in the calibration transect: median values of 68.5 vs 33.0 individuals m^{-2} (Mann-Whitney rank sum test $U = 984$, $n1 = 20$, $n2 = 160$, $p < 0.005$) and of 7.5 vs 4.0 species m^{-2} (Mann-Whitney rank sum test $U = 700.5$, $n1 = 20$, $n2 = 160$, $p < 0.001$). As a consequence, the accumulation of species was faster during the preliminary than during the calibration transect and the number of uniques began to level off. Despite an 8-fold more intensive sampling effort, 8 species found in the preliminary transect were not collected in the calibration transect. All these 8 species were infrequent (species occurrence: 1–3/20 samples, species abundance: 1–8 individuals) (Appendix 1). All but one of the 11 frequent species of the calibration transect were also found among the 20 frequent species of the preliminary transect. However *Hypoponera* sp.4, present in 28/60 samples and ranked 8th most frequent species in the calibration transect was only found in 1/20 samples of the preliminary transect.

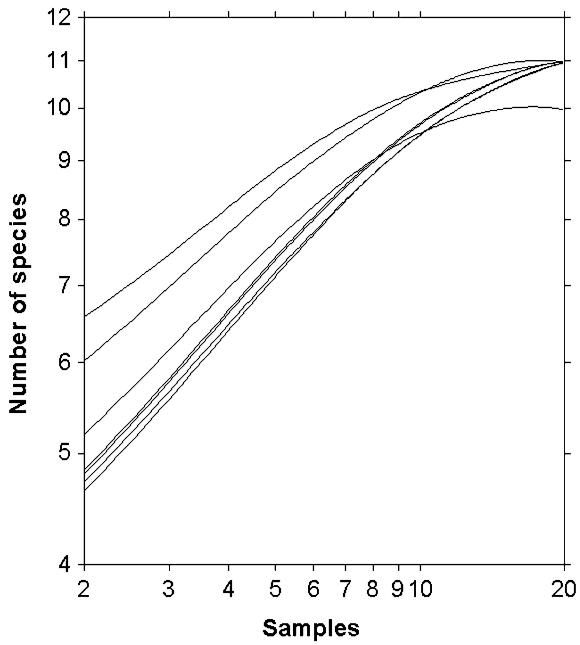

Fig. 8. Sample-based rarefaction curves of the 11 frequent species (i.e. present in at least 10% of the whole 160 samples) for each of the 8 A.L.L. standardized transects (20 samples at intervals of 10 m) which composed the calibration transect (160 samples at intervals of 1.25 m). Each curve represents the expected number of frequent species collected for a given sampling effort. Both axes were scaled logarithmically to better distinguish between curves.

The rarefaction technique allows to adjust a series of samples to a common number of individuals so that species richness can be compared among samples. To evaluate the performance of the rarefaction method to buffer the measure of S against seasonal variations, rarefaction curves were calculated for both the preliminary transect and the calibration transect (decomposed into 8 A.L.L. subtransects so that both the number of samples and the sampling interval were identical to those of the preliminary transect) (Fig. 9). The expected species richness for the largest common species occurrence (77) was 32.5 for the preliminary transect and 27.6 ± 1.7 for the other 8 transects.

When the α parameter of the log series is used to predict the rarefied species richness of the preliminary transect for 77 occurrences one obtains a value of $S = 20.7 \ln(1 + (77/20.7)) = 32.1$ species. The same method applied to the other 8 transects yielded 27.8 ± 1.7 species for 77 occurrences.

Discussion

Composition and spatial structure of the leaf litter ant community

The leaf litter ant community was composed of a few numerically dominant ants and of numerous rare species. Eighty-three percent of the 66 species encountered in the calibration transect were present in $< 10\%$ of the total area sampled. Even more, 44% of the species collected were known from only one or two samples (i.e. $< 1.25\%$ of the surface sampled). Eleven species were frequent (present in over 10% of the samples of the calibration transect). These dominant species were predominantly Myrmicinae belonging to genera such as *Pheidole* and *Solenopsis* as it is often the case with Winkler extracts (Ward 2000). Preliminary data suggest that many of the frequent species probably nest in the soil. Individuals of all 11 frequent species but *Crematogaster* sp.2 – an

