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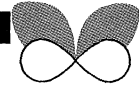
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Assessing completeness of Mexican sphinx moth inventories through species accumulation functions

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Abstract. Accumulation curves were fitted to faunal lists for moths of the family Sphingidae for three Mexican sites. Information coming from both museum data and *ad hoc* inventory efforts was used and compared. Two different accumulation models were used to extrapolate predictions of fauna sizes, and a non-parametric method was used to validate the

results of the models. One of the models was found to provide practical and informative extrapolations of fauna size, with the non-parametric method also being useful when detailed information on specimen frequencies is available.

Key words. Sphingidae, moths, accumulation curves, Mexico

INTRODUCTION

The rapid rate of human-caused perturbation of natural systems demands the application of quick and reliable tools for estimation of species-richness, especially, for areas in which some taxa are little known, e.g. invertebrates in tropical zones (Erwin, 1982, 1988; May, 1988; Stork, 1988; Gaston, 1991). For example, few Mexican localities have thorough inventories of biological diversity (Ramamoorthy *et al.*, 1993): our experience suggests that not more than about fifty Mexican localities have been exhaustively collected for Papilionid and Pierid butterflies. For moths the number is much lower.

Estimation of species richness of taxa in a given area may be achieved by modelling of species accumulation curves (Soberón & Llorente, 1993). In practical terms, such models may yield predictions of increases in richness expected for a given level of additional collection effort (Soberón & Llorente, 1993; Colwell & Coddington, 1994). At the same time, these models can facilitate the planning of field activities or the evaluation of biological inventories already completed (Clench, 1979; Lamas, Robbins & Harvey, 1991; Prendergast *et al.*, 1993). Since the use of accumulation curves is still relatively new, more experience is required regarding their usefulness. In this paper we present a

simple protocol for assessing the exhaustiveness of a biological inventory performed in the field or using information from museums. We employ data from three Mexican localities to analyse and estimate values of richness in both situations. In order to compare the accuracy of these estimates, we also use a non-parametric technique for estimating the asymptotic values of the analysed cases (Chao, 1984, cited in Colwell & Coddington, 1994). Finally, we discuss the relative values of the different methods, and implications of changes in measures of effort.

METHODS

Sphinx moth field data

We collected sphingids using uv light traps at a tropical rain forest at the Lacandon rain forest, near the Estación de Biología Chajul, Chiapas (Chajul) (16° 05' N 90° 56' W), from October 1991 to July 1993, for a total of 160 sampling nights. Detailed descriptions of the site are provided in Medellín (1994). In all, eighty-one species of Sphingidae were recorded. Collecting sites included rain forest edge, grasslands, forest understory, river borders, and secondary vegetation. Daily collecting effort averaged 12 h of continuous trapping. We also recorded the numbers of individuals per trap and the number of traps set each night. After

