

Assessment of large-vertebrate species richness and relative abundance in Neotropical forest using line-transect censuses: what is the minimal effort required?

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Abstract Line-transect sampling is a strategy commonly used to assess richness and abundance of large diurnal vertebrates in tropical forests, but the relationships between the sampling effort (measured as transect length in km) and the accuracy of the estimates based on the field data have rarely been investigated. Using data from 17 distinct surveys in French Guiana, we demonstrated that 85 km of transect are sufficient to extrapolate species richness whatever the forest type and the disturbance level of the habitat. Concerning species abundances, reliable estimations were obtained after 40–90 km of transects for large birds, howlers, tamarins, and agoutis. In contrast, relative abundances of capucins, sakis, and unguates, were still not stabilized after 100 km but can still be reliably assessed with this effort. These species have larger home range than the former, and the accuracy of abundance assessment may be related to use of space. Since species with small area requirements regularly use their entire home range, abundance prediction with a moderate sampling effort may be facilitated. On the contrary, species with large home ranges may exhibit strong seasonal habitat partitioning, therefore decreasing the accuracy of abundance estimation on a low-effort survey. This analysis provides the first evidence of the minimal efforts required to assess large vertebrate richness and relative abundance of some species in a neotropical rainforest. We encourage similar works on other sites, to collect additional information on the influence of forest productivity and species assemblage composition on the minimal required sampling effort. This would permit confident extrapolations of species richness and abundance in other Neotropical forests and may provide efficient guidelines to

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integrate the predictive analytical tool developed in this work in future biodiversity management plans.

Keywords Macrofauna · Sampling · Richness · Abundance · Line-transect · Neotropics

Introduction

Specific richness and relative abundances of species are basic attributes of animal communities that can be used as simple and integrative measures to investigate the relationships between population structure and biotic and abiotic patterns of habitats, to quantify anthropic disturbances, and to monitor biodiversity management plans (Begon et al. 1996; Gotelli and Colwell 2001). Both ecology and conservation programs, habitat management and assessment of ecosystem status require the determination of the richness and the abundance of target species, as baseline data for calculation of biomass, productivity, and as an estimate for population trends. Methods available include presence/absence data, capture/mark-recapture, point methods, index plots, track counts, photoidentification, molecular DNA typing, strip transects, and line-transect sampling (e.g., Wilson et al. 1996; Silveira et al. 2003; Tosh et al. 2004; Smallwood and Fitzhugh 1995; Prigioni et al. 2006; Lees and Peres 2006). The latter is a well-recognised strategy commonly used to survey large mammals and birds in tropical rainforests (Voss et al. 2001; Haugaasen and Peres 2005a). This method consists in determining and counting species encountered along a census walk of fixed length, replicated until a large enough cumulated distance (Brockelman and Ali 1987; Southwell 1996; Peres 1999) is obtained. However, despite numerous theoretical developments and field test applications (Skorupa 1987; Whitesides et al. 1988; Garcia 1993; Brugière and Fleury 2000), relationships between the total effort, i.e. the unit census walk multiplied by the number of repetitions, and the reliability of calculated richness and abundances has scarcely been investigated for large forest species. A brief overview of recent studies conducted in neotropical forests shows that the total implemented sampling efforts were highly variable, with cumulated survey length ranging from 40 to 600 km (Bodmer et al. 1997; Carillo et al. 2000; de Thoisy et al. 2000; Lopes and Ferrari 2000; Peres 2000; Sorensen and Fedigan 2000; Wright et al. 2000; Cullen et al. 2001; de Thoisy et al. 2005; Haugaasen and Peres 2005a; Haugaasen and Peres 2005b).

In neotropical forest habitats, Emmons (1984) estimated that a cumulated survey length of 100 km can provide reliable estimations of large species richness. Regarding species abundances, the estimation of densities (i.e., number of individuals per unit area) is difficult to achieve as it requires a large number of independent sightings and may require a sampling effort of hundreds of kilometres (Peres 1999). Calculated densities are therefore often replaced by a measurement of relative abundances, expressed as a sighting rate (i.e., number of individuals per unit distance), which is assumed to require a lower sampling effort for reliable assessments (Carillo et al. 2000; de Thoisy et al. 2005; Lopes and Ferrari 2000; Wright et al. 2000).

Large frugivorous birds, large-bodied mammals and primates are widely used as indicators of habitat disturbance and direct pressures on fauna, including logging, fragmentation (Lopes and Ferrari 2000; Dalecky et al. 2002) and hunting (Bodmer et al. 1997; Peres 2000; Peres 2001; de Thoisy et al. 2005). Indeed, such sensitive species are prone to anthropogenic pressures, leading to a decrease of species diversity, and dramatic shifts of relative abundances. Our aim was to facilitate the reliable use of such sensitive species as indicators for inter-site comparison and site monitoring, by determining the minimal

sampling effort needed to accurately assess species richness and the relative abundance of some species. Based on line-transects conducted on 17 forest sites in French Guiana, we first used easily available extrapolation procedures (EstimateS[®], Colwell 2005) to predict species richness based on the species accumulation curves from 0 to 100 km effort. Second, we considered the 12 species present in most of surveyed areas, either disturbed or not, including monkeys, large birds and ungulates, to determine the minimal sampling effort needed to obtain a rapid and reliable assessment of their relative abundances.

