Assessing the completeness of bat biodiversity inventories using species accumulation curves

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Summary

1. In this study we used species accumulation models to solve one of the most serious problems encountered when comparing species richness between different communities. The problem is how to compare data among inventories in which different methodologies or measures of sampling effort have been employed. The methods used here for bats may be applied to any other biological group. We fit two asymptotic models to species accumulation curves for bat inventories to evaluate local or within-community diversity (alpha) and landscape diversity (gamma) in central Veracruz, Mexico.

2. Species accumulation models allow us to: (i) measure within-inventory efficacy and completeness; (ii) obtain an estimate of species richness that is based on a standardized measure of sampling effort, which makes valid comparisons between inventories possible; and (iii) estimate the minimum sampling effort required to reach a satisfactory level of completeness.

3. The applied models fit well in all cases ($r^2 > 0.95$). The linear dependence model predicted lower asymptotes and the Clench model predicted higher asymptotes than the observed species richness. These models are useful as predictors representing the lower and upper limits between which the true species richness value should lie.

4. Alpha diversity for bats in all vegetation communities (11–18 species) was lower than the gamma diversity (20 species), suggesting that species richness and the sampling effort required are related to environmental heterogeneity.

5. We propose that 90% of the total fauna predicted by either of the models is an acceptable standardized value for comparing species richness between communities.

6. We assessed the within-inventory completeness as the proportion of the models' asymptote, where 90% is the desired minimum level of completeness. Except in palm stands, all bat inventories had an acceptable level of completeness, at least for the linear dependence model.

7. For conditions similar to those of our study area, the minimum effort required to obtain a satisfactory level of completeness is 5–18 nights for plant communities and 18 nights for more heterogeneous landscapes.

8. We make recommendations for improving the efficacy and completeness of bat surveys based on the application of species accumulation models.

Key-words: alpha and gamma diversity, Chiroptera, cumulative models, sampling effort.

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Introduction

Among the different geographical scales at which biodiversity can be inventoried, analysis of species at the landscape level can be very useful. Studies at the landscape level are particularly valuable for detecting and evaluating the effects of anthropogenic activities (modification and fragmentation of natural communities over time), and also for comparing the biodiversity of different geographical areas (Halffter 1998). In practice, in order to study species diversity at the landscape level, we must make an effort to select a study group carefully (such as an indicator

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group) that will reflect accurately changes in diversity under a variety of environmental conditions. Species inventories may, however, be misleading when lists of species are compiled, because (i) within inventories, there is no indication of how complete such lists may be (Soberón & Llorente 1993), and (ii) in most cases, between inventories, it is not possible to compare directly or combine data because of incompatible sampling methods, terminology or data handling systems (Dennis & Ruggiero 1996). However, with a standardized measure of species richness, one that considers within-inventory efficacy and completeness, it should be possible to compare species inventories from different places, different times or those compiled with different sampling techniques. Without standardization such comparisons will lack the rigour required for valid and meaningful interpretation.

One way of assessing inventory completeness and standardizing the comparisons of different inventories is through the use of species accumulation models fitted to species accumulation curves (Soberón & Llorente 1993), in which the cumulative number of species is plotted against some measure of the effort it took to obtain that sample (Hayek & Buzas 1997). The measure of effort can be the number of individuals observed, number of samples, traps, trap-days or some other measure of area or time (Soberón & Llorente 1993; Colwell & Coddington 1994; Hayek & Buzas 1997; Longino & Colwell 1997). The curves of species accumulation models reach an asymptote when the probability of adding a new species to the list approaches zero, but are non-asymptotic if this probability does not reach zero (Soberón & Llorente 1993).

Species accumulation models allow: (i) measures of inventory efficacy and completeness within a given study, and (ii) valid comparisons between studies based upon a standardized measure of sampling effort. The use of species accumulation functions can result in better planning and sampling protocols by providing reliable estimates of the minimum effort required to obtain an efficient inventory, and, consequently, can result in notable savings in time and field expenses (Soberón & Llorente 1993).

The purpose of this study was to test the fit and compare the predictions of two asymptotic models of species accumulation applied to neotropical bat inventories on two spatial scales of biodiversity: alpha diversity within seven vegetation communities, and gamma diversity at the landscape scale. This approach was selected to: (i) assess completeness within inventories; (ii) obtain a comparable estimate of species richness based on a standardized methodology; and (iii) estimate the minimum effort required to reach an arbitrary, but acceptable, minimum level of completeness.

