

Characterizing termite assemblages in fragmented forests: A test case in the Argentinian Chaco

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Abstract Termites are major decomposers in tropical ecosystems. To characterize their assemblages in terms of taxonomical and functional composition, Jones and Eggleton (2000, *Journal of Applied Ecology* 37, 191–203) recently proposed a standardized sampling protocol based on belt transects of 100 m × 2 m. We evaluated the representativeness of samples obtained by this protocol, and its suitability to calculate diversity statistics, by replicating it in an area of naturally fragmented subtropical forest. We sampled six 100 m transects in separate small forest islets, and one transect extended to 500 m in a large islet, recording presence/absence data (occurrences) of termite species in successive quadrats of 5 m × 2 m. In the large islet, strips of 100 m within the 500 m transect produced extremely variable species richness figures. This variability was primarily due to heterogeneity in the spatial distribution of soil-dwelling termites. Combining non-contiguous quadrats allowed us to span a broader diversity of microhabitats for an equal effort, providing less variable results and faster species accumulation. Individual transects of 100 m in small forest islets yielded too few samples to allow reliable estimations of total species richness, although these transects when pooled constituted a useful data set for comparison with other sites. In the focal habitat, a single 100 m transect appeared therefore inadequate to allow a reliable characterization of the termite assemblage, even at the level of a single forest islet. To improve the rate of species accumulation and to obtain diversity statistics allowing intersite comparisons, we suggest the use of smaller, non-contiguous quadrats, and that sampling be continued until stable diversity estimates are obtained. In the habitat studied, such an alternative protocol could be adequately combined with a standardized protocol for collecting ground-dwelling ants.

Key words: community composition, habitat fragmentation, Isoptera, sampling standardization, spatial heterogeneity, species accumulation, species richness estimates.

INTRODUCTION

Termites are major components of tropical ecosystems, in which they perform an important ecological function as decomposers (Holt & Lepage 2000) and emitters of greenhouse gases (Sugimoto *et al.* 2000). Recent studies suggest that environmental degradation or disturbance may cause severe and long-lasting modifications of termite assemblages (Eggleton *et al.* 1995, 2002; Black & Okwakol 1997). However, a major hurdle to the assessment of these effects is that it is difficult to obtain a reliable characterization of such assemblages, which would allow intersite comparisons (Eggleton & Bignell 1995).

Termites being social insects, the unit of interest for biodiversity studies has to be defined beyond the individual level. Focusing on numbers of colonies is not satisfactory, because the size of individual colonies may differ considerably between or even within species (Lepage & Darlington 2000). An acceptable compro-

mise is to focus on occurrences, that is, recording presence/absence data for each species within a series of predefined quadrats. Although non-quantitative in terms of numbers of individuals or biomass, occurrence records at least provide an estimation of the probability of encounter with the various species, or of the fraction of the total area in which each species occurs. For those reasons, this procedure is commonly advised to evaluate the diversity of leaf-litter ants (Longino 2000; Fisher & Robertson 2002; Lepage *et al.* 2004).

To characterize Amazonian termite assemblages, DeSouza and Brown (1994) introduced a procedure of systematic sampling along belt transects of 110 m × 3 m. More recently, Jones and Eggleton (2000) suggested adopting a protocol based on 100 m × 2 m transects, including soil scrapes (see also Bignell & Eggleton 2000). A variant was proposed by Cancellato (2002), who suggested using six transects per habitat, each comprising five 5 m × 2 m quadrats at 15 m intervals. These methods introduce rigour into the sampling process by standardizing sampling effort. Compared to comprehensive surveys conducted in

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three equatorial forests of Asia & Africa, Jones and Eggleton (2000) obtained with single belt transects about one-third (31–36%) of the species present in the source assemblage, with little bias toward specific taxonomical categories or feeding guilds. Their protocol has been widely used across the world in recent years, mostly in equatorial forests (review in Davies *et al.* 2003a). However, up to now, the reproducibility of results obtained by this method and the representativeness of standardized samples with respect to their source assemblages have not been evaluated.

In the present study, we repeatedly applied the standardized protocol of Jones and Eggleton (2000) to assess its representativeness in a subtropical ecosystem and to evaluate its potential to calculate reliable diversity statistics. We worked in a naturally fragmented forest, which can be considered as a metacommunity, whose constitutive parts are a multitude of fragments of various sizes and degree of isolation. Our investigation was carried out at both levels. An extended transect of 500 m was positioned within a large islet of forest to evaluate the reproducibility and representativeness of the method at the local community scale. In addition, six standard transects were sampled in distant islets of forest to test how well this procedure characterized the metacommunity.

STUDY SITE AND METHODS

Study site

Field work took place in October 1999 and October 2001, in Parque Nacional Río Pilcomayo, Formosa Province, Argentina (latitude S 25°07', longitude W 58°10'). This protected area of about 500 km² is situated on the south bank of the Río Pilcomayo, in the eastern, humid part of the Gran Chaco. Average annual rainfall in the park is about 1200 mm, with a short dry period (0–3 months) in the southern winter, between June and September. Temperature fluctuates broadly, with an annual average of 22–24°C and occasional winter frosts (Pujalte *et al.* 1995).

The park is a mosaic of vegetation types, depending primarily on inundation frequency. The present study was limited to the semideciduous forest (*monte fuerte*), which occupies 20–22% of the park area (Pujalte *et al.* 1995), but displays a considerable degree of natural fragmentation amidst a palm savanna (*pastizal*) matrix (Fig. 1).

Sampling

We applied the standardized protocol proposed by Jones and Eggleton (2000), consisting of 100 m long

transects, divided into 20 successive quadrats of 5 m × 2 m. A maximum of one man-hour was spent in each quadrat searching for termites in all potential microhabitats, including wood, leaf litter, soil (a dozen 12 × 12 × 10 cm scrapes), visible nests and galleries up to a height of 2 m. Searching time was reduced if all microhabitats could be adequately searched in less than one man-hour.