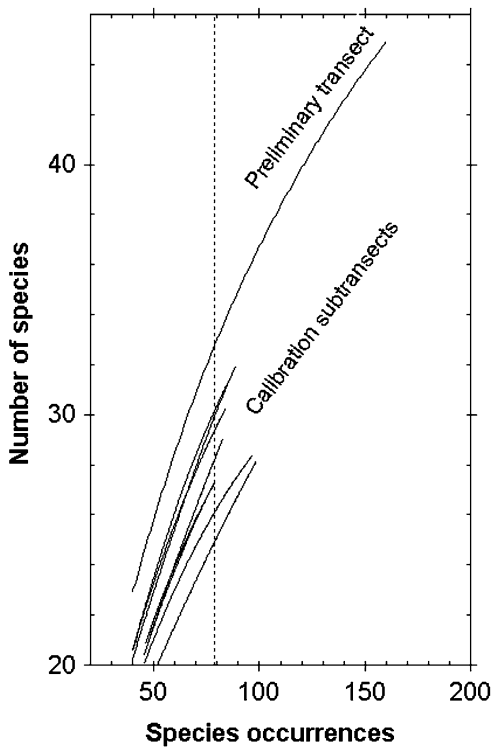

Fig. 9. Temporal variations of species richness between the preliminary transect (A.L.L. protocol: 20 quadrats of 1 m^2 at intervals of 10 m) and the calibration transect (8-fold oversampled A.L.L. protocol) sampled 9 months later at the same station but in colder weather conditions. Comparison of species richness between the two period for an identical sampling protocol (A.L.L.) and a common number of species occurrences (dotted line).

arboreal species – were found among 100 soil samples collected at the same locality (unpubl.). Queens were found among these soil samples for *Solenopsis* sp.1, *Brachymyrmex physogaster*, *Paratrechina* sp.2, *Octostruma rugifera* and *Hypoponera* sp. prox. *trigona*. Nesting in the soil might be advantageous to buffer against extreme temperature variations experienced in the Chaco region (Burgos 1970).

Because ants live in colonies varying largely in size, it is not possible to conclude that two occurrences of the same species in neighbour quadrats correspond to two distinct colonies. This would require additional information (such as presence of reproductives in nests, tests of antagonism, genetic or chemical analyses) that is time-consuming and incompatible with a rapid evaluation of community diversity. In this respect the analysis of community diversity of colonial organisms such as ants differ from the analysis of diversity of non colonial organisms where what is taken into account is the number of specimens of each species encountered during the inventory. In the context of the current diversity inventory "species frequency" should be understood as "species numerical dominance", a measure that is ecologically meaningful anyway. Unfrequent species showed little clumping in their spatial distribution (Fig. 1) suggesting that their colony size is small. Frequent species appeared generally clumped but it is unclear if the aggregates are constituted by one or several colonies.

Diversity estimates vs sampling design

Diversity measures vs number of samples

The number of samples collected had a much stronger influence than sampling interval and extent on measures of community species richness. At the scale of the 200 m transect, species richness increased logarithmically with the area sampled and the number of uniques was still rising (Fig. 2). When an inventory is nearly completed uniques decline (Longino 2000, Longino et al. 2002). At a larger scale, the slope of the species accumulation curve may change and result in a sigmoidal curve (Longino et al. 2002). Even if there is a limited number of species in the community considered, the species accumulation curve may hardly reach a plateau in a speciose environment like most tropical and subtropical forests because of rare species (Longino et al. 2002). These rare species may correspond to species normally not living in the habitat considered or to species generally not collected with the method considered.

Species evenness was particularly sensitive to the sampling effort. Values of 0.87 were obtained with 5 samples, far from the 0.37 corresponding to 160 samples (Fig. 5). It is a trivial consequence of the fact that the commonness or rarity of species can not be assessed accurately with a few samples. With only 5 samples, for example, any species collected has a frequency at least equal to 20%. With 160 samples species frequencies may range from 0.625 to 100%. Comparison of equitability of species distribution among assemblages may thus be misleading especially if the number of samples considered is different.

Diversity measures vs sampling interval, extent and grain

For a fixed number of samples, the influence of sampling interval was slight on species richness and was even less conspicuous on species evenness (Fig. 5).

Species richness tended to be lower when the sampling interval was below 10 m (Fig. 5). This could be interpreted as the result of spatial autocorrelation for distances below 10 m, especially for the most frequent species since unfrequent species generally showed little clumping in their spatial distribution (Fig. 1). Over 10 m the sampling interval did not affect much S. This result is consistent with the findings of Fisher (1999) who observed that in Madagascar forests, rates of species accumulation were not improved beyond an interval of 5 m. Species evenness was almost insensitive to the sampling interval probably because the number of

samples is probably the major factor that affect evenness as already discussed. The effect of sampling interval on H ($= \ln S + \ln E$) is almost exclusively explained by the response of S since E was nearly constant for a fixed number of samples. In other words, H was lower for sampling intervals below 10 m.