Neotropical bats are easily sampled and are often abundant in numbers of both species and individuals (Findley & Wilson 1983). In the Neotropics, as many as 100 sympatric species may be found. In addition to their taxonomic richness, the diet of this group is very diverse, including fruit, pollen, nectar, small vertebrates, insects and other arthropods, as well as blood. Neotropical bats also influence other organisms through pollination, seed dispersal and insect predation. For these reasons, this group has been proposed as a promising indicator for analysing biodiversity in relation to community structure patterns (Kalko 1997) and ecosystem modification (Fenton *et al.* 1992; Kalko 1997).

Methods

STUDY AREA

The study area was located in central Veracruz, Mexico, in the municipality of Jalcomulco, between $19°17'$ and $19°22'$ N latitude and $96°43'$ and $96°49'$ W longitude. Altitude ranges from 350 to 700 m a.s.l. The area is characterized by plateaux and deep ravines with high slopes, as well as valleys and limestone hills. The mean annual temperature is $22°C$ and mean annual rainfall is 1500 mm. As for most areas of central Veracruz, human activities have led to changes in land use and the fragmentation of natural communities. However, this impact has not been extreme in the study area. Fragments of undisturbed communities and riparian corridors remain almost intact between modified ecosystems, which together form a landscape mosaic.

The study area covers approximately $42 km^2$ (Fig. 1) and comprises the following vegetation communities: tropical subdeciduous ($2·05 km^2$) and deciduous forest ($11·63 km^2$), riparian vegetation ($1·37 km^2$), palm stands ($3·35 km^2$), secondary vegetation ($12·35 km^2$), mango plantations ($10·37 km^2$) and corn fields ($0·80 km^2$), as defined by Castillo (1995) based on floristic inventories and environmental characteristics. For the purposes of this study, we considered these vegetation communities to be homogeneous units (α level) relative to the landscape (γ level).

FIELD SAMPLING METHODS

Fourteen sampling sites were distributed throughout the seven vegetation types of the study area: three in subdeciduous forest, three in deciduous forest, three in secondary vegetation, two in mango plantations, one in riparian vegetation, one in a palm stand and one in a corn field (Fig. 1). At each sampling site, bat surveys were made every 2 months from July 1995 to June 1997, except when there was a full moon to avoid capture bias due to the lunar phobia (Morrison 1978). Note that by analysing the samples
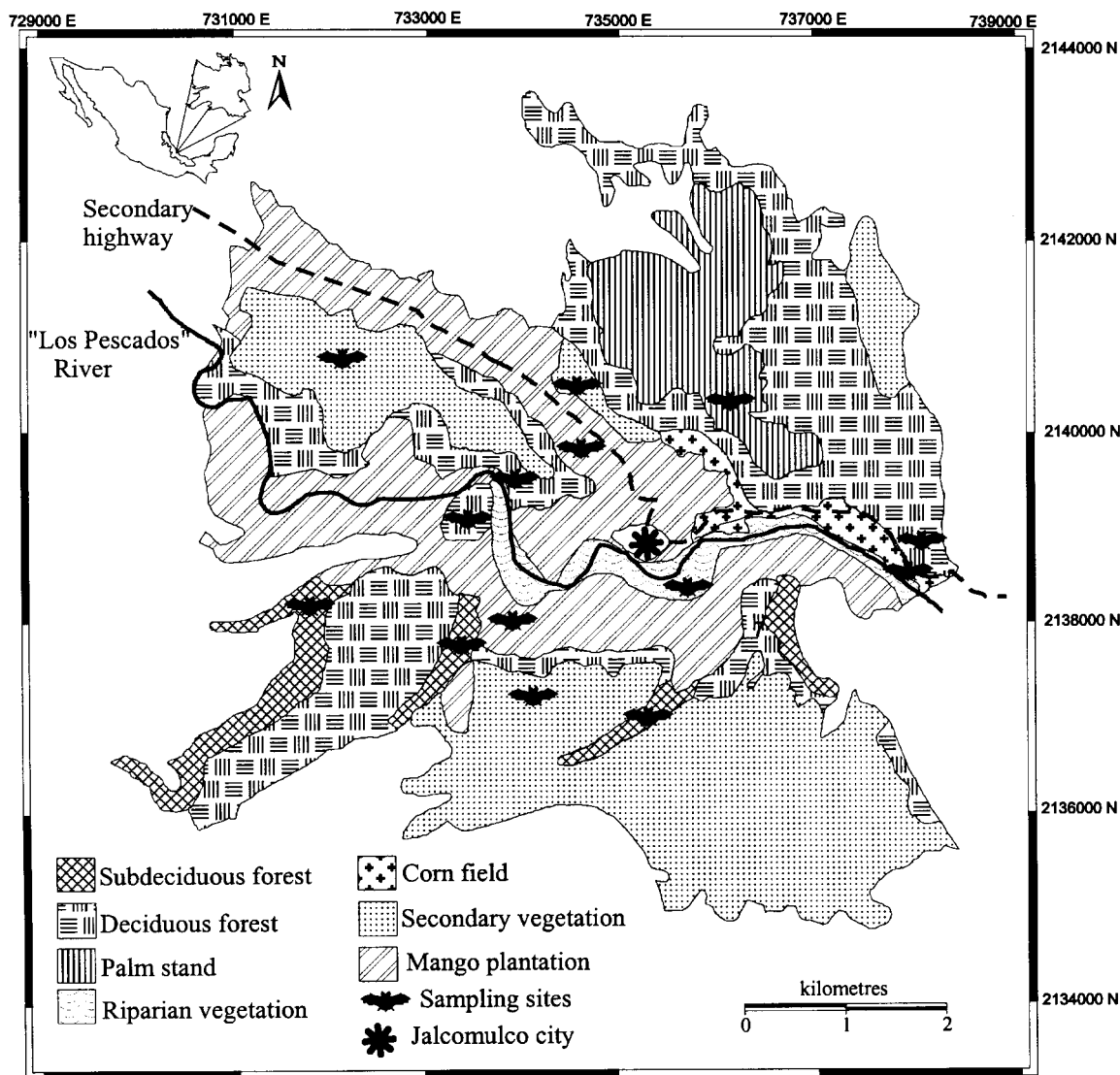
Fig. 1. Location of the study area where bat inventories were carried out, in the northern Neotropics, in central Veracruz, Mexico. The area covered approximately $42 \, km^2$.