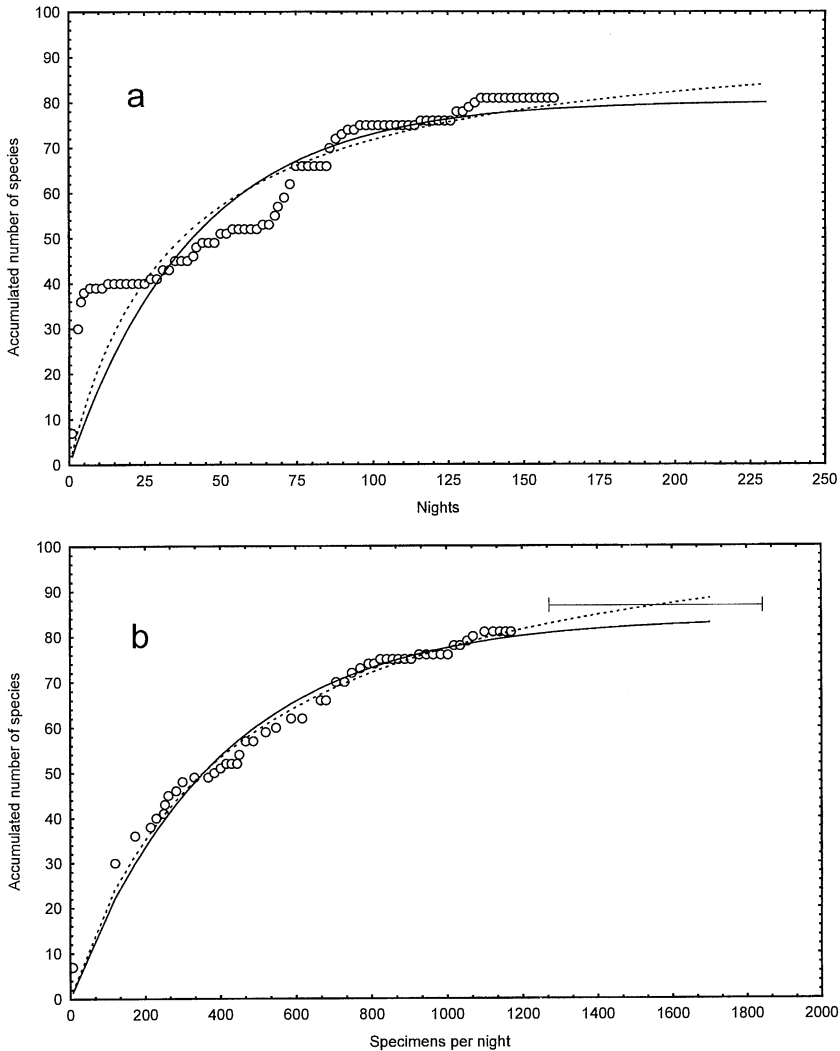


Fig. 1. Accumulation curves for the Sphingidae of Chajul, Lacandon Forest, Chiapas, México, where the unit of effort is: (a) nights, and (b) collected number of individuals per night. The circles represent the accumulated number of species, the solid line corresponds to the Bertalanffy's equation and the dashed line to Clench's equation. The bar in (b) represents the total number of species estimated using Chao's equation.

preparation, individuals collected were oven-dried and labelled. Identifications of moths were made based on the entomological collections of the Instituto Nacional de Biodiversidad from Costa Rica (InBio) and with the help of its curators.

Sphinx moth museum data

We assembled information from museum collections corresponding to two other Mexican localities. One is

the Estación de Biología Chamela, Jalisco (Chamela), located in a large area of tropical deciduous forest in western Mexico. The second site is El Vigía, Veracruz (Vigía) which used to lie at the ecotone of cloud forest and tropical rain forest (Ross, 1975). We used the entomological collections of the Instituto de Biología at the Universidad Nacional Autónoma de México, recording collecting data from all specimens from both localities. The species from each locality were ordered

according to the date of capture, and all collecting dates per species were included. According to Pescador (1994, pers. comm.), his sampling in Chamela was done with a uv light trap at a fixed site, very near the buildings of the station. Alfonso Pescador (pers. comm.) estimates the list to be almost complete, which is supported by further collecting realized by one of us (JLC) in the general area of Chamela. We have no information regarding collection methods at Vigía, nor any expected fauna size based on expert assessments.

Data analysis

We built accumulation curves for the sphinx moth faunas at the three localities and, using non-linear regressions (a quasi Newton algorithm, Statsoft, 1991), fitted the faunistic data to two accumulation functions. The two models we used were the von Bertalanffy's model,

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

and the Michaelis-Menten function, henceforth called the Clench's function because he was the first author applying it in this context (Clench, 1979):

$$S(t) = a \cdot t / (1 + b \cdot t) \quad (2)$$

where, for both curves, $S(t)$ is the expected size of the list, a is the slope at the beginning of the collection, b is a parameter related to the shape of the accumulation of new species during the collection, t is the collecting effort (e.g. some unit of time), and a/b is the asymptote (Soberón & Llorente, 1993).