Methods

Study sites and surveys

All the samples were collected during the dry season (July–December), from 1998 to 2003. Line-transect censuses were conducted on 17 sites in various forest habitats in French Guianan forests (Fig. 1). Thirteen of the sites were located in moist upland forest, as this evergreen forest type is the most common on the Guianan shield with its well-drained, ferrallitic, oligotrophic soils characterized by a high tree diversity, dominated by Lecythidaceae, Caesalpinaceae, Chrysobalanaceae and Sapotaceae (de Granville 1988). Four sites were located in transition forests, found on the old alluvial coastal plain, where dominant

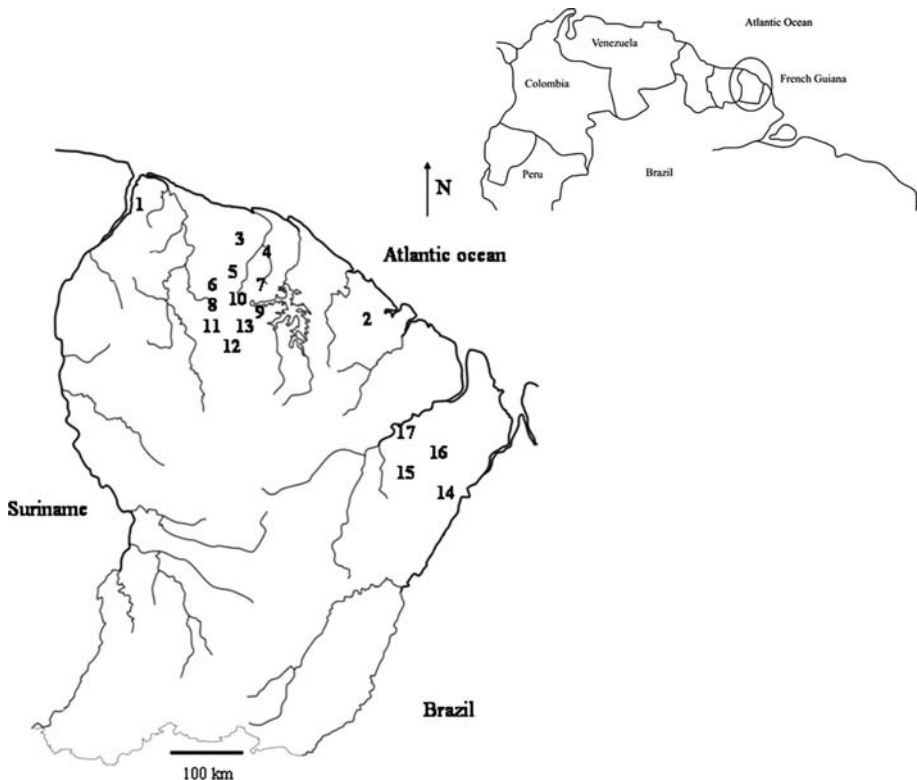


Fig. 1 Locations of study sites sampled by line-transects

tree species are *Parinari campestris*, *Licania* sp. (Chrysobalanaceae), *Protium heptaphyllum* (Burseraceae), *Inga* spp. (Mimosaceae), and *Euterpe oleraceae* (Arecaceae) (de Granville 1988). Three of the 17 sites were free from human pressure, whereas the remaining 14 faced different human disturbance levels, including hunting and/or selective logging (Table 1).

Briefly, the line-transect sampling consisted in walking slowly (1–1.3 km/h), on a single linear forest track measuring 4–5 km, in a homogeneous habitat in terms of forest structure (similar plant species assemblages) and observed human threats. The survey on this single track was repeated daily until a cumulated distance of c.a. 100 km was reached (mean distance = 100.5 ± 4.0 km, $n = 17$ sites). The walk was conducted from 08:00 to 12:00, and 15:30 to 17:30, and hence, strictly nocturnal species were not observed. As we considered the entire large mammals and large birds species assemblage, that temporal window allowed us to maximize the probability of detecting the target species, and therefore obtaining a realistic estimation of the species composition at each site. Although sampling efficiency may differ between species, which have different activity patterns, our aim was not to determine the absolute values of species abundances. Our abundance measurements were rather the best compromise between data relevance and study feasibility considering multispecies assemblages over a large set of sites. Census walks were stopped during rain, and species detected on the return walk were not considered for diversity or abundance estimates. As far as possible, following logistic constraints, the census tracks implemented in rather close sites (e.g., sites 3–12, and 14, 15, 16, 17, Fig. 1) were performed alternately. This allowed each site to be surveyed every 3–4 days and reduced the probability of sighting recapture of the same individuals. All surveys were performed by a single well-trained person to avoid potential biases in the ability to detect and identify species. The assessment of abundance, expressed as a kilometric index, i.e. number of sightings/km, was restricted to the species recorded at least three times during the 100 km of the sampling effort, and present in all the forest types and levels of disturbance. This allowed us to define a sampling effort valid for the widest set of common species, excluding species for which a particular habitat feature (natural and/or anthropic) would strongly affect presence/absence.

Table 1 Characteristics of the areas surveyed: location, human pressure, and forest types

Site	Location ^a	Hunting	Logging	Forest type
Coswine	1	Low	No	Transition forest
Matiti	2	High	No	Transition forest
Patagaie A	3	High	Selective logging, ancient	Transition forest
Patagaie B	4	High	Selective logging, ancient	Transition forest
Counami A, 1998	5	Low	No	Moist upland forest
Counami A, 2000	6	High	No	Moist upland forest
Counami A, 2001	7	High	Selective logging, recent	Moist upland forest
Counami B, 1998	8	Low	No	Moist upland Forest
Counami B, 2000	9	High	No	Moist upland forest
Counami B, 2001	10	High	Selective logging, recent	Moist upland forest
Counami T, 1998	11	No	No	Moist upland forest
Counami T, 2000	12	No	No	Moist upland forest
Counami T, 2001	13	Low	No	Moist upland forest
RNT	14	No	No	Moist upland forest
RN2	15	Low	No	Moist upland forest
RN3	16	High	No	Moist upland forest
RN1	17	Low	No	Moist upland forest