To test the representativeness of a belt transect at the local scale, we sampled a strip of 500 m × 2 m, corresponding to five consecutive 100 m transects, in a large forest islet. This work took place in October 2001. We started 5 m from the edge, to prevent interference from savanna specialists, and proceeded towards the centre of the islet (Fig. 1). To interpret the pattern of species distribution, we assessed three environmental variables, all of which integrate a number of elementary factors likely to influence termite distribution. In addition, these variables are conspicuous to the observer and easily measured. The first variable was distance to forest edge. The second was the number of rosettes of terrestrial bromeliads in each quadrat. *Pseudananas sagenarius* (Arruda) Camargo was the most abundant bromeliad, followed by *Aechmea distichantha* Lemaire. The third was the proportion of canopy closure, estimated from hemispherical images taken every 10 m along the transects with a Nikon Coolpix 950 digital camera fitted with a fisheye converter FCE8. Canopy closure was quantified with the free software *Gap Light Analyser* version 2.0 (Frazer *et al.* 1999).

To test the protocol at the metacommunity scale, one 100 m transect was sampled in each of six islets of *monte* spread over a distance of approximately 14 km (Fig. 1). Five transects were sampled in October 1999 and one in October 2001.

Data analysis

Termite samples were identified to species or morpho-species. We distinguished herein two major feeding groups, corresponding to groups I + II (wood-feeders, including litter-feeders) and III + IV (soil–wood interface-, humus- and soil-feeders) of Donovan *et al.* (2001). Matrices of species by transect quadrats were constructed, and filled with occurrence data (presence = 1, absence = 0). One occurrence was defined as the presence of one species in one 5 m × 2 m quadrat, no matter how many encounters with this species occurred in the quadrat or how many individuals were present.

To evaluate how much variation in observed species richness and other diversity statistics could be due to the position of the sampling strip, we considered the initial 100 m strip (quadrats 1–20) of the 500 m transect, then moved the considered strip by 10 m (quadrats 3–22) and repeated the operation to the end

of the transect (quadrats 81–100). This yielded 41 partially overlapping strips of 100 m. We tested an increase of the sampling extent by repeating this process with strips of 200 m (a total of 31 strips). We also tested modifications of the sampling interval by considering sets of 20 quadrats at intervals of 10 m (i.e. taking one quadrat out of two, 62 combinations) or 20 m (one quadrat out of every four, 24 combinations),

and 40 quadrats at intervals of 10 m (22 combinations).

Smoothed species accumulation curves (sample-based rarefaction curves of Gotelli & Colwell 2001), total species richness (TSR) estimates and other diversity statistics were computed using the free software *EstimateS*, version 5.0.1 (Colwell 1997). By this method, all sampling units are randomly ordinated,