We also used a non-parametric function derived by Chao (Colwell & Coddington, 1994), which is based on the lower frequency classes in the total sample. That equation is as follows:

$$S(t) = S_{obs}(t) + [c(t)^2/2d(t)] \quad (3)$$

where $S_{obs}(t)$ is the observed number of species in the sample at 'effort' t , $c(t)$ is the number of observed species represented by only a single individual in the sample, and $d(t)$ is the number of observed species represented by two individuals in the sample, both at accumulated 'effort' equalling t .

Finally, we explored the effects of basing extrapolations on different measures of effort. First, we carried out all calculations based on 'nights' and then as 'number of individuals collected per night.' This manipulation allowed us to explore the implications of different assumptions in the analysis. We used the

accumulation functions to extrapolate species numbers; our experience with the sphingid and other data sets indicated that extrapolation to the asymptote is unreliable so we constrained our extrapolations to twice the last effort value.

RESULTS

Sphinx moth accumulation curves

Fifty-six species of Sphingidae have been recorded in Chamela (Pescador, 1994), sixty-eight species in el Vigía, and eighty-one species in Chajul.

All the accumulation curves for the three localities showed asymptotic shapes (Figs 1–3). The Chamela data showed a small jump at the end of the curve that will be discussed below.

Figs 1a, 2a and 3a, based on 'nights' as the unit of effort, presented a more irregular shape of the species accumulation curves. This difference resulted from equating effort with time elapsed, which does not necessarily coincide with actual numbers of specimens collected. By employing the 'number of individuals collected per night' as a measure of effort, the shape of the accumulation curve became more regular (Figs 1b, 2b and 3b). We believe that actual numbers of specimens collected represent a better measure of effort, because under the alternative measure, a night with a single specimen collected increments a 'night's' effort by the same amount as a night with ten specimens.

Estimated richness values

Using von Bertalanffy's equation, estimated richness values were lower or equivalent than the last observed point of richness (Figs 1–3; Table 1). In contrast, Clench's equation yielded a more reasonable extrapolation (Figs 1–3) to the number of species, increasing estimated totals by a percentage consistent with what experienced workers would expect.

Chao's equation (3) also offered reasonable estimates of total species number in Chajul, but probably overestimated Chamela. We do not have an expert opinion about the likely number of species in El Vigía, and so could not assess its Chao estimates.

Changing the unit of effort

The proportion of variance explained remained high when the unit of effort was changed. However, the