Sampling extent followed the same general pattern as sampling interval (Fig. 5): lower species richness and heterogeneity for short sampling extent, evenness independent of extent for a given sample size. This is easily understood since extent is closely related to both interval and number of samples. Beyond an extent of 100 m^2, doubling the extent did not allow to collect more species (considering a given number of samples). This result has to be considered for a local scale. At regional or geographic scale a high species turnover between samples should occur.

An increase of sampling grain had a similar effect than a corresponding increase of the number of samples collected on species richness. Evenness decreased proportionaly less for an increase of grain than for a corresponding increase of the number of samples. As a result, an increase of grain caused a proportionally greater increase of heterogeneity (H) than a corresponding increase of the number of samples (Fig. 6). The accrual of species for a given area sampled is faster for a small compared to a large grain due to spatial dependence (Malsch 2000) and to the use of species occurrence. Compared to sampling interval and extent, it was the grain that had the stronger effect on S, a result consistent with those of Palmer and White (1994).

Reproducibility of diversity measures

The density of species m^{-2} varied two-fold at an interval of 9 months (median = 4.0 vs 7.5 species m^{-2}). During the cold season significantly fewer species were collected with an A.L.L. transect than during warmer weather (30 vs 45 species). Individual-based rarefaction (based on species abundance data) is commonly used to compensate for variations of species density and to compare the species richness among communities of similar taxonomic composition and coming from similar habitats (the smaller sample is supposed to be a random sample of the larger set) (Sanders 1968, Simberloff 1972, Krebs 1999). The rarefaction method is based on the frequency of each species (see Hayek and Buzas 1997 for details). The rarefaction of data sets corresponding to colonial organisms such as ants inventoried without clear identification of colonies has some peculiarities for two main reasons. First, as already discussed above, species numerical dominance rather than species frequency (calculated with the number of colonies present) is measured. Second, no more than one single species occurrence can be counted in a sampling unit (even if more than one colony is present) and some information on species spatial aggregation is lost. This bias can be reduced by using a sampling interval that is large and a sampling grain that is small in comparison to colony size. By contrast to individual-based rarefaction curves, which generally lie under sample-based rarefaction curves because of the spatial aggregation of individuals (Gotelli and Colwell 2001), the occurrence-based rarefaction curve is generally very slightly above the sample-based rarefaction curve. On Fig. 2 the sample-based rarefaction curve was superimposed on the occurrence-based rarefaction curve.

In our study, occurrence-based rarefaction only partially compensated for the variations of species density (32.5 instead of 27.6 species obtained for 77 cumulated occurrences) and yielded a result very close to the one obtained by using Fisher's α to rarefy (32.1 species). The rarefaction curve for the preliminary transect was above, rather than between, individual rarefaction curves of the 8 A.L.L. transects performed 9 months later. A possible explanation is that the sub-community sampled with Winkler extracts is larger during warm weather conditions. On the one hand, the probability to collect species from other strata than the leaf litter (i.e. species nesting in the soil or in trees) should increase with the higher number of foragers often associated with warmer temperatures (Levings 1983). On the other hand, an increased number of foragers should also increase the probability to collect species living in small colonies and present in low numbers in the sampling unit or species present in its surroundings. After a 9-month interval numerically dominant leaf litter ant species were not different. With activity traps (pitfalls), more marked seasonal differences among foraging ants may be observed in the Argentinian Chaco (Bestelmeyer and Wiens 1996).

Representativeness of a single A.L.L. transect

A single A.L.L. transect with Winkler samples collected on average $< 45\%$ of the species present in the leaf litter ant community. In a cocoa plantation in Brasil, a similar proportion of the leaf litter ant fauna present in 0.87 ha was captured on average with 20 Winkler samples (50/106 = 47%, Delabie et al. 2000b).

All frequent species were collected with a single A.L.L. transect. Nevertheless the estimation of species proportion remained approximative because of the limited number of samples. With 20 samples, unfrequent species that occur by chance in 2 samples earn a frequency of 10% whereas a higher sampling effort would reveal that they are in fact rare. Conversely, common species may appear uncommon even though they are generally collected in at least 1 of the 20 samples.