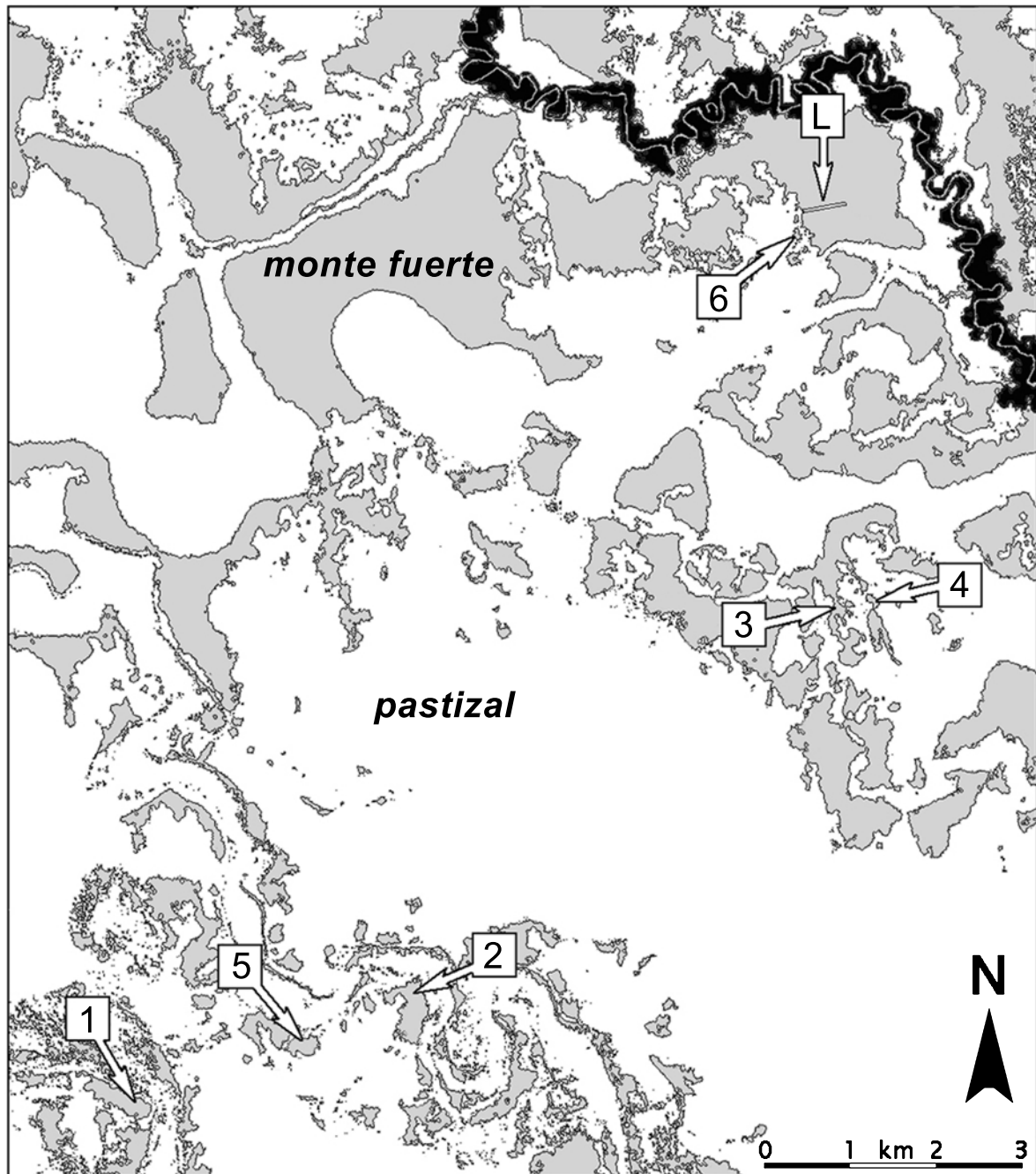


Fig. 1. Map of the study site, showing mosaic of habitats and position of transects. Small-islet, 100 m long transects are numbered 1–6, as in Table 1. L, Large-islet, 500 m long transect. White, herbaceous vegetation and palm savannas (*pastizal*); Grey, semideciduous forest (*monte fuerte*); Black, Rio Pilcomayo, bordered by riparian forest, marks the border between Argentina (to the south) and Paraguay.

without replacement. Curves are then calculated to describe how the number of occurrences, of observed species, of uniques (species found only once), of duplicates (species found exactly twice), and several diversity statistics vary as samples accumulate. The program repeats this procedure as instructed (1000 times) and calculates average values. Three non-parametric estimators of TSR were used: Chao 2 (Chao 1987), Jackknife 2 (Smith & van Belle 1984; Palmer 1991), and Incidence-based Coverage (ICE: Lee & Chao 1994). Detailed formulae for the calculation of these estimators are available in the online user guide of *EstimateS* (Colwell 1997) and in Chazdon *et al.* (1998). Additionally, *EstimateS* also calculated an estimator of the asymptote of the mean species accumulation curve fitted to the Michaelis-Menten equation (MMMean; see Raaijmakers 1987 for details), and Fisher's parameter α (Fisher *et al.* 1943).

RESULTS

Species distribution and representativeness of a standardized transect at the local community scale

Nineteen species in 129 occurrences were recorded from the 100 quadrats of the 500 m transect (Table 1). A close association emerged between the occurrence of termite species and the density of terrestrial bromeliads. The number of bromeliad rosettes per transect quadrat of 10 m² was a significant predictor of termite occurrence (multiple linear regression analysis, $r = 0.774$, $P < 0.001$), but distance to forest edge ($P = 0.78$) and canopy openness ($P = 0.49$) were not. Increased occurrence in bromeliad patches mostly involved soil- or interface-feeding termites, whereas wood-feeding species were more evenly distributed along the transect (Fig. 2).

Table 1. List of species records by transect

Family – Species	Food type	Small islets – Transect No.						Large islet Transect L
		1	2	3	4	5	6	
Kalotermitidae								
<i>Rugitermes rugosus</i>	W	2	3	1	1	–	1	8
<i>Neotermes</i> sp. A	W	1	2	1	1	1	1	3
<i>Neotermes</i> sp. B	W	1	–	–	–	–	–	2
<i>Neotermes</i> sp. C	W	1	–	–	1	–	–	–
<i>Tauritermes taurocephalus</i>	W	–	–	–	2	–	1	3
<i>Tauritermes</i> sp.	W	–	1	–	–	–	–	–
<i>Cryptotermes chacoensis</i>	W	–	–	1	–	–	1	–
Rhinotermitidae								
<i>Heterotermes longiceps</i>	W	–	2	3	–	–	–	7
Termitidae – Nasutitermitinae								
<i>Nasutitermes</i> sp. A	W	–	–	3	4	–	–	13
<i>Nasutitermes</i> sp. B	W	1	4	–	–	4	–	3
<i>Nasutitermes</i> sp. C	W	–	–	–	–	–	–	1
<i>Diversitermes diversimilis</i>	W	–	2	–	–	–	–	7
<i>Procornitermes striatus</i>	S	1	–	1	–	1	–	2
<i>Procornitermes triacifer</i>	S	–	–	–	–	–	1	3
Termitidae – Termitinae								
<i>Microcerotermes strunckii</i>	W	–	1	–	9	1	2	7
<i>Onkotermes brevicorniger</i>	S	1	–	–	–	–	–	–
<i>Termes nigrinus</i>	S	–	1	3	–	–	5	8
<i>Dihoplotermes inusitatus</i>	S	–	–	–	–	–	–	16
<i>Neocapritermes opacus</i>	S	–	–	–	–	–	1	3
Termitidae – Apicotermitinae								
<i>Anoplotermes</i> sp. A	S	1	–	–	–	–	–	14
<i>Anoplotermes</i> sp. B	S	–	–	2	–	1	1	21
<i>Anoplotermes</i> sp. C	S	–	–	1	–	–	3	5
<i>Anoplotermes</i> sp. D	S	–	–	1	–	–	–	–
<i>Aparatermes</i> sp. G	S	–	–	–	–	–	1	3
Total occurrences		9	16	17	18	8	18	129
Species		8	8	10	6	5	11	19

Values show number of occurrences (presence of a species in one quadrat of 5 m × 2 m). –, species not detected; S, wood–soil interface, humus, or soil; W, wood or litter.

Nomenclature follows Constantino (1998), except for *Onkotermes brevicorniger* (transferred from *Synhamitermes* by Constantino *et al.* 2002) and *Cryptotermes chacoensis* (described in Roisin 2003).