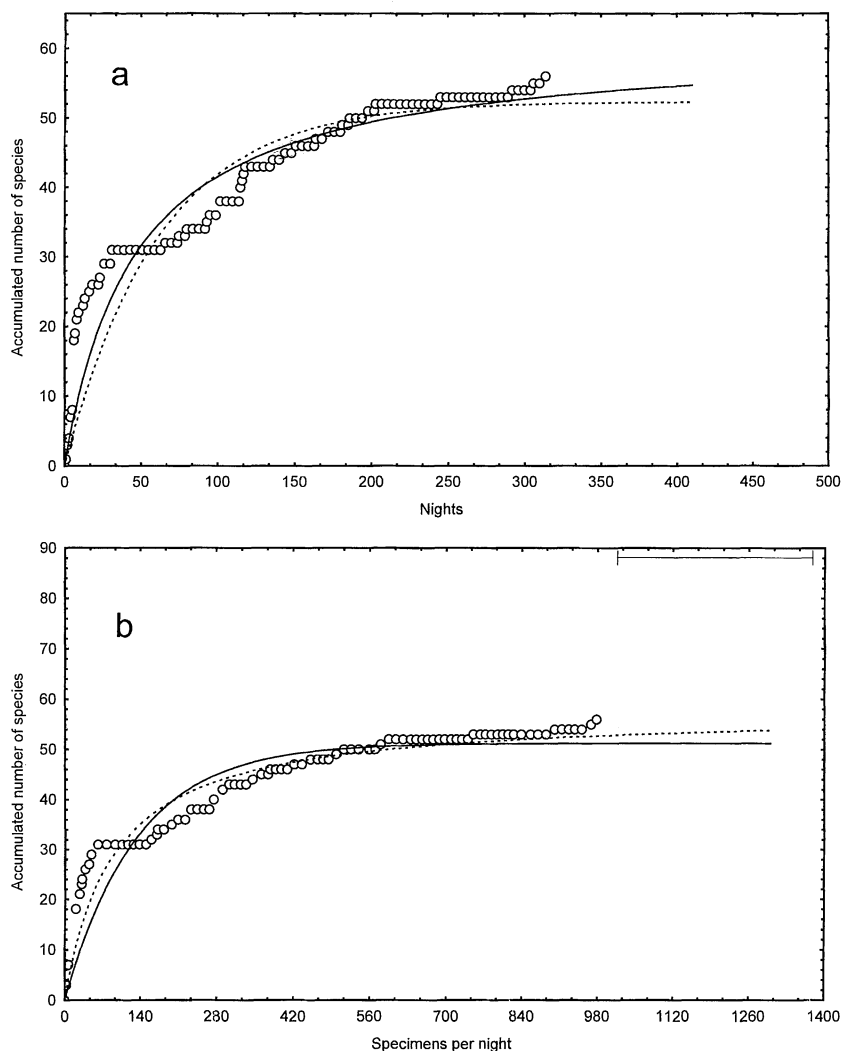


Fig. 2. Accumulation curves for the Sphingidae of Chamela, Jalisco, México, where the unit of effort is: (a) nights, and (b) collected number of individuals per night. The circles represent the accumulated number of species, the solid line corresponds to the Bertalanffy's equation and the dashed line to Clench's equation. The bar in (b) represents the total number of species estimated using Chao's equation.

asymptotes and the slopes at the origin were different (Table 1).

DISCUSSION

Methodological rigor is necessary for the assessment of both the results of biotic inventories (Sykes, Horrill & Mountford, 1983; Miller & Wiegert, 1989;

Prendergast *et al.*, 1993) and their process (Lamas *et al.*, 1991; Raguso & Llorente, 1991; Soberón & Llorente, 1993). This study presents a method for analysing the completeness of a list obtained either from museum specimens or field data, requiring specification of the unit of effort, the accumulation model to be fitted, and an extrapolation time.

Choosing a proper unit of time proves to be very important since it affects the values of both parameters.

Table 1. Statistics of the non-linear functions

Effort unit	Species estimator	Par.	EBLa 81(*)	EBCh 56(*) 56(+)	EVi 68(*)
Nights	Bertalanffy $S(t) = alb[1 - \exp(-bt)]$	t_r	160	317	170
		a	1.93	0.84	1.23
		b	0.024	0.016	0.016
	Clench $S(t) = at/(1 + bt)$	$S(2t_r)$	80	52	73
		a	2.785	1.303	1.419
		b	0.0288	0.0214	0.0141
Specimens per night	Bertalanffy	t_r	1179	981	300
		a	0.214	0.384	0.93
		b	0.0025	0.0075	0.014
	Clench $S(2t_r)$	$S(2t_r)$	84	51	68
		a	0.258	0.643	1.182
		b	0.0023	0.0112	0.0136
Frequency abundance data	Chao $S(t) = Sobs + (c^2/2d)$	c	10	14	13
		d	8	3	8
		$S(t)$	87	88	78
		$V St$	18.8	326.8	39.8

For the accumulation curves: Par. = regression parameter, a = slope at the beginning of the collection, b = accumulation parameter during the collection, t = collecting effort, t_r = last effort value, a/b = asymptote, Sobs = observed number of species in the sample, $S(2t_r)$ = predicted number of species at twice the last recorded effort.