Species richness for an increased sampling effort could be inferred with little error (average underestimation of 10%) by either a parametric log series or a curve-fitting extrapolation model (Soberón and Llorente 1993). Both approaches outperformed non-parametric methods (Fig. 7). With 20 samples and even with 160 samples, non-parametric estimators were far from reaching a stable estimate of total species richness. Other studies also obtained poor results with non-parametric methods. The analysis of 500 Winkler samples taken from 0.87 ha of cocoa plantation revealed that Jackknife 1 and ICE estimators did not reach an asymptote before 300 samples (Delabie et al. 2000b). The strong dependence of non-parametric estimators to sample size has also been observed in other ant inventories (Fisher 1996, 1998, 1999, Longino et al. 2002). Non-parametric estimators can be considered as the minimum richness in the habitat (Longino et al. 2002).

The oversampling of the A.L.L. protocol demonstrated that Shannon's index H was very similar among replicates whereas species richness, species occurrence and abundance varied substantially from one replicate to another. Beyond 22 samples (ca 70 species occurrences), ln E decreased by the same amount as ln S so that H ($H = \ln S + \ln E$) changed only from 2.9 to 3.2 (10%) when the number of samples considered changed from 22 to 160. The stability of H is a characteristic of the log series distribution (Hayek and Buzas 1997). H was affected by temporal variations of species density and a value of 3.4 was obtained for the preliminary A.L.L. transect during warmer weather conditions. This higher value was the reflect of differences in species richness (45 vs 30 ± 2 species) rather than of species evenness (0.66 vs 0.64 ± 0.03).

The heterogeneity of species spatial distribution was high (0–13 species m^{-2}) and the average faunal similarity between quadrats was low (Jaccard index = 0.18). This explains why diversity results obtained with replicated A.L.L. transects inside the same sampling extent were variable. As already clearly demonstrated by of Palmer and White (1994), no single species accumulation curve exists for a habitat, but instead a collection of curves can be drawn and their extrapolation may lead to quite variable results.

How these results could be generalized to other communities is still speculative because only a few communities have been inventoried intensively. A log series distribution of species occurrence was also observed in a leaf litter ant community from a Brazilian cocoa plantation (Delabie et al. 2000b, Leponce et al. 2003b) and from the Amazonian forest (Leponce et al. 2003a). In the former study the parametric log series and the Soberón and Llorente models also yielded the best estimates of species richness for 500 samples with the data from 25 samples. By combining several collection methods in order to inventory the complete ant fauna of a Costa Rican rainforest, Longino et al. (2002) obtained a log normal rather than a log series distribution of species occurrence. Collection methods taken individually yielded distributions close to a log series. It should also be noted that vascular plants may exhibit species spatial distributions very similar to those observed in the leaf litter ant community studied here (see Fig. 2 in Palmer 1995).

Conclusions

The standardization of sampling protocols is an important step to allow quantitative comparisons between communities in space and time. A single standardized A.L.L. transect with Winkler samples appears as the minimum sampling effort necessary for characterizing the leaf litter ant assemblage studied. Indeed, with 20 samples: 1) all frequent species were included; 2) the Shannon's index of diversity became little dependent of sample size; 3) the species accumulation curve entered in a stable logarithmic phase and species richness for an 8-fold increased sampling effort could be inferred with a precision of ca 10%. As stressed by Cao et al. (2002), equal-sized samples may however differentially represent the communities from which they are drawn. The autosimilarity between replicated A.L.L. transects drawn from the community sampled was near 50% (Jaccard Index), a value that guarantees some degree of representativeness and should allow to measure between-site complementarity (Cao et al. 2002). With a single transect $< 45\%$ of the local ant fauna was collected and the relative frequency of species was not always representative. One or two additional transects allowed to collect respectively $< 60\%$ and $< 72\%$ of the local ant fauna (Fig. 2) and are probably preferable to a single transect in most situations, especially in the case of assemblages more diverse than the one studied. With eight transects, the species accumulation curve was not asymptotic yet, indicating that a higher sampling effort is required to estimate the total species richness of the assemblage (Leponce et al. 2003b). The density of species m^{-2} varied twofold after a 9-month interval. As a result, despite the use of identical sampling protocols, measures of species richness were on average 50% (45 vs 30 species) higher during warmer weather conditions and could only be partially corrected by rarefaction. Our results emphasize the need to compare diversity among communities for a similar number of species occurrences and whenever possible to conduct inventories in similar weather conditions and at a period where most species are active in order to maximize the number of species collected per sampling effort. In the case of a log series distribution, the widespread Fisher's log series α (Fisher et al. 1943) and Shannon's index were the most appropriate diversity indexes. The former was

useful to rarefy or abundify species richness and the latter was robust against sample size effects. Finally, both parametric and Soberón and Llorente extrapolation methods yielded a fair estimate of total species richness along the transect, a minimum value of species richness for the assemblage sampled.