^a The number refers to the Fig. 1

Table 2 Total of mammal and bird species recorded during the 17 line-transects conducted in French Guianan rainforests. Codes of the species used for abundance calculations are indicated in brackets

Primates	Ungulates	Carnivores
<i>Alouatta seniculus</i> (Ase)	<i>Mazama americana</i> (Maz)	<i>Nasua nasua</i>
<i>Ateles paniscus</i>	<i>Mazama gouazoubira</i> (Maz)	<i>Galictis vittata</i>
<i>Cebus apella</i> (Cap)	<i>Pecari tajacu</i> (Pta)	<i>Eira barbara</i>
<i>Cebus olivaceus</i>	<i>Tayassu pecari</i>	<i>Speothos venaticus</i>
<i>Saimiri sciureus</i>	<i>Tapirus terrestris</i>	<i>Lontra longicaudis</i>
<i>Pithecia pithecia</i> (Ppi)		<i>Leopardus wiedii</i>
<i>Saguinus midas</i> (Smi)	Rodents	<i>Leopardus tigrinus</i>
	<i>Dasyprocta leporina</i> (Dle)	<i>Leopardus pardalis</i>
Xenarthres	<i>Sciurillus pusillus</i>	<i>Puma concolor</i>
<i>Tamandua tetradactyla</i>	<i>Sciurus aestuans</i>	<i>Panthera onca</i>
<i>Myrmecophaga tridactyla</i>	<i>Myoprocta acouchy</i>	
<i>Choloepus didactylus</i>		Birds
<i>Bradypus tridactylus</i>		<i>Psophia crepitans</i> (Pcr)
		<i>Crax alector</i> (Cal)
		<i>Tinamus major</i> (Tma)
		<i>Penelope marail</i> (Pma)

As a result, target species were primates, large terrestrial mammals, and large frugivorous birds (Table 2).

Species richness

At each site, the cumulated distance from the beginning of the transect was recorded for each contact with an individual and/or a group in case of social species. Species accumulation curves were then set up following the sampling effort. The total richness estimation was calculated using the asymptotic Michaelis–Menten function (Colwell and Coddington 1994) with the EstimateS 7.5[®] software (Colwell 2005). The estimated total richness was assessed by functional extrapolation with two indicators, MMruns and MMmeans (Colwell 2005). These two methods are recognised as efficient richness estimators, commonly used to achieve this task (Colwell et al. 2004). The first method, MMruns, computes estimates of the values for each pooling level, for each randomization run, and then averages over randomization runs. The second method, MMmeans, computes the estimates for each sample pooling level just once, based on the species accumulation curve (for more details on these methods, see Colwell 2005). The two estimators were computed to obtain an Extrapolated Species Richness (ESR) calculated for every 5 km sampling (from 5 to 100 km of survey) aiming to compare their capabilities. With both methods, the ESR calculated after 100 km sampling (ESR_{100}) was compared to that calculated earlier during sampling (ESR_i). This allowed the determination of the minimal sampling effort needed to obtain a relevant estimation of species richness, defined as an ESR_i value differing from ESR_{100} by no more than one species (i.e., when $ESR_{100} + 1 \text{ species} \geq ESR_i \geq ESR_{100} - 1 \text{ species}$).

Species abundance

At each site and for each target species, the Kilometric Index (KI) was calculated every 5 km from the beginning of the survey, up to 100 km. Among the diversity of species recorded, including primates, frugivorous birds, rodents, ungulates, xenarthra, and carnivores (Table 2), 12 were present in most of the sites and sighted at least 3 times along the

transects. These 12 species were considered for relative abundance calculation. The correlation coefficient (r) between final KI measured after 100 km of survey (KI_{100}) and values calculated earlier during the sampling (KI_i) was used to evaluate the quality of the relationships; the sampling effort was considered sufficient when the r -value was greater than 0.9. This ensures that more than 80% ($r^2 \geq 0.81$) of KI_{100} variability was explained after a survey effort equal to KI_i . The shape of the relationship between the above mentioned r -value and the sampling effort was used to identify significantly different groups of species. The 20 r -values (one per 5 km effort) for the 12 species were used as input data to pattern the species using the self-organizing map (SOM; Kohonen 2001). This ordination method is recognized as a powerful tool due to its ability to deal with both linear and nonlinear data, (Chon et al. 1996; Lek and Guegan 2000; Park et al. 2003; Lek et al. 2005). The SOM performs a nonlinear projection of the multivariate data onto a low dimension. The input data are the 12 species \times the 20 r -values; the output data are a two-dimensional network of neurons arranged on a rectangular grid, where each neuron is connected to its nearest neighbours on the grid and stores a set of connection intensities. The SOM map provides a realistic ordination of the different species, according to the closeness of the shape of their r -value curves. Following species ordination, a hierarchical cluster analysis (Ward distance) was used to detect the cluster boundaries on the SOM map, and therefore to distinguish the different groups of species based on the shape of their r -value evolution curves through sampling effort. This SOM method is expected to be much more powerful than classical ordination methods in ecological fields (Brosse et al. 2001; Giraudel and Lek 2001; Brosse et al. 2007).