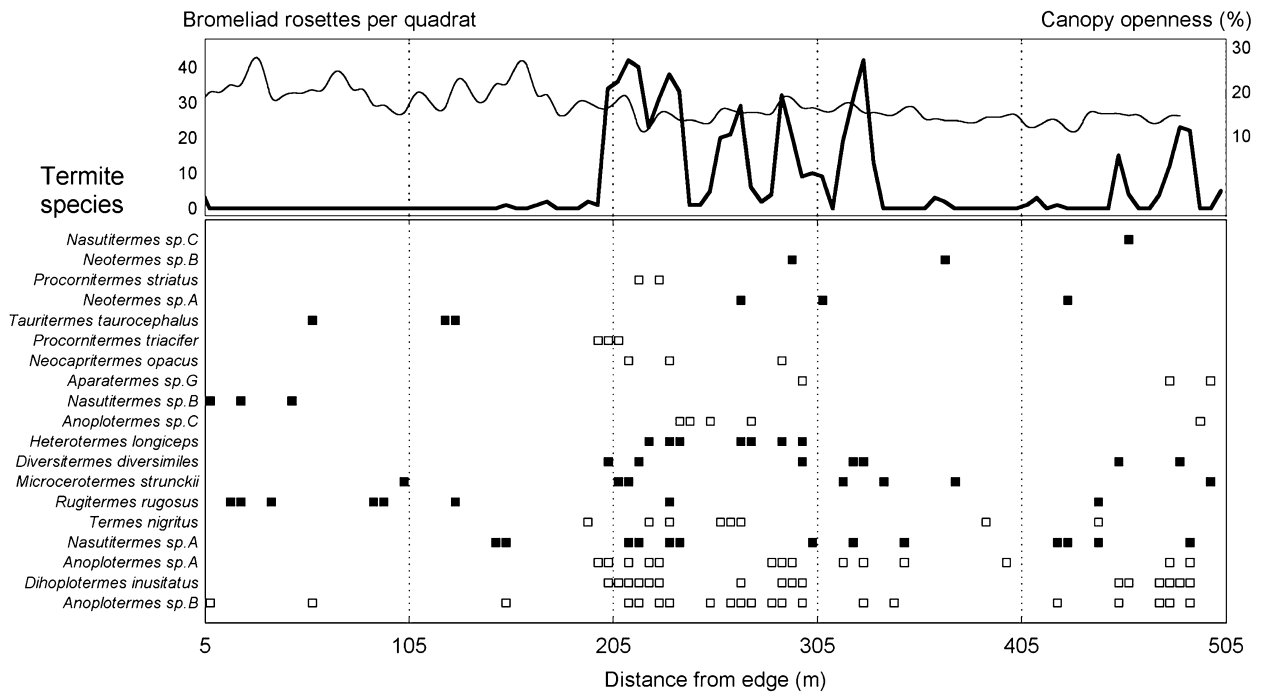


Fig. 2. Distribution of termite species along the 500 m transect, in relation with density of (—) terrestrial bromeliads and (—) canopy openness. Species are ranked in order of occurrence frequency. Each square represents the presence of a species in one quadrat: (■) wood/litter feeders; (□) soil/interface feeders.

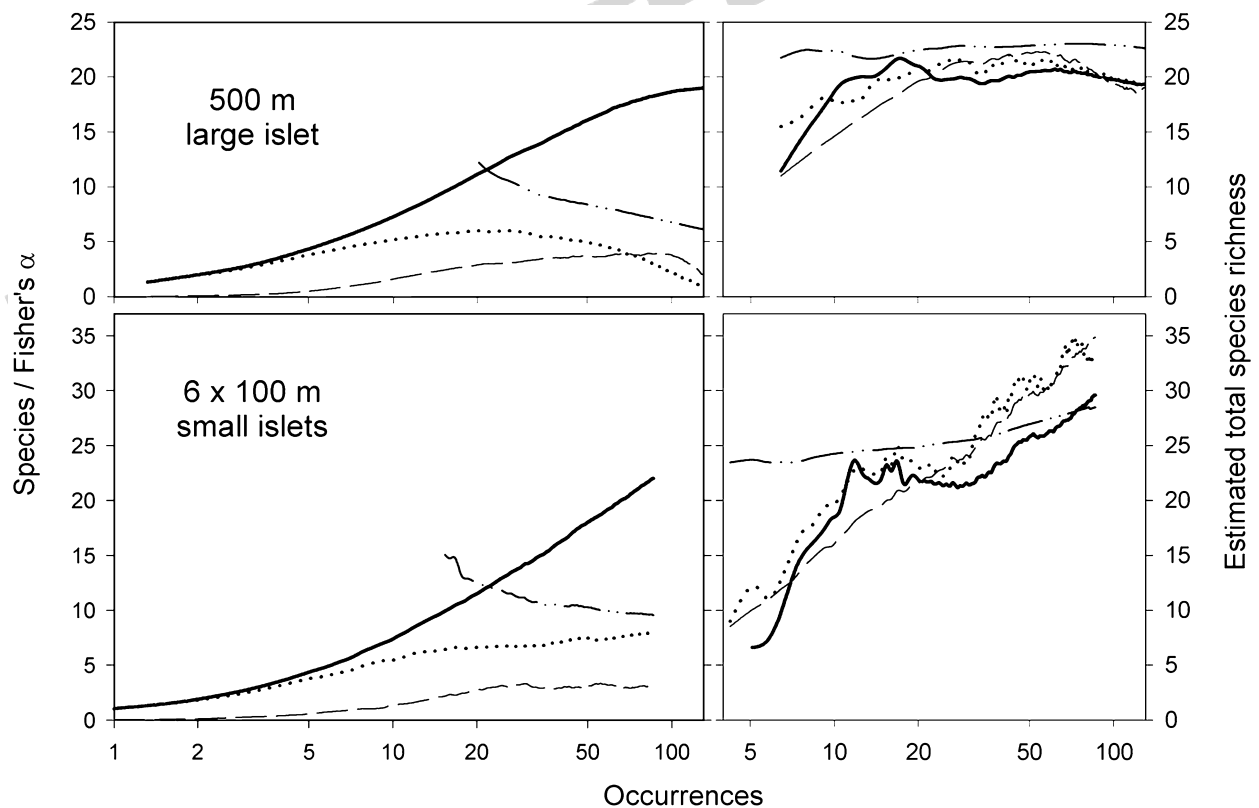


Fig. 3. Biodiversity statistics for the 500 m transect in a large islet of monte (top), and the six 100 m long small-islet transects combined (bottom), calculated by *EstimateS* from 1000 randomizations of sample order, and plotted against the number of occurrences (log scale). Left: (—) Average observed species richness; (.....) number of uniques; (---) number of duplicates; and (—) Fisher's α . Right, total species richness estimated by four methods: (—) ICE; (.....) Chao 2; (---) Jackknife 2; and (—) Michaelis-Menten Mean fit.