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Appendix 1. Species found in the preliminary and in the calibration transect. Frequency of occurrence in the 20 and 160 samples respectively.

Subfamily – Species	Preliminary transect %	Calibration transect %
Formicinae		
Brachymyrmex physogaster	45.0	56.9
Camponotus (*Myrmosphincta*) sp.11	0.0	1.9
Camponotus (*Myrmaphaenus*) sp.13	5.0	0.0
Camponotus (*Pseudocolobopsis*) sp.17	0.0	0.6
Camponotus (*Myrmothrix*) *renggeri*	0.0	3.1
Camponotus arborens	0.0	1.3
Camponotus crassus	15.0	9.4
Myrmelachista sp.2	0.0	0.6
Paratrechina pubens	20.0	2.5
Paratrechina sp.2	50.0	30.0
Myrmicinae		
Acromyrmex hispidus fallax	10.0	1.3
Apterostigma sp. *complex pilosum*	0.0	1.9
Cephalotes minutus	5.0	3.8
Crematogaster corticicola	5.0	3.1
Crematogaster euterpe	5.0	0.0
Crematogaster montezumia	5.0	1.3
Crematogaster sp.11	0.0	0.6
Crematogaster sp.14	0.0	1.3
Crematogaster sp.2	45.0	17.5
Crematogaster sp.5	15.0	0.0
Crematogaster sp.7	0.0	0.6
Cyphomyrmex rimosus	25.0	5.6
Megalomyrmex drifti	0.0	0.6
Myrmicocrypta foreli	5.0	0.0
Octostruma rugifera	60.0	23.8
Oxyepoecus sp.1	0.0	0.6
Pheidole aberrans	0.0	6.9
Pheidole radoszkowskii reflexans	20.0	10.6
Pheidole sp.30	0.0	0.6
Pheidole sp.1	45.0	17.5
Pheidole sp.21	5.0	0.0
Pheidole sp.22	15.0	7.5
Pheidole sp.4	5.0	5.0
Pyramica crassicornis	5.0	1.3
Pyramica denticulata	15.0	13.1
Pyramica gr. appretiatus sp.1	0.0	1.3
Pyramica gr. appretiatus sp.2	10.0	0.0
Pyramica sp.2	5.0	4.4
Rogeria scobinata	20.0	6.3
Solenopsis sp.1	95.0	76.9
Solenopsis sp.13	0.0	0.6
Solenopsis sp.15	0.0	1.3
Solenopsis sp.2	10.0	6.9
Solenopsis sp.5	5.0	0.0
Solenopsis sp.7	0.0	0.6
Solenopsis sp.8	25.0	1.3
Strumigenys ogloblini	15.0	0.6
Strumigenys sp. *prox. elongata*	0.0	0.6
Wasmannia sp.1	50.0	41.3
Wasmannia sp.3	0.0	2.5
Ponerinae		
Amblyopone sp.1	0.0	0.6
Anochetus diegensis	0.0	2.5
Discothyrea neotropica	5.0	5.0
Ectatomma edentatum	10.0	8.1
Ectatomma permagnum	10.0	0.0
Gnamptogenys striatula	25.0	2.5
Heteroponera sp.1	0.0	1.9

Appendix 1. (Continued).

Subfamily – Species	Preliminary transect %	Calibration transect %
Hypoponera clavatula	5.0	0.6
Hypoponera opaciceps	0.0	2.5
Hypoponera opacior	15.0	2.5
Hypoponera sp.4	5.0	17.5
Hypoponera sp.5	0.0	0.6
Hypoponera sp. *prox. opaciceps*	5.0	1.9
Hypoponera sp. *prox. trigona*	30.0	16.9
Hypoponera sp.1	0.0	0.6
Leptogenys consanguinea	5.0	1.3
Odontomachus bauri	5.0	2.5
Odontomachus meinerti	0.0	0.6
Pachycondyla ferruginea	5.0	0.6
Pachycondyla harpax	10.0	2.5
Pachycondyla gr. villosa sp.1	0.0	0.6
Prionopelta punctulata	10.0	0.6
Typhlomyrmex pusillus	0.0	0.6
Pseudomyrmecinae		
Pseudomyrmex gracilis	0.0	1.9