Results

Species richness

A total of 34 species were sighted on all the 17 surveys; in each area, the total number of species recorded after the total sampling effort ranged from 9 to 23 (see Appendix 1). The observed species richness in pristine or slightly disturbed areas (19 ± 2 species) was significantly higher than in areas with medium or strong hunting pressure, where only 15 ± 3 species were recorded (Mann–Whitney test: $z = 2.19$, $P = 0.01$). The 17 richness accumulation curves indicated a tendency to stabilise before 100 km sampling effort (Fig. 2). However, despite an attenuation of the slope of the curve according to the effort, there was no strict stabilisation of the observed richness, and some rare species (e.g., spider monkey *Ateles paniscus* recorded for the first time at km 97 on site 5; lowland tapir *Tapirus terrestris* recorded at km 96 on site 11) and/or cryptic species (e.g., tamandua *Tamandua tetradactyla* sighted at km 95 on site 8; three-toed sloth *Bradypus tridactylus* sighted at km 99 on site 9) were still detected toward the end of the effort. The species number estimated with both MMmeans and MMruns methods was far above total species number observed at 100 km (+23–26%), but the difference between observed and estimated richness after a sampling effort of 100 km was constant among sites, with a significant correlation between observed and estimated richness after a sampling effort of 100 km ($r^2 = 0.808$, $P < 0.0001$ and $r^2 = 0.807$, $P < 0.0001$, with MMmeans and MMruns, respectively).

For the 17 surveys, the evolution of the extrapolated richness using the MMmeans calculation procedure from 5 to 100 km sampling effort produced a much smoother curve than MMruns (Fig. 3). At each site, ESR_{90} , ESR_{95} and ESR_{100} had a very low standard deviation, suggesting that the extrapolation process became stabilized at the end of the initial

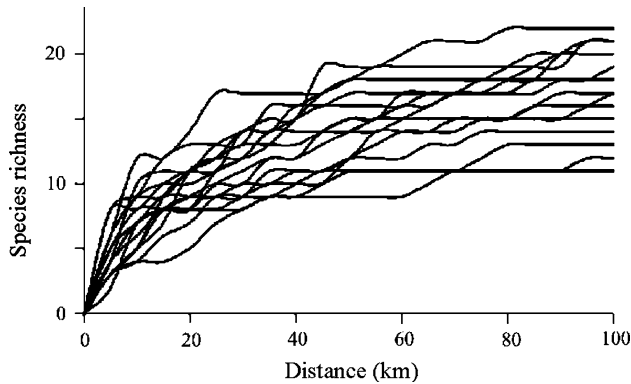


Fig. 2 Species richness observed according to the cumulated distance of the survey (in kilometres) for the 17 line-transect censuses

effort. Further, the minimal distance required to get an acceptable value of ESR_i (i.e., $ESR_{100} + 1 \text{ species} \geq ESR_i \geq ESR_{100} - 1 \text{ species}$) ranged from 25 to 85 km according to the site. MMmeans and MMruns extrapolation methods gave different results, although the difference was not significant (Student t -test, $t = 1.56$, $P = 0.131$): 63.8 ± 17.0 km for MMruns, and 51.6 ± 26.3 for MMmeans. This minimal effort was not related to forest type (Mann–Whitney test for comparison of upland moist forest sites *vs.* other forest types, $z = 0.86$, $P = 0.4$), level of disturbance (Kruskal–Wallis test between sites of high, medium, and low level of disturbance, $h = 0.7$, $P = 0.7$), and extrapolated number of species (linear regression, $r^2 = 0.02$; $P = 0.9$).

Species abundance

For the 12 target species, the Kilometric Indexes (KI) determined after 100 km of survey showed large variations, according to species and sites (Fig. 4; Appendix 1). Hunting pressure explains most of this variation. For instance, sighting rates of howler monkeys *Alouatta seniculus* and black curassows *Crax alector* were much lower in areas with medium or high hunting pressure than in areas with nil or low hunting pressure (Mann–Whitney tests, $z = -2.91$, $P = 0.004$ and $z = -2.52$, $P = 0.01$, respectively). Based on the r -value profiles of each species through sampling effort, the SOM patterned the species and clearly identified two groups, shown as two clusters in Fig. 5. Seven species were grouped in the first cluster (Cluster A in Fig. 5): the howler *Alouatta seniculus*, the tamarin *Saguinus midas*, the agouti, and the four species of frugivorous birds. For these species, r -profiles, although showing a high discrepancy according to the species, exhibited a logarithmic shape. The estimation of abundance reached stable values after 100 km of sampling effort, and according to the species, a relevant estimation of KI_{100} (i.e., $r > 0.9$) was possible between 40 and 90 km of sampling (Fig. 6).

Cluster B corresponded to two primates: the white-faced saki *Pithecia pithecia* and the capuchin *Cebus apella*, and two ungulates: collared peccary *Pecari tajacu* and the brocket deers (*Mazama gouazoubira* and *M. americana*). This group includes species for which the r -values profile was linear shaped (Fig. 6), showing that the relative abundance of each species did not fully stabilize up to 100 km. For these species, abundances could nevertheless be reliably estimated ($r > 0.9$) after 90 km of sampling.