The number of uniques started to decrease after only 20 occurrences. The species accumulation curve initially followed a logarithmic progression, but levelled off towards 19 species (Fig. 3). Non-parametric estimates of TSR rapidly levelled off just above the observed number of 19 species, whereas the Michaelis-Menten fit gave a higher estimate (22.5 species; Fig. 3).

Fractioning the 500 m transect into shorter strips resulted in considerable fluctuations of the number of occurrences and observed species, as well as of TSR estimates and Fisher's α parameter (Fig. 4). In 100 m strips, the observed species richness varied from 5 to 16, which represented 26–84% of the total observed species richness. In 200 m strips, from 11 to 17 species (58–90% of the total) were obtained. The number of occurrences fluctuated, respectively, in the ranges 8–61 (100 m) and 25–82 (200 m). Highest richness and occurrences were observed in strips covering the middle part of the transect, where bromeliads were most abundant. Fisher's α was relatively constant near 6.15 for all strip lengths near the middle section. This index was lower for 100 m strips near the edge, and showed two peaks for 100 m strips comprising both bromeliad-rich and bromeliad-free zones. TSR estimates ICE, MMMean and Chao 2 based on 200 m strips were more or less constant and usually slightly lower than those based on the whole transect length, whereas 100 m strips yielded very variable values, starting well below 10 near the edge to reach near 20 in

the bromeliad fields. Fluctuations were important for all indices, especially Chao 2 (not shown on Fig. 4 because the absence of duplicates in some strips resulted in indefinite values of this estimator).

Species accumulation curves constructed from contiguous quadrats revealed a considerable dispersion and tended to remain below the curve corresponding to the whole 500 m transect (Fig. 5). Introducing a sampling interval of 10 m between the centre of the sampling units reduced the dispersion of the data, and also reduced the bias with respect to the whole 500 m transect curve. Further reduction in data dispersion resulted from introducing intervals of 20 m.

Representativeness of a standardized transect and diversity measures at the metacommunity scale

Single standardized transects of 100 m (20 quadrats) in distant islets of *monte* yielded 8–18 occurrences and 5–11 species. Five of these species, all rare (three uniques and two duplicates), were not recorded from the large islet of forest sampled by the calibration transect (Table 1).

Single small-islet transects provided too few occurrences to allow extrapolations of any kind. However, the six transects pooled conveyed useful information on the termite assemblage in the metacommunity. They summed up to 86 occurrences, representing 22 species.

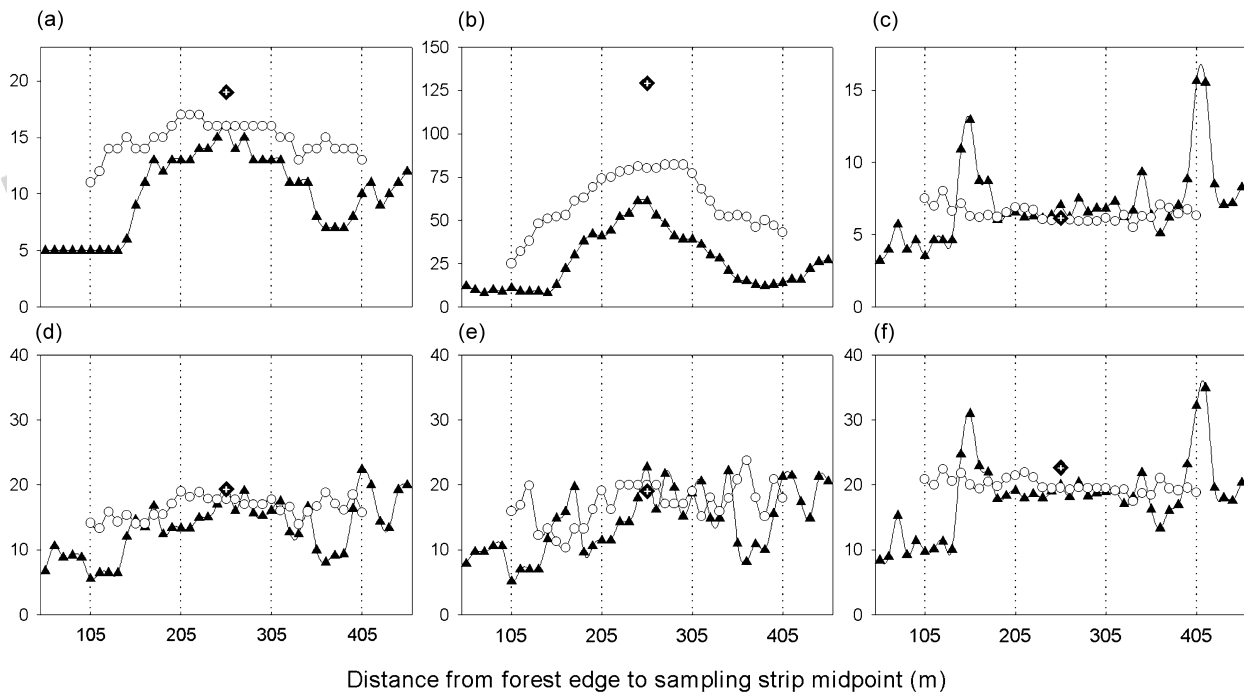


Fig. 4. (a) Observed species richness, (b) occurrences, (c) Fisher's α and total species richness (TSR) estimates for (d) ICE, (e) Jackknife, and (f) MMMean, from (◆) the whole 500 m transect and partially overlapping strips of (▲) 100 m (20 quadrats), or (○) 200 m (40 quadrats) in the large forest islet. Parameter variation is shown with respect to the position of the sampled strip centre.

The species accumulation curve presented an almost perfect logarithmic growth, and gave no sign of levelling off, while the number of uniques and duplicates was not declining (Fig. 3). Fisher's α declined as sampling progressed to become almost stable at 9.55. All estimates of TSR for the meta-community were still rising steeply after 86 occurrences (Fig. 3).