from the seven plant communities as separate inventories, we are assuming that samples might not be statistically independent in space or time. Spatially, sampling sites were separated by an average of 3 km, which is a distance easily travelled by bats. Temporally, data came from successive sampling occasions conducted at the same sites.

In each survey, the order in which the sites were sampled was set at random. Bats were captured with standard mist nets (38-mm mesh, 2·5 m high and 12 m wide) set at ground level. Nets were opened at dusk for 1–3 h, for one night at each sampling site. Different numbers of nets (4–10) were set in each sampling site, depending on the characteristics of the vegetation and the ease of deploying the nets. Even so, sampling effort was the same for each vegetation type (see below). Because only the lower 2·5 m of the forest was sampled during part of the night, this work is restricted to species belonging to

the families Phyllostomidae and Mormoopidae (see below). These bats fly at ground level during the first period of the night and thus can be captured with mist nets.

Nets were monitored every 30 min and individual bats were identified to species with field keys (Coates-Estrada & Estrada 1986; Emmons 1990; Alvarez, Alvarez-Castañeda & López-Vidal 1994; Medellín, Arita & Sánchez 1997). Bats were marked with plastic collars and released at the site of capture.

MEASUREMENT OF SAMPLING EFFORT

Sampling effort in bat research using mist nets has been quantified by different approaches such as (i) the number of netting nights regardless of the number of nets used (Fleming, Hooper & Wilson 1972);

(ii) net-nights, with a constant number of nets (Findley & Wilson 1983); (iii) number of individuals captured (Brosset *et al.* 1996; Rautenbach, Fenton & Whiting 1996); (iv) net hours with a specified number of nets (Fenton *et al.* 1992; Estrada, Coates-Estrada & Meritt 1993); (v) sampling time (dos Reis & Muller 1995); and (vi) net metres per hour (Medellín 1993).

We used the product of the net area (total metres) and the total number of hours that the nets remained open for a given site (Medellín 1993). Medellín (1993) summed total metres of net and multiplied this by the total number of hours per sampling period. Here, we propose an approach that better reflects our sampling methods: total net metres per hour (m h^{-1}) was calculated per night for each sampling site. This way, the sum of total m h^{-1} can be calculated for a given site and these data can be reported by sampling period or by vegetation type, giving the same grand total of sampling effort. As a different number of nets was set for different periods at each sampling site, we increased the number of sampling nights for those sites where effort was less, and added the effort of all the sampling sites for a given vegetation type to standardize sampling effort (Table 1). In heterogeneous habitats that differ in structure and area, this method is very useful because the total required m h^{-1} for every vegetation type can be obtained, even when a different number of nets of varying lengths is used and sampling periods vary in duration owing to habitat restrictions or weather conditions.

However, once we had standardized the sampling effort in the way described, we were forced to use the number of nights as a measure of sampling effort in order to obtain an adequate fit to the cumulative models, because values of m h^{-1} do not rise gradually in inventories. As an average, one of our sampling nights equals 225 m h$^{-1.}$ This is equivalent to setting 6·25 nets, each net measuring 12 m in length, during the first 3 h after sunset.