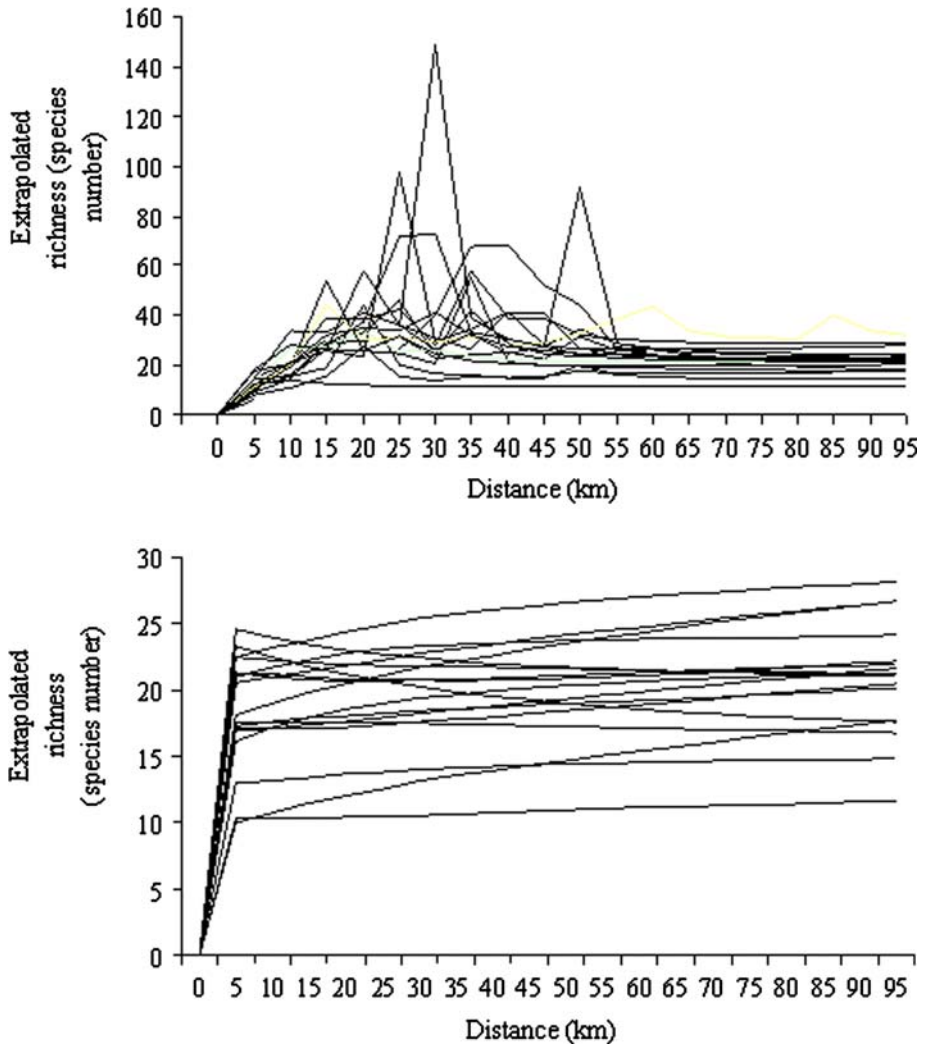


Fig. 3 Extrapolated species richness in the 17 sites calculated using MMruns (up) and MMmeans (low) methods (Colwell 2005)

Discussion

Line-transect sampling is widely used to monitor game species abundances in both pristine and harvested forests (Cullen et al. 2001; Lopes and Ferrari 2000; Peres 2000; Wright et al. 2000). It has been applied to large fauna in different forest structures aiming to understand complex relationships between animal communities and environmental factors such as soil fertility, habitat structure, floristic composition, and human threats (e.g., Haussagen and Peres 2005a, b). Our results confirm that line-transect sampling can be a reliable tool to estimate the richness of large vertebrates and the relative abundances of several target species in neotropical forests. Although the number of species recorded during diurnal surveys

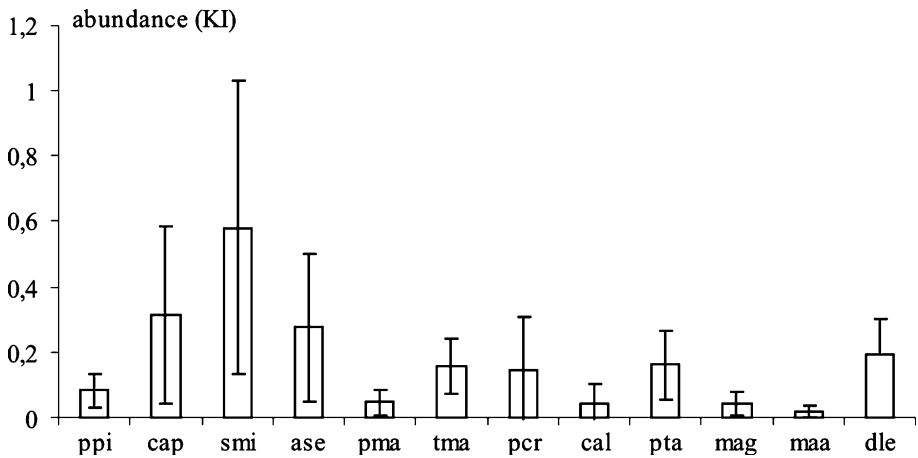


Fig. 4 Abundances expressed as Kilometric Index (mean \pm standard deviation of the 17 surveys) for the 12 target species. Species' codes refer to Table 2