DISCUSSION

Species distribution and biodiversity statistics at the local scale

The results of the 500 m transect revealed an extreme variability in termite species distribution. Soil- or wood-soil interface-feeding species were concentrated in the bromeliad fields. This phenomenon introduced a level of patchiness in termite distribution at a much larger scale than the gregarious behaviour of individual foragers. Such spatial heterogeneity could not be expected *a priori* from the Chacoan *monte*, but has important consequences on the representativeness and reliability of standardized samples.

The species accumulation curve based on the 500 m transect in the large forest islet levelled off to reach a plateau at 19 species, whereas the number of uniques and duplicates were decreasing. The inventory of this particular islet was therefore complete, or nearly so. Yet, even at the level of this local assemblage, a single 100 m transect was not sufficient to reach a reliable estimate of TSR and other biodiversity statistics. A first difficulty resulted from the low species density, and accordingly low number of occurrences, recorded from strips situated outside of the bromeliad patches. According to Condit *et al.* (1998), samples of at least 100 individual stems are advisable to characterize the diversity of a botanical plot, and 50 individuals are a strict minimum. In this study, more than half the 100 m strips extracted from the 500 m transect yielded fewer than 25 occurrences, and only five strips (out of 41), centred near the middle of the largest bromeliad patch, provided more than 50. Those figures were greatly improved by the use of 200 m strips, since 24 of the 31 combinations provided 50 occurrences or more.

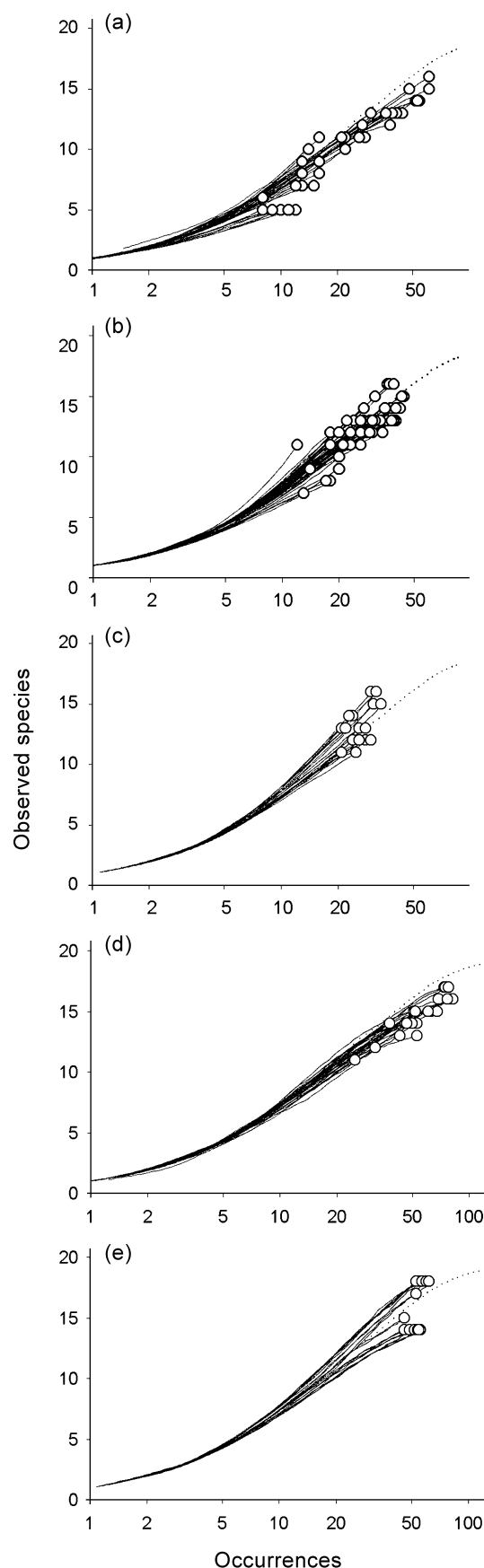


Fig. 5. Species accumulation curves, plotted against the number of occurrences (log scale), obtained by varying the interval between quadrats along the 500 m transect. (a) 20 quadrats contiguous over 100 m, (b) 20 quadrats at 5 m intervals over 200 m, (c) 20 quadrats at 15 m intervals over 400 m, (d) 40 quadrats contiguous over 200 m and (e) 40 quadrats at 5 m intervals over 400 m. Open dots emphasize end point of each curve. Dotted curve corresponds to the whole 500 m transect (100 contiguous quadrats).

A second hurdle resulted from habitat heterogeneity, which elicits clumping of soil-dwelling species at a spatial scale approaching that of the standard transect length (100 m). Clearly, transects sampled different termite assemblages if they ran across bromeliad fields or if they did not. This may explain why species *vs.* occurrences curves generated from single 100 m strips remained below the curve corresponding to the whole 500 m transect. In the focal habitat, this is another reason to recommend that sampling be extended beyond a single 100 m strip. This bias can be reduced by extending the length of the sampled strip, but also by introducing non-sampled intervals between quadrats, to expand the variety of microhabitats sampled without substantial increase in the amount of work required.

Species distribution and biodiversity statistics at the metacommunity scale

As in the large islet, individual 100 m transects provided too few occurrences to allow reliable statistical treatment. However, once pooled, they summed up to 86 occurrences. The six transects combined resulted in a steeper species accumulation curve than the single 500 m transect, which could be due to several factors. First, because the sampled islets were spread over ± 14 km and were highly subject to edge effects, they may present together a higher diversity of microhabitats than a single large islet, in spite of the internal heterogeneity of the latter. Second, isolation by distance may have allowed the persistence of different assemblages in separate islets, making their overall richness higher than that of single, though large, islet. The distal part of the species accumulation curve corresponding to the six small-islet transects combined was almost linear, indicating a logarithmic progression (Fig. 3). This curve showed no sign of saturation, which was consistent with the increasing number of uniques. The TSR estimates were still rising steeply with sample size, and remained thus unreliable. Because the inventory was far from complete, comparisons with other sites might be attempted only on the basis of parameters of the species accumulation curve, or indices such as Fisher's α (Gotelli & Colwell 2001).