(*) = number of species recorded for each locality, (+) = number of species estimated by experts as a likely total.

For the method of Chao: c = number of observed species represented by only a single individual in the sample, d = number of observed species represented by two individuals in the sample, $S(t)$ = expected size of the list, $V St$ = variance estimator that applies to $S(t)$. After Chao (1984), and Soberón & Llorente (1993).

We prefer to use individuals captured per night, since this measure better approximates some 'true' effort that ideally would include the effectiveness of the collection method employed, total time of use, proficiency of the user, etc. Besides, 'specimens per time unit' in general produces more regularly shaped curves than in the sphingid data, as well as in many other datasets we have analysed.

The two models applied are not equivalent in their properties. The von Bertalanffy function reaches the asymptote too fast, and consistently underestimates the expected fauna size in Chajul and Chamela. Clench's equation, on the other hand, provides a slower approach to the asymptote that allows more sensible extrapolation. Because sphingids are vagile and given the complex tropical habitats of the three sites, we suspected *a priori* that the Clench model would provide a better fit to the data (Soberón & Llorente, 1993), since the equation of Clench models a process in which

the probability of adding new species is non-linear and slower than in von Bertalanffy's. As suggested by Colwell and Coddington (1994), to decide among the many models of accumulation of new species in a collecting process experience will be of paramount importance. In this work we add experience to regard the Clench model as useful for medium sized faunas on moderately small tropical sites. We do not consider the von Bertalanffy as a good model of the accumulation of new species, at least for our group and sites

The extent of effort extrapolated is also of importance. The asymptote itself may yield unreasonably high values, as it is the case in Chajul. Depending on the parameters, the effort required to reach values very near the asymptote may be also unreasonably large. Our use of twice the last value of effort was arbitrary. With the data we used, this meant adding about a year of additional effort, which seemed

