



## Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae)

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**Abstract.** Thirteen tropical montane cloud forests (TMCFs) in Honduras and adjacent El Salvador were evaluated for species diversity and endemism in leaf litter inhabiting Curculionidae (weevils) and Staphylinidae in June and August of 1994. Totals of 26,891 specimens representing 293 species of Curculionidae, and 7349 specimens representing 224 species of Staphylinidae, were collected. Regional endemism was high with 173 species (58.7% of total) of Curculionidae and 126 species (56.3% of total) of Staphylinidae, restricted to single sites. Measures of diversity (number of observed species [Sobs]; number of endemic species) and estimates of biodiversity (Chao 2, first and second order Jackknife and Bootstrap richness estimators) are given for each site for Curculionidae and Staphylinidae. Priority-areas analyses based on Sobs ('Greedy'), Sobs, Chao 2, number of endemic species, site complementarity and higher taxonomic diversity (Curculionidae only) are presented. Weak or lack of correlation was noted between site area and site diversity for either Curculionidae or Staphylinidae. The optimum sequence for site conservation was determined based on Sobs ('Greedy'). Four sites are identified as the highest conservation priorities; Parque Nacional Montecristo, P.N. La Muralla, P.N. Santa Barbara and P.N. Comayagua. Identification as high priority sites supports their designation as Parques Nacionales rather than the less diverse Reservas Biologias or Reservas Vidas Silvestres. While closely approximating performance of Sobs ('Greedy'), no one of Sobs, number of endemics, Chao 2 or site complementarity give results equivalent to the optimum sequence based on Sobs ('Greedy') and the latter is concluded to be the best method for establishing conservation priorities in TMCF. Results of the analyses based on one of Curculionidae or Staphylinidae differ in the ordering of site priorities based on each of Sobs, Chao 2 or number of endemics at each site, with at best, weak positive correlations between results based on each taxon. Data from other taxa are necessary to determine if one of Curculionidae or Staphylinidae emerges as the better surrogate for general patterns of biodiversity in TMCF. Conservation strategies in Central America should emphasize the importance of TMCF particularly in view of high regional endemism. In formulating these strategies, consideration needs to be given to the preservation of many small regional preserves rather than fewer larger preserves. Data from inventories of other taxa should be included where available and all biological data should be integrated with social and cultural issues of regional importance.