CONCLUSIONS

Pitfalls and general recommendations

The standardized sampling protocol was first aimed at producing a representative sample of a local termite community in terms of functional and taxonomic

composition, especially for equatorial forests. For this purpose, it has the merit of being relatively rapid, of sampling most microhabitats (exceptions being the canopy and the soil below a depth of 10 cm), and of offering high efficiency per unit of effort (Bignell & Eggleton 2000; Jones & Eggleton 2000). Problems arise when one attempts to use data obtained by this protocol to draw quantitative comparisons of diversity instead of faunal comparisons between sites.

The first pitfall arises from the fact that the transect protocol standardizes sampling effort only. Because many factors independent of species richness and relative abundance may produce strongly unequal samples for an equal effort, several authors have recommended standardizing data processing on the basis of equal numbers of individuals, instead of equal effort (Condit *et al.* 1996, 1998; Gotelli & Colwell 2001), although this procedure has some drawbacks as well. For instance, the magnitude of differences between species-rich and species-poor environments, or even the ranking of communities may depend on sample 'grain', that is, the size of elementary sampling units (Palmer & White 1994), and on total sample size (Lande *et al.* 2000; Cao *et al.* 2002). To those restrictions of universal relevance regarding standardization by sampling effort alone, this study further suggests an increased likelihood of data misinterpretation in the particular case of termites, in view of their sensitivity to habitat heterogeneity.

A key issue then becomes the definition of the ideal size, number and positioning of the sampled quadrats. Positioning the quadrats along transects presents the advantage that narrow strips generally run across a higher variety of habitats than squares of the same area, and are therefore more efficient at accumulating species (e.g. for trees: Condit *et al.* 1996). We showed that introducing intervals between sampled quadrats is a way to reduce the variability of the data without increasing the required amount of work, because encompassing a larger range alleviates effects of habitat heterogeneity. Spacing also reduces risks that single colonies occupy by chance two or more adjacent quadrats, thereby slowing down species accumulation and biasing frequency-based statistics. In the same habitat, positioning one sample every 10 m was found satisfactory for leaf-litter ants (Leponce *et al.* 2004), in agreement with the standardized A.L.L. protocol proposed for sampling these insects (Agosti & Alonso 2000). Our results suggest that one quadrat every 10 m might be adequate for termites as well, although the low number of occurrences recorded did not permit a detailed analysis of spatial patterns. Moreover, this would facilitate running simultaneously ant and termite protocols. A 20-m interval might allow an even higher rate of species accumulation but would result in impractical long transects.

Quadrat size should be small enough to allow numerous replications, but large enough to cover several suitable microhabitats and provide good chances of encounter with termite species whose foraging range encompasses the area. If the proposed quadrat width of 2 m appears reasonable, there is no reason to design rectangular quadrats instead of square ones. Furthermore, a quadrat area of 10 m² seems excessive in some habitats, frequent species being often subject to multiple encounters per quadrat (e.g. see records in Davies *et al.* 2003b). A good compromise could be to sample squares of 5 m² (2.25 m × 2.25 m), which would allow a doubling of the number of quadrats for the same effort.

The number of quadrats should be adapted in order to obtain sufficient numbers of occurrences, allowing statistical treatment of the data. For this purpose, unless the density of species is very high, 20 quadrats of 10 m² (as proposed by Jones & Eggleton 2000), or even 30 (Cancello 2002; Sena *et al.* 2003) may often be insufficient. Around 80 such quadrats at the local (large islet) scale and more than 200 quadrats at the meta-community scale would be advisable in the present ecosystem. Even higher numbers would be required if quadrat area were reduced by half. Sampling a total area of 200 m² (the standard of Jones & Eggleton 2000) with quadrats of 5 m² at 10 m intervals requires a range of 400 m. It is however, not necessary to carry out sampling along a single linear transect, which is often impossible in disturbed or fragmented habitats. Parallel transects can be set up, provided the distance between quadrats remains sufficient. Two parallel transects of 200 m, or four of 100 m, spaced by intervals of at least 10 m, would be more practical in many situations. This procedure should be repeated so as to obtain a sufficient number of individual occurrences (more than 100 are recommended, see Condit *et al.* 1998).

Our basic recommendations for future studies, as long as intersite comparisons of termite diversity are intended, are (i) to use transects with non-contiguous quadrats (ii) to extend sampling as necessary to obtain a sufficient number of individual occurrences, considering indicators of inventory completeness such as decrease in uniques, shape of species accumulation curves and stabilization of diversity indices. The availability of data treatment methods that compensate for differences in sampling effort would still permit cautious comparisons with results obtained by other standardized protocols, such as those of Jones and Eggleton (2000) or Cancello (2002).