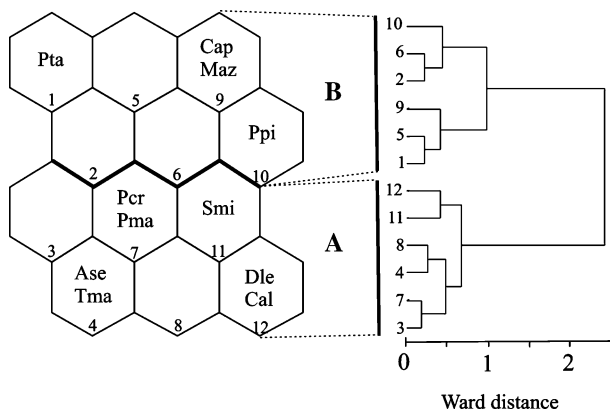


Fig. 5 Classification of the species using the Self-organising map (SOM), based on the evolution of the *r*-values between the Kilometric Index (KI) after 100 km (KI_{100}) and KI calculated for a lower effort (lower distance). After SOM patterning, species were classified into two clusters based on hierarchical cluster analysis. In the SOM, the numbers (1–12) correspond the units of the hierarchical analysis. The bold lines indicate the boundary between the two clusters on the SOM. Species codes are given in Table 2

may be limited in comparison to the actual richness of the fauna in neotropical forests, standardized line-transects are a good surrogate to the determination of the total richness which would require a much more intensive and long-term study. With this method comparative studies can be carried out between sites, as data collection is based on a similar set of species. Moreover, as richness constitutes a first and simple attempt to estimate macrofauna community status, the temporal investment needed to measure this faunal index is of primal importance for conservation programs. After empirical observations providing a rough estimation of species richness of large diurnal mammals and birds in neotropical rainforests (Emmons 1984; de Thoisy 2000; Voss et al. 2001), our data showed that although species diversity accumulation curves did not stabilise after 100 km of sampling, the extrapolated richness could be estimated below this distance, whatever the total species richness of

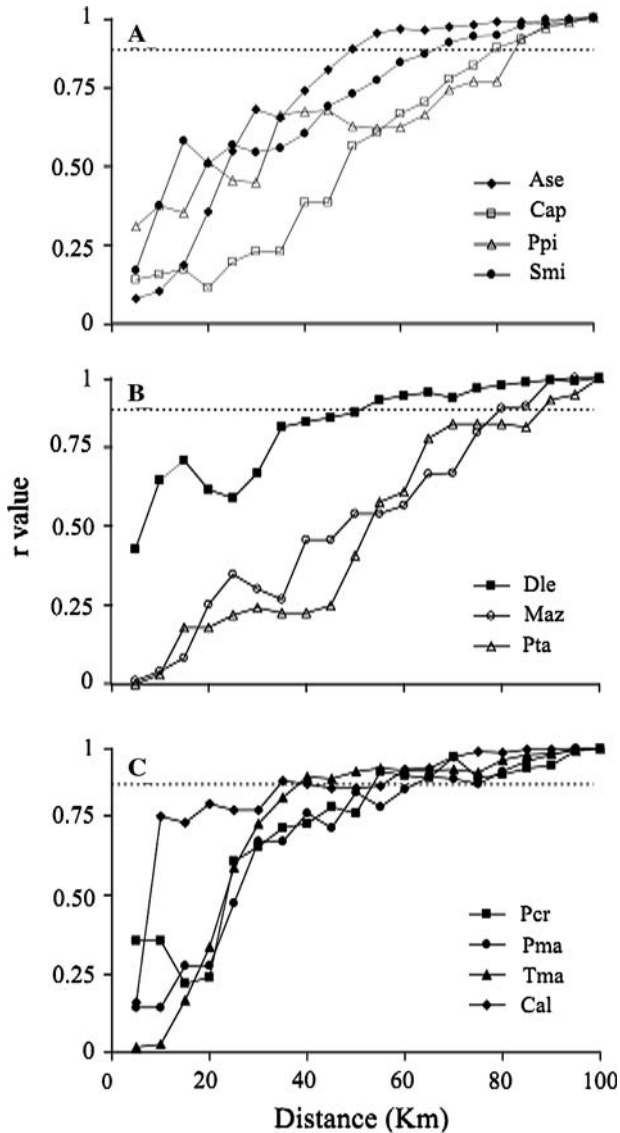


Fig. 6 Correlation coefficient (r -value) between species abundance (Kilometric Index, KI) estimated after 100 km sampling and abundance estimated for a lower sampling distances. The dashed line indicates an r -value of 0.9. Black symbols indicate species exhibiting a logarithmic r -value curve (cluster A on Fig. 5), open symbols indicate species exhibiting a linear r -value curve (cluster B in Fig. 5). (a) Primates, (b) Rodents and Ungulates, (c) Birds. Species codes are given in Table 2

the site or the strength of human disturbance. From our data set, a total survey effort of 80–90 km appears effective, as it is the largest effort needed to stabilize richness assessments. Interestingly, this effort is independent of the levels of threat on species and/or habitats. Namely, the hunting pressure has been previously identified as a major cause of local richness decrease in ungulates, large birds and primates (Bodmer et al. 1988; Begazo and

Bodmer 1998; de Thoisy et al. 2005). In the sites considered here, hunting was also the major disturbance affecting overall macrofauna diversity, but disturbed sites did not require a significant higher effort for a reliable assessment of their richness, meaning that this method is suitable for estimating the impact of human disturbance on game species richness.