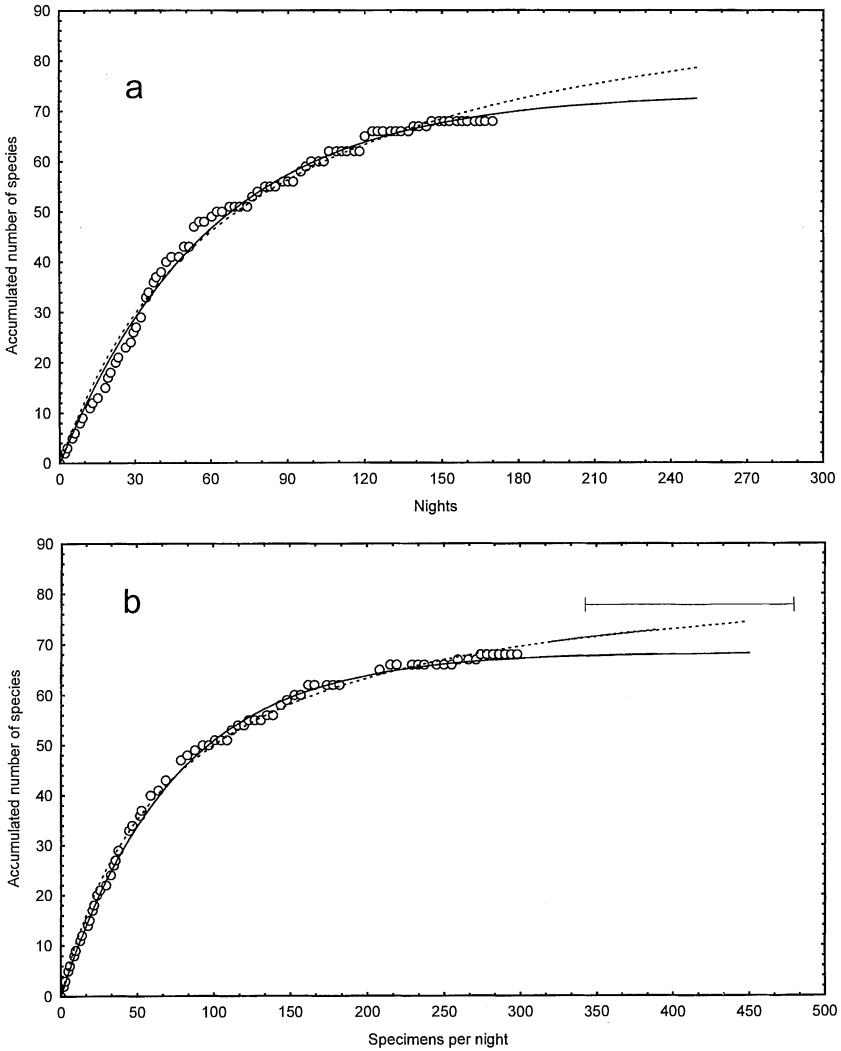


Fig. 3. Accumulation curves for the Sphingidae of El Vigía, Veracruz, México, where the unit of effort is: (a) nights, and (b) collected number of individuals per night. The circles represents the accumulated number of species, the solid line corresponds to the Bertalanffy's equation and the dashed line to Clench's equation. The bar in (b) represents the total number of species estimated using Chao's equation.

a reasonable amount for the scale of the areas and the fauna. In the case of the much more complex butterfly fauna of the Parque Nacional Manu, at eastern Peru, significant numbers of new species are being discovered after 5 years of work (R. Robbins, pers. comm.).

Finally, to check our estimates, we used an independent statistic, the method of Chao (Colwell & Coddington, 1994). This approach requires detailed data on frequencies of species and, therefore, we

restricted its application to the inventory data. The Chao prediction for Chajul is consistent with our results for Clench's equation, and also with *a priori* estimates by D. Janzen (pers. comm.), but does not agree with our assessment for Chamela.

Patterson (1994), argues that accumulation curves should be restricted to local scales, because at a continental scale they are fraught with problems due essentially to ecosystem heterogeneity and uneven

Table 2. Comparisons of the advantages and disadvantages of the use of museum and field Sphinx moths data using species accumulation functions

Feature	Museums data	Field data
Quality of information (systematization and arrangement data)	Low to high	High
Gathering time	Fast	Slow
Cost	Low	High
Heterogeneity among sampling effort units	Low to high	Low
Availability of relative abundance data of species	Low	High
Possibility in the conversion of the effort units	Low	High
Possibility of planning field trips	High	High
Possibility of estimating local richness values	Low to high	High

sampling. Sampling problems can also occur at the scales of hundreds of hectares, as in our work. Accumulation curves are not a property of the faunas or floras, but of the interaction between the observer methods, how comprehensive the sampling is in space and time, and of the ethology and ecology of the species in question. In our examples, spatially restricted sampling at Chamela may explain the little jump at the end of the curve that makes extrapolation difficult. We do not believe that this jump means that many more species will be found at Chamela, but rather that the single-site sampling was sensitive to vagaries of moth flight patterns.

In conclusion, Clench's equation provided a sensible extrapolation for both Chajul and Chamela. In the case of the Chajul, where good information about frequencies of individuals was available, Chao's method confirmed the results of the accumulation curve approach. Information about collecting effort should be obtained in all biological inventories to allow quantitative comparisons (Soberón & Llorente, 1993; Remsem, 1994) (see also Table 2). For museum data, good information on 'specimens per unit time' may be difficult to obtain, because many museums do not include all specimens in the curated collection, or the taxonomist may reject specimens for a variety of reasons. These difficulties can be avoided by careful record-keeping in field notes. Despite this, we find that the predictions of Clench's equation are reasonable for an extrapolation of twice the last recorded effort.

Given the increasing use of comparisons of biotic checklists for assessing richness patterns and their

significance, the methodology developed here may allow practical quantitative analyses of the substantial information contained in entomological collections. We are currently testing these methods for larger scales (on the order of thousands of square kilometres), using museum information.

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