STUDY GROUP

In the study area, we recorded bats (Microchiroptera) from six families. We restricted the analysis of biodiversity to the families Phyllostomidae and Mormoopidae, which belong to common taxonomic and biogeographic units. Both are members of the superfamily Noctilionoidea and their distribution is restricted to the Neotropics (Simmons 1998). Representatives of these families were collected regularly in all vegetation types. Members of four other families were captured (Emballonuridae, Natalidae, Vespertilionidae and Molossidae), but they were not included in our biodiversity analysis because they belong to different natural groups (Simmons 1998) and cannot be captured easily with mist nets. We used mist nets because they are the most common, easiest and least expensive capture devices, although they are biased to under-represent some of the species known to be adept fliers, such as vespertilionids (Aldridge & Rautenbach 1987; Rautenbach, Fenton & Whiting 1996; Kalko 1997) and emballonurids (Kalko 1997). The survey at ground level also underestimates the presence of molossids that often forage for insects above the canopy (Bonaccorso 1979; Rautenbach, Fenton & Whiting 1996; Fenton & Griffin 1997; Kalko 1997). We did not capture members of the family Noctilionidae (Noctilionoidea), because these restrict their flight activities over rivers, which were not sampled in this study (Bonaccorso 1979). Unlike Fenton *et al.* (1992), we did not restrict the study group to the family Phyllostomidae because mormoopids are also easily captured with mist nets. Mormoopid bats are slow-flying hawking insectivores that fly within 3 m of the ground (Bonaccorso 1979). Their inclusion increased the scope of the analysis because they belong to a different trophic guild.

DATA ANALYSIS

We analysed patterns of bat species accumulation against sampling effort for seven vegetation types and the landscape mosaic. To assess the completeness of the inventory method relative to the sampling effort invested, and to project species accumulation curves, we fit two asymptotic models (reviewed by Soberón & Llorente 1993) to our species accumulation data.

Table 1. Capture effort for neotropical bat inventories in the seven plant communities and the landscape mosaic

Vegetation type (area, km^2)	Number of sampling sites	Total capture nights	m h^{-1}
Subdeciduous forest (2·05)	3	24	3853
Deciduous forest (11·63)	3	20	3850
Riparian vegetation (1·37)	1	14	3858
Palm stand (3·35)	1	14	3858
Secondary vegetation (12·35)	3	18	3858
Mango plantation (10·37)	2	16	3846
Corn field (0·80)	1	14	3873
Landscape mosaic (41·92)	14	120	27 001

The linear dependence model is based on the concept that the number of species collected decreases linearly as sampling effort increases:

$$S(t) = a/b[1 - \exp(-bt)]$$

where t is a measure of effort (in our case number of nights), $S(t)$ is the predicted number of species at t, a represents the rate of increase at the beginning of the sampling, and b is species accumulation. Soberón & Llorente (1993) recommended this model for situations where the taxon is well known or the study area is relatively small and could theoretically reach an asymptote over a finite period of time. We used Lamas, Robbins & Harvey's (1991) equation for estimating the time required to register a proportion of the total fauna as predicted by the asymptote (tq):

$$tq = -1/b \ln(1 - q)$$

where q is the desired proportion of the total fauna for which the required time is estimated.

The Clench model assumes that the probability of adding species to the list decreases with the number of species already recorded, but increases over time:

$$S(t) = at/(1 + bt).$$

Soberón & Llorente (1993) recommend this model for larger areas than those where the linear dependence model would be applied, or for taxa for which the probability of adding new species will increase as more time is spent in the field, until an upper limit is reached. For this model, we applied Soberón & Llorente's (1993) equation for tq:

$$tq = q/[b(1 - q)].$$

Our bat survey was carried out over a relatively small area (42 km^2); however, as rare species continued to appear with increased sampling time, we decided to fit both asymptotic models to our data to compare their predictions under different habitat conditions. For both models, the predicted asymptote was calculated as a/b.

The species accumulation curves were obtained by taking the number of survey nights as sampling effort. To eliminate the influence of the order in which nights were added to the total, the sample order was randomized 100 times using EstimateS software (Colwell 1997). This produces smoothed species accumulation curves (Fig. 2) by repeated random reordering of the samples (Longino & Colwell 1997). We fitted the asymptotic models to these smoothed curves.