Concerning abundances, kilometric indices for 7 of the 12 considered target species stabilized before 100 km of sampling (r -value > 0.95 , Fig. 6), thus validating the reliability of the line-transect method for these species. For these seven species, the sampling effort required to reliably predict abundance can be reduced from 30 to 65%, with an r -value remaining above 0.9, i.e., the reduced effort still provides a highly reliable prediction. This predictive ability may be of interest for conservation programs assessing the abundance of endangered species or species considered as biological indicators. There, the reduction of sampling effort to determine the relative abundance of large monkeys and frugivorous birds could be of interest, as these species are considered as overall indicators of hunting impacts on wildlife communities (Peres 1997; Brooks and Strahl 2000; Peres and Lake 2003). The reduction of sampling effort therefore provides interesting insights concerning rapid assessment of some major game species' abundance, site follow-up, between-site comparisons, but also population trends. However, for 5 species, corresponding to cluster B in Fig. 5, KI values were still not stabilized after a sampling effort of 100 km. That effort could nevertheless provide a relevant estimation of abundances, with an r -value of up to 0.9 at 95 km (Fig. 6). The discrepancy between species gathered in the clusters A and B was not related to social structure (gregarious vs. solitary), nor to differences in samples size (i.e., differences in relative abundance), as KI_{100} values of species belonging to the two clusters did not significantly differ (Mann–Whitney test: $z = 0.945$, $P = 0.35$). In contrast, home range sizes could explain this structure: species that require a higher sampling effort have larger home range sizes (Mann–Whitney test, $z = -2.26$, $P = 0.02$) (Table 3). The importance of the home range size in the accuracy of predictions made from data collected during field sampling has been previously suggested (Defler and Pintor 1985), and may be related to habitat use. Species with small area requirement are more liable to regularly use their entire home range for foraging (e.g., for howler monkeys, see Julliot 1992), and are expected to be recorded at a constant probability along the sampling effort, hence a limited sampling effort is sufficient to reliably predict species abundance. On the contrary, most species with

Table 3 Minimal sampling effort (sampling distance, in km) needed to estimate large mammal and bird richness and relative abundance for seven mammal and four bird species. Home range sizes recorded from bibliography are indicated. See Table 2 for species codes

	Minimal distance (km)	Home range (ha)
Species richness	85	
Species abundance		
Ase	50	40 (Julliot 1992)
Cap	>100	350 (Zhang 1995)
Ppi	>100	100 (Vié et al. 2001)
Smi	70	35 (Kessler 1995)
Dla	55	2–3 (Dubost 1988)
Maz	>100	300 (Vogliotti 2003)
Pta	>100	200 (Henry and Judas 1999)
Pcr	55	75 (for <i>P. leucoptera</i> : Sherman 1995)
Pma	65	no data available
Tma	40	3 (Erard et al. 1991)
Cal	60	180 (I. Jimenez, pers.comm.)

large home ranges show strong seasonal spatial variation, with foraging activities preferably concentrated in precise geographic subunits (see Zhang 1995 for capuchins *C. apella*, Henry and Judas 1999 for collared peccaries *P. tajacu*). Therefore, depending on season, phenology, and location of resources, the probability of presence of an animal in a given unit of its home range is not constant through time, and thus the probability of sighting it is not constant all along the sampling effort. Hence, the minimal sampling effort increases significantly with species home range (Fig. 7, $r^2 = 0.595$; $P < 0.01$). Lastly, home range overlap between neighbouring conspecific groups is also expected to influence the census effort, since a large overlap would reduce the number of spatially independent units. However, home range overlap is known to be very low in pristine and continuous forests, due to limiting amounts of resources, whether in rodents (Dubost 1988), ungulates (Henry and Judas 1999), or monkeys (Julliot 1992). This contrasts with the high levels of home range overlap found in secondary and/or heavily disturbed forests (e.g., Keuroghlian et al. 2004 for peccaries; Crockett 1996 for howler monkeys).

In brief, the present work clearly showed that monitoring well-identified target species using a diurnal line-transect provides reliable data for species management plans. Nevertheless the line-transect design used here has some limitations. First, most of the species considered during our surveys were potential indicators of habitat status due to their sensitivity to threats. These human-induced disturbances often conceal associated environmental factors that may affect species diversity and abundances (Kay et al. 1997; Peres and Janson 1999). For other species, abundances may not be recorded with a short-term effort and hence other methods (e.g., camera trapping, track counts, and nocturnal transects; Silveira et al. 2003) and/or higher-effort sampling have to be implemented. Although the design of the survey track is an important issue, the census walk is often restricted to a rather short section, i.e., 4–6 km repeated until a sufficient effort is obtained, due to logistic and field constraints (Haugaasen and Peres 2005a). This implies potentially important drawbacks due to the risk of multiple sightings of a single animal (i.e., pseudoreplication effect) or to the inability to accurately prospect the available habitats in heterogeneous environment. We therefore recognise that our sampling design is not optimal, but it reflects the sampling strategy employed by environmental management agencies for rapid assessment of species richness and abundances. Of course, to obtain more relevant data, and therefore more robust richness and abundance assessments, we strongly recommend the use of longer transects or the prospection of several tracks to characterise a single site.

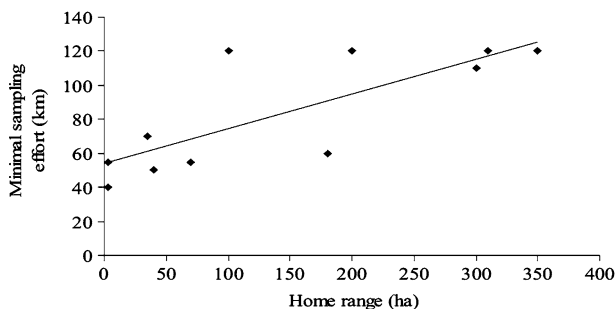


Fig. 7 Correlation between home ranges of some large vertebrates in Neotropical forests and minimal sampling effort required to assess their abundance. Species' codes are given in Table 2

In addition, many forest species are cryptic and forest habitat provides limited visibility, consequently the observers have to be trained. The detectability of species may also be influenced by the level of disturbance of the site. Animals in non-remote areas may become shier, or on the contrary may exhibit higher rates of dispersal, with consequences on the ability to record their presence (e.g., Johns 1985). The detectability of animals may also be influenced by the period of the day and of the year, in relation to their behavioural plasticity drawn by seasonal and inter-annual variations of resource availability. For instance, comparative surveys in pristine forests (Trinité Nature Reserve, French Guiana) showed that sighting rates of howler monkeys, spider monkeys, and black curassow were 20% higher during the wet season, whereas sighting rates of the brown capuchin, tamarins, agouti and *Penelope marail* were 30–50% lower (M. Dewynter, pers comm). Therefore, our results cannot be generalized to larger temporal scales nor to other forest types without previous assessment of their reliability, and we strongly encourage future studies to extend our results. For instance, a phenology index, related to the frugivorous diet of most of the target species (large birds, monkeys) could be designed to adjust the line-transect index. To avoid this issue, single-season surveys are recommended.