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REFERENCES

- Agosti D. & Alonso L. E. (2000) The ALL protocol. A standard protocol for the collection of ground-dwelling ants. In: *Ants. Standard Methods for Measuring and Monitoring Biodiversity* (eds D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz) pp. 204–6. Smithsonian Institution Press, Washington, D.C.
- Bignell D. E. & Eggleton P. (2000) Termites in ecosystems. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T. Abe, D. E. Bignell & M. Higashi) pp. 363–87. Kluwer Academic Publishers, Dordrecht.
- Black H. I. J. & Okwakol M. J. N. (1997) Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. *Appl. Soil Ecol.* **6**, 37–53.
- Cancello E. M. (2002) Termite diversity along the Brazilian Atlantic Forest. In: *Proceedings of the XIV International Congress of IUSSI – The Golden Jubilee Proceedings, 27 July–3 August 2002, Hokkaido University, Sapporo, Japan* p. 164. Hokkaido University, Sapporo.
- Cao Y., Williams D. D., Larsen D. P. (2002) Comparison of ecological communities: the problem of sample representativeness. *Ecol. Monogr.* **72**, 41–56.
- Chao A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**, 783–91.
- Chazdon R. L., Colwell R. K., Denslow J. S., Guariguata M. (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. In: *Forest Biodiversity Research, Monitoring and Modeling. Conceptual Background and Old World Case Studies* (eds F. Dallmeier & J. A. Comiskey) pp. 285–309. UNESCO and Parthenon Publishing Group, Paris and New York.
- Colwell R. K. (1997) EstimateS: Statistical estimation of species richness and shared species from samples [updated 26 February 1999]. Available from: <http://viceroy.eeb.uconn.edu/EstimateS>.
- Condit R., Foster R. B., Hubbell S. P., Sukumar R., Leigh E. G. Jr., Manokaran N., Lao S. L., LaFrankie J. V., Ashton P. S. (1998) Assessing forest diversity on small plots: calibration using species-individual curves from 50-ha plots. In: *Forest Biodiversity Research, Monitoring and Modeling. Conceptual Background and Old World Case Studies* (eds F. Dallmeier & J. A. Comiskey) pp. 247–68. UNESCO and Parthenon Publishing Group, Paris and New York.
- Condit R., Hubbell S. P., LaFrankie J. V., Sukumar R., Manokaran N., Foster R. B., Ashton P. S. (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *J. Ecol.* **84**, 549–62.

- Constantino R. (1998) Catalog of the living termites of the New World (Insecta: Isoptera). *Arquiv. Zool.* **35**, 135–231.
- Constantino R., Liotta J., Giacosa B. (2002) A reexamination of the systematic position of *Amitermes brevicorniger*, with the description of a new genus (Isoptera, Termitidae, Termitinae). *Sociobiology* **39**, 453–63.
- Davies R. G., Eggleton P., Jones D. T., Gathorne-Hardy F. J., Hernández L. M. (2003a) Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *J. Biogeogr.* **30**, 847–77.
- Davies R. G., Hernández L. M., Eggleton P., Didham R. K., Fagan L. L., Winchester N. N. (2003b) Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. *J. Trop. Ecol.* **19**, 509–24.
- DeSouza O. & Brown V. K. (1994) Effects of habitat fragmentation on Amazonian termite communities. *J. Trop. Ecol.* **10**, 197–206.
- Donovan S. E., Eggleton P., Bignell D. E. (2001) Gut content analysis and a new feeding group classification of termites. *Ecol. Entomol.* **26**, 356–66.
- Eggleton P. & Bignell D. E. (1995) Monitoring the response of tropical insects to changes in the environment: troubles with termites. In: *Insects in a Changing Environment* (eds R. Harrington & N. E. Stork) pp. 473–97. Academic Press, London.
- Eggleton P., Bignell D. E., Hauser S., Dibog L., Norgrove L., Madong B. (2002) Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agric. Ecosyst. Environ.* **90**, 189–202.
- Eggleton P., Bignell D. E., Sands W. A., Waite B., Wood T. G., Lawton J. H. (1995) The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *J. Trop. Ecol.* **11**, 85–98.
- Fisher R. A., Corbet A. S., Williams C. B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**, 42–58.
- Fisher B. L. & Robertson H. G. (2002) Comparison and origin of forest and grassland ant assemblages in the high plateau of Madagascar (Hymenoptera: Formicidae). *Biotropica* **34**, 155–67.
- Frazer G. W., Canham C. D., Lertzman K. P. (1999) *Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation*. Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY [updated 10 October 2003]. Available from: http://www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm.
- Gotelli N. J. & Colwell R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–91.
- Holt J. A. & Lepage M. (2000) Termites and soil properties. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T. Abe, D. E. Bignell & M. Higashi) pp. 389–407. Kluwer Academic Publishers, Dordrecht.
- Jones D. T. & Eggleton P. (2000) Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *J. Appl. Ecol.* **37**, 191–203.
- Lande R., DeVries P. J., Walla T. R. (2000) When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* **89**, 601–5.
- Lee S.-M. & Chao A. (1994) Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* **50**, 88–97.
- Lepage M. & Darlington J. P. E. C. (2000) Population dynamics of termites. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T. Abe, D. E. Bignell & M. Higashi) pp. 333–61. Kluwer Academic Publishers, Dordrecht.
- Leponce M., Theunis L., Delabie J. H. C., Roisin Y. (2004) Scale dependence of diversity measures in a leaf-litter ant assemblage. *Ecography* **27**, 253–67.
- Longino J. T. (2000) What to do with the data?. In: *Ants. Standard Methods for Measuring and Monitoring Biodiversity* (eds D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz) pp. 186–203. Smithsonian Institution Press, Washington, D.C.
- Palmer M. W. (1991) Estimating species richness: the second-order jackknife reconsidered. *Ecology* **72**, 1512–3.
- Palmer M. W. & White P. S. (1994) Scale dependence and the species-area relationship. *Am. Nat.* **144**, 717–40.
- Pujalte J. C., Reca A. R., Balabusic A., Canevari P., Cusato L., Fleming V. P. (1995) *Unidades Ecológicas Del Parque Nacional Rio Pilcomayo*. Administración de Parques Nacionales, Buenos Aires.
- Raaijmakers J. G. W. (1987) Statistical analysis of the Michaelis-Menten equation. *Biometrics* **43**, 793–803.
- Roisin Y. (2003) *Cryptotermes chacoensis*, a new species from native South American inland habitats (Isoptera: Kalotermitidae). *Sociobiology* **42**, 319–27.
- Sena J. M., Vasconcellos A., Gusmão M. A. B., Bandeira A. G. (2003) Assemblage of termites in a fragment of cerrado on the coast of Paraíba State, northeast Brazil (Isoptera). *Sociobiology* **42**, 753–60.
- Smith E. P. & van Belle G. (1984) Nonparametric estimation of species richness. *Biometrics* **40**, 119–29.
- Sugimoto A., Bignell D. E., MacDonald J. A. (2000) Global impact of termites on the carbon cycle and atmospheric trace gases. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T. Abe, D. E. Bignell & M. Higashi) pp. 409–35. Kluwer Academic Publishers, Dordrecht.