We assessed the completeness of our bat inventory by calculating the proportion of the maximum number of species (asymptote) registered at the end of sampling. By definition, reaching 100% richness would require an infinite effort, and the rate of species recorded per effort invested decreases markedly
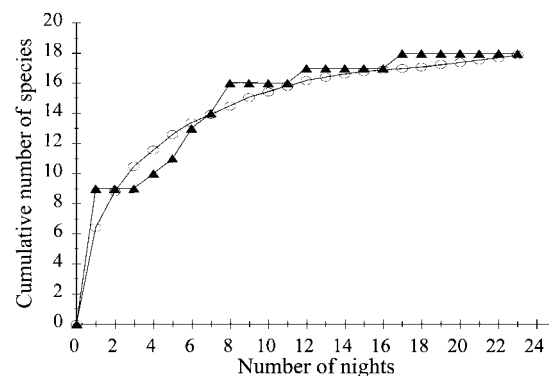

Fig. 2. Bat species accumulation curve (▲) in subdeciduous rainforest and the smoothed average curve produced by 100 random reorderings (○).

as the curve approaches the asymptote (Soberón & Llorente 1993). Thus, the effort required to register a species increases substantially as the proportion of species captured approaches the total number of species present. We selected 90% of the total fauna as a conservative, but satisfactory, level of inventory completeness for the purpose of making valid comparisons, and estimated the effort required to reach this level. We used a non-linear regression (Sigma Stat; Jandel Corporation 1995) to fit the two models to the smoothed curves of the observed data.

Results

We recorded 16 species of Phyllostomidae: *Micronycteris microtus* Gray, *Glossophaga soricina* Pallas, *Anoura geoffroyi* Gray, *Carollia brevicauda* Schinz, *Artibeus jamaicencis* Leach, *A. lituratus* Olfers, *A. intermedius* Allen, *Centurio senex* Gray, *Dermanura phaeotis* Miller, *D. tolteca* Saussure, *D. watsoni* Thomas, *Sturnira lilium* E. Geoffroy St-Hilaire, *S. ludovici* Anthony, *Platyrrhinus helleri* Peters, *Chiroderma salvini* Dobson and *Desmodus rotundus* E. Geoffroy St-Hilaire; and four species of Mormoopidae: *Mormoops megalophylla* Peters, *Pteronotus parnelli* Gray, *P. davyi* Gray and *P. personatus* Wagner.

The species accumulation curves and fitted models for the seven vegetation types and the landscape mosaic (Fig. 3) reached an asymptote, except for the palm stand (Fig. 3d). Both species accumulation models fit the observed data very well for all vegetation types ($r^2 > 0.95$; Table 2). However, the linear dependence model predicted a lower asymptote than that predicted by the Clench model for all vegetation types. Considering the nature of the models, we propose the use of financial terms, such as those used for forecasting confidence intervals in the stock market, to describe the predictions derived from our models. Consequently, for our data the linear dependence model predicts the 'floor' or lower limit,
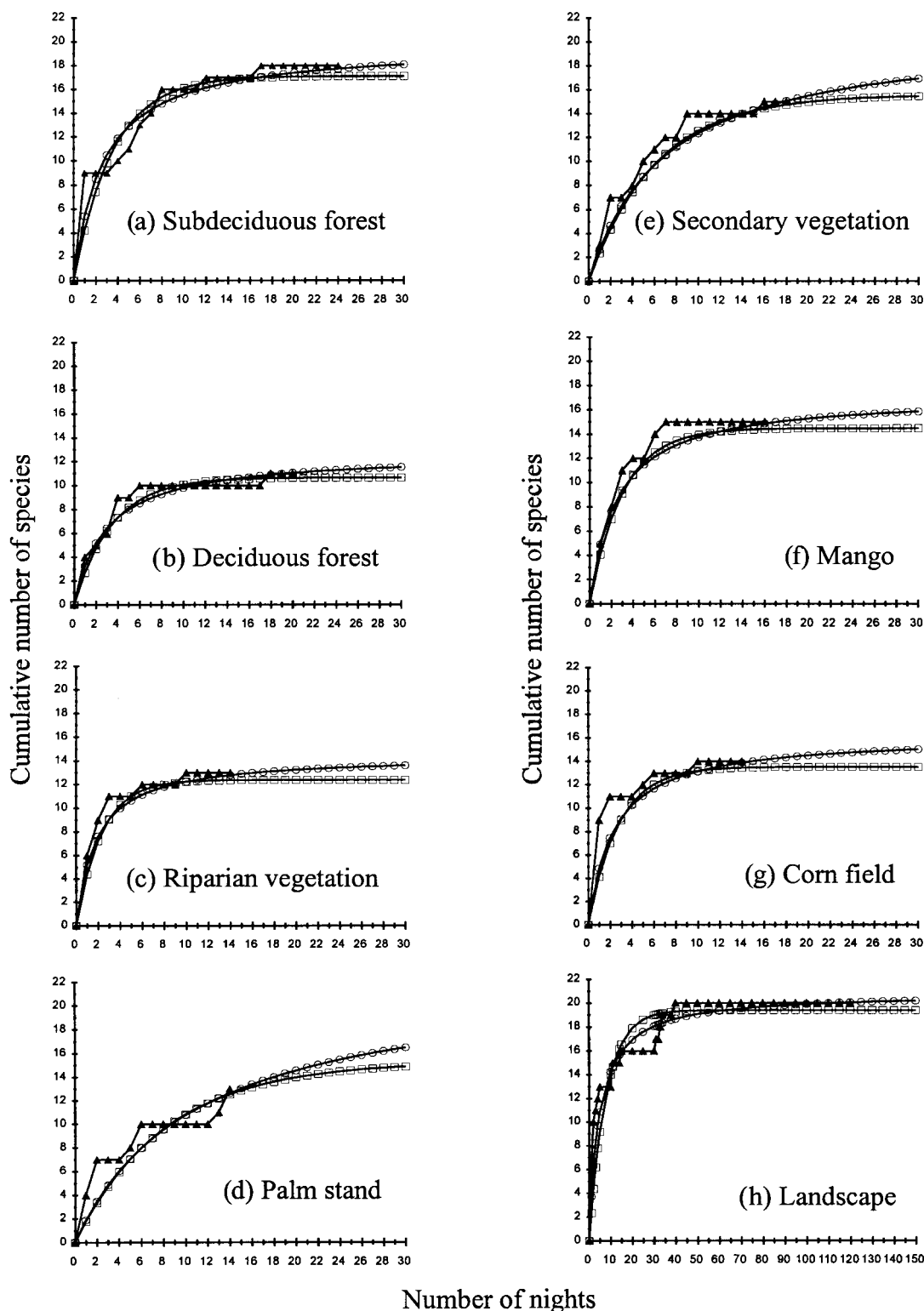
Fig. 3. Original and fitted bat species accumulation curves for the seven vegetation types and the landscape mosaic. ▲ = observed data; ○ = prediction of the Clench model; and □ = prediction of the linear dependence model.

and the Clench model represents the 'ceiling' or upper limit, and the true species accumulation curve should lie between them.

In the landscape mosaic inventory we captured 20 species of phyllostomids (16) and mormoopid (four)

bats. Richness for the seven vegetation types ranged from 11 to 18 species. Except for secondary vegetation and the palm stand, the asymptote predicted by the linear dependence model was even lower than the number of species already registered, indicating

Table 2. Number of species recorded, parameters and predictions of two species accumulation models fitted for each plant community and the landscape mosaic, where a is the slope at the beginning of the sampling, b is a parameter related to the shape of the accumulation of new species during the sampling, t is the sampling effort, a/b is the asymptote and r^2 is the coefficient of determination

Vegetation type	Number of species	Linear dependence model $S(t) = a/b[1 - \exp(-bt)]$				Clench model $S(t) = at/(1 + bt)$			
		a	b	a/b	r^2	a	b	a/b	r^2
Subdeciduous forest	18	4·80	0·28	17·1	0·97	7·48	0·38	19·7	0·99
Deciduous forest	11	3·10	0·29	10·7	0·99	4·38	0·35	12·6	0·99
Riparian vegetation	13	5·44	0·44	12·4	0·97	8·15	0·56	14·4	0·99
Palm stand	13	1·89	0·12	15·3	0·99	2·06	0·09	22·5	0·99
Secondary vegetation	15	2·54	0·16	15·6	0·99	3·01	0·14	20·8	0·99
Mango plantation	15	4·80	0·33	14·5	0·97	6·88	0·40	17·2	0·99
Corn field	14	4·94	0·36	13·4	0·98	6·96	0·43	16·2	0·99
Landscape mosaic	20	2·49	0·13	19·4	0·95	4·53	0·22	20·8	0·99

that for the rest of the vegetation communities more than 100% of the predicted asymptote was registered (Table 3). According to this lower limit, the bat inventory for the palm stand failed to reach a satisfactory level of completeness (85%) at the level of effort invested (13 net nights), while inventories for the remaining vegetation types and the landscape mosaic recorded more than 95% of the total fauna. Only the inventories in the riparian vegetation, subdeciduous forest and the landscape mosaic reached more than 90% of the upper limit predicted by the Clench model (Table 3).

Considering that each model yields different predictions owing to their underlying assumptions (Soberón & Llorente 1993), comparisons must be made based upon the predictions of the same model. Here, we compared the standardized measure of species richness as a function of the linear dependence model (17·5 species = gamma diversity for the landscape; 9·6–15·4 species = alpha diversity for the vegetation communities) or as a function of the Clench model (gamma = 18·7 species; alpha = 11·3–20·3 species).

With the lower and upper limits, we calculated the minimum effort required to reach an acceptable level of completeness under similar environmental conditions. To obtain the lower estimate of richness, the required effort ranged from five to 19 nights for vegetation type inventories, and 18 nights were required for the landscape mosaic (Table 3). For the upper limits, the minimum effort required lay between 16 and 98 nights for inventories of small homogeneous areas like the vegetation types studied here, and 41 nights for a larger heterogeneous area (landscape; Table 3).

Discussion

The use of asymptotic functions fitted to species accumulation curves increases the rigour of comparisons because it assesses the completeness of an inventory (Palmer 1990; Soberón & Llorente 1993; Colwell & Coddington 1994; Longino & Colwell 1997). Both the magnitude and the urgency of the task of assessing biodiversity make extrapolation and prediction critical components of research agendas in this field (Colwell & Coddington 1994). Species accumulation models provide a predictive tool for conservation and biodiversity studies, and also provide a planning tool for designing sampling

Table 3. Comparison of two different models that describe the growth of the cumulative curve, including the estimated sampling effort (expressed in number of nights) required to record an acceptable proportion (90%, see the data analysis in the methods section) of the diversity

Vegetation type	Linear dependence model		Clench model	
	% of the asymptote recorded	Sampling effort required	% of the asymptote recorded	Sampling effort required
Subdeciduous forest	105·14	8·1	91·56	23·7
Deciduous forest	103·19	7·9	87·16	25·9
Riparian vegetation	105·01	5·2	90·39	15·9
Palm stand	85·13	18·6	57·73	98·4
Secondary vegetation	96·28	14·1	71·94	62·3
Mango plantation	103·59	6·9	87·31	20·9
Corn field	103·47	6·3	86·53	20·9
Landscape mosaic	103·14	17·9	96·10	41·3

protocols (Soberón & Llorente 1993). Thus, application of these models is highly recommended when comparing species diversity from different communities or landscapes, or from areas with different degrees of perturbation, especially if indicator groups are being used.

Except for the palm stand, our bat inventories demonstrate a satisfactory level of completeness, at least for the lower limit predicted by the linear dependence model (Table 3). In the palm stand, one species was added to the list on the penultimate survey night and two more species were added on the last night. Contrary to expectation, these three new species recorded in the palm stand are not considered rare in this landscape. Furthermore, one of the species captured on the last night, *Sturnira ludovici*, was the most abundant species. This probably means that these species have stable populations in the landscape but are tourists species or vagrants (*sensu* Gaston 1996) in palm stands. Their presence in this vegetation type is restricted to brief periods because the habitat does not provide sufficient resources to maintain populations. Thus, species such as *S. ludovici* are tourists for one or more vegetation types, but are not on the larger landscape scale.

Although our survey for the palm stand took into consideration spatial heterogeneity, we did not consider temporal heterogeneity. This factor, perhaps in a random fashion, may explain the ephemeral presence of these species. Unlike the other vegetation types, the palm stand does not have a well-defined bat species composition. The number of species captured in this community probably reflects a greater influence from tourist species (random events) than that which occurs in other communities. The presence of tourist species might indicate a lack of stability in the indicator group for a given community. That is, they do not form a community that approaches saturation, but rather a non-stable community open to occasional, transitory elements such as tourist species.

In the relatively small vegetation communities we recorded a lower number of species and our inventories reached the asymptote more rapidly than in the larger more heterogeneous landscape. For each plant community we recorded a number of species that represents the alpha diversity under current environmental conditions. The gamma diversity of the landscape mosaic results from the complementarity (*sensu* Colwell & Coddington 1994) of different alpha diversities. This value of gamma diversity is more strongly associated with the heterogeneous landscape mosaic as a whole, than with any particular type of plant community. Thus, compared with the landscape, to obtain an acceptable level of completeness less effort is required for each of the vegetation types, with the exception of the palm stand. The effort required to survey the landscape is not simply the sum of the effort required for each vegetation type, because many species are shared between these elements.

For comparative studies within a landscape or between landscapes, it is important to have a reliable method for obtaining rapid estimates of species richness. However, reports of bat species accumulation curves (Brosset *et al.* 1996; Findley & Wilson 1983; Estrada, Coates-Estrada & Meritt 1993; dos Reis & Muller 1995) use different units of sampling effort and do not apply any model for an objective assessment of inventories. To our knowledge, only Medellín (1993; see also Soberón & Llorente 1993) fits the linear dependence model to his results of bat surveys done in the Lacandona evergreen forest of southern Mexico, when he captured bats with mist nets and other methods between April 1982 and November 1986. He found that species accumulation was related to sampling effort measured in number of sampling nights. The linear dependence model was fitted to the accumulation pattern of 50 bat species, 44 of which were captured with mist nets (29 phyllostomids, two mormoopids and 13 species from other families). The model was applied to the raw data of the cumulative species curve without sample order randomization. The linear model applied to his data predicts an asymptote of 56·38 species (of which he captured 88·68%) and indicates that, using his field methods, 49 nights are required to register 90% of this total fauna. The standardized measure (90% of the asymptote) of bat richness for the Lacandona forest would be 50·7 species. This richness is substantially greater than any of the values of alpha and gamma diversity obtained for our study site, even when only the phyllostomid and mormoopid species that Medellín captured are considered. The Lacandona tropical evergreen forest is partially included in the Montes Azules Biosphere Reserve, which covers approximately 331 200 ha (Medellín 1993). The greater bat species richness and required sampling effort are probably related to the high structural heterogeneity of the plant community, and the large area covered by this primary community.

Our findings allow us to propose specific recommendations for bat surveys under similar conditions. Some of these suggestions may also be applied to other groups.

Habitat heterogeneity

Our results suggest that sampling effort is related to habitat heterogeneity, which therefore should be taken into account. Measures of habitat complexity and heterogeneity such as those proposed by August (1983) can be related to sampling effort required under different conditions, and allow for a reliable estimate of species richness.

Seasonal variation

Sampling protocols should take seasonal variation in species composition and abundance into account. Depending on the biogeographic and environmental characteristics of the study area, collecting effort should be distributed throughout the year (as in this study) or can be restricted to the season in which abundance peaks. Once sampling has been standardized with respect to season, capture sequence can be randomized, thus avoiding temporal bias in the predictions of the species accumulation curves.

Minimum required effort

Within our study area and with our methodology, in order to reach the predicted lower limit of species richness (linear dependence model) 5–18 nights are required in small homogeneous areas to register 90% of the total bat fauna present, while larger more complex landscapes require at least 18 nights. For different sampling designs or under different ecological conditions and biogeographical regions, inventory completeness should be assessed to estimate the minimum effort needed and, once estimated, can be applied to similar sites.

The use of other methods in addition to mist nets

Using species accumulation curves, Longino & Colwell (1997) assessed the individual and joint efficacy of different sampling methods for ants and, consequently, proposed sampling designs that involved several complementary methods of collection. For bats, inventory methods can be adapted to include sets of species other than those that fly at ground level during the first 3 h after nightfall and can be captured with mist nets. Harp traps (Francis 1989) and other specialized traps can be used for capturing bats under different environmental conditions. In temperate regions bat species identity has been established by detecting their echolocation calls with ultrasound receivers (Vaughan, Jones & Harris 1997). Recent research has improved detection techniques that take advantage of the fact that different species of neotropical bats use different echolocation signal designs as they have adapted to a particular niche (Allen 1996). However, in the Neotropics, where Phyllostomidae species predominate, mist netting is a more appropriate sampling method than acoustic detection (Fenton *et al.* 1992), because phyllostomids are 'whispering bats' that emit low intensity sounds that are rarely registered with detectors (Arita & Fenton 1997; Kalko 1997). A comparison of the efficacy of different sampling techniques should be used to optimize bat species detection and improve inventory completeness.

Our bat inventories worked efficiently (*sensu* Longino & Colwell 1997), as species accumulation curves quickly rose and reached an asymptote as a function of sampling effort. The four recommendations made above can improve the sampling efficacy for bat inventories, making bats a potential group for measuring and monitoring biodiversity. Many authors discuss and assess the ideal characteristics of biodiversity indicator groups (Noss 1990; Pearson & Cassola 1992; Halffter & Favila 1993; Pearson 1994; Favila & Halffter 1997; Halffter 1998). For selecting such groups, researchers should also consider methods that allow the species accumulation curve to reach rapidly an asymptotic phase relative to sampling effort, as shown in this paper.

Our results for bats show three practical applications of species accumulation models, including assessment of within-inventory completeness, estimating a standardized measure of species richness for comparisons between inventories, and estimation of the minimum effort required for a complete inventory. This can lead to important improvements in sampling design, as money, time and effort should be invested efficiently to maximize species capture as a function of cost. With the assessment of inventory completeness, a reliable standardized measure of richness can be obtained for meaningful comparisons between species inventories, even when the sampling effort differs.

Acknowledgements

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