The present work, based on a large set of data, indicates the minimal effort needed to reliably estimate both species richness and the relative abundances of some large neotropical rainforest mammals and birds, using line-transect sampling. With the direct correlate of time and money saving, field effort reduction should constitute a significant help for both long-term studies of managed areas and biodiversity evaluation in new sites. However, the results should be considered with caution as the robustness of the estimators may be related to the diversity and the abundance of vertebrate assemblages. The minimal sampling effort defined here therefore needs to be tested in different types of Neotropical forests (e.g., with contrasted forest productivity) before being generalized. Once validated and applied to well-identified target species (e.g., threatened, indicator, or keystone species), the line-transect may be a useful tool for monitoring species and habitat management plans. Finally, from a wider point of view, the proposed standardization of the sampling effort could facilitate comparisons between sites from different neotropical areas, and therefore may help give a more general view on neotropical macrofauna richness and abundance. Despite the limits presented above, we propose that the transect method is a valuable and simple tool for assessment of both species richness and the abundance of several large species in neotropical forest habitats. We therefore encourage future research to use a similar approach on other animal communities and in other habitats, to gather additional information on the influence of forest productivity and species assemblage composition on the minimal required sampling effort. This would enable confident extrapolations of species richness and abundance in other Neotropical forests and may provide efficient guidelines to integrate the predictive analytic tool developed in this work into future biodiversity management plans.

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Appendix 1

Number of records (number of individuals per km) for the 34 species and the 17 sites. See Fig. 1 for sites location. In the case of social species, are given number of groups/number of individuals

Sites:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Primates																	
<i>Alouatta seniculus</i>		2/7	5/26	7/19	7/36	5/11	2/8	6/32	3/8	1/3	13/68	10/35	9/22	13/52	15/67	2/9	6/60
<i>Ateles paniscus</i>					1/3	2/6		1/2	1/3		4/10	6/15	2/2	6/20			
<i>Cebus apella</i>	5/26	3/20			4/23	3/32	6/36	8/82	3/15	3/12	7/74	1/5	3/28	12/74	6/39	1/5	9/62
<i>Cebus olivaceus</i>			4/44	5/19	1/5	1/12		12/1		3/16	1/18	1/10		3/20	1/8		4/35
<i>Saimiri sciureus</i>		9/115							1/15								
<i>Pithecia pithecia</i>	8/15	7/12	3/6	2/4	4/12	4/10	4/6	5/8	2/4	7/12	3/8	6/14	8/16		2/3		2/6
<i>Saguinus midas</i>	17/89	37/210	6/37	4/24	10/52	2/11	16/95	15/66	9/43	16/71	14/73	13/65	5/26	5/24	6/33	5/27	6/38
Xenarthres																	
<i>Tamandua tetradactyla</i>					1	2	3	1	1	2	1	1					1
<i>Myrmecophaga tridactyla</i>					1	1	1	1	1		1						
<i>Choloepus didactylus</i>							1										
<i>Bradypus tridactylus</i>				1					1								
Rodents																	
<i>Myoprocta acouchy</i>	16	5	5	5	13	2	14	21		10		9	10	9	2	6	1
<i>Dasyprocta leporina</i>	19	9	5	4	38	25	21	50	18	22	16	16	9	12	11	25	18
<i>Sciurillus pusillus</i>					2	3					2	2	1		1	1	1
<i>Sciurus aestuans</i>	3	2	3	2	1	1	1	1	3		1	2					
Carnivores																	
<i>Nasua nasua</i>			10				4/35	2/10					5/123		1		5
<i>Galictis vittata</i>											1						
<i>Eira Barbara</i>	1	1		1	2	1			2		1	2		1	1	1	2
<i>Speothos venaticus</i>				3													
<i>Lontra longicaudis</i>											3						
<i>Leopardus wiedii</i>											1					1	
<i>Leopardus tigrinus</i>																	
<i>Leopardus pardalis</i>																	
<i>Puma concolor</i>												1					1
<i>Panthera onca</i>													2				

Appendix 1 continued

Sites:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Ungulates																	
<i>Mazama americana</i>		6		2			3	3	4	4	3	3	2	6	5		3
<i>Mazama gouazoubira</i>	2		2		1	3	3	4	3	1	3	4	5	4	3		3
<i>Pecari tajacu</i>		2/5	2/10		1/5	2/15	4/19	15/30	3/14	4/20	1/3	6/35	2/9	5/34	2/6	6/10	3/14
<i>Tayassu pecari</i>		2/17		1/6		3/40						1/10	4/120	2/30	2/32		
<i>Tapirus terrestris</i>					1		1	1			2						
Birds																	
<i>Psophia crepitans</i>		2			7/37			3/21			3/8	5/10	3/20	10/54	4/35		5/26
<i>Crax alector</i>		1			3	7	2				10	10	5	13	23		7
<i>Tinamus major</i>	28	9	11	6	13	9	25	18	12	27	29	18	23	9	11	9	13
<i>Penelope marail</i>	5	5	5		2	11	2	10	13	1	3	4	1	6	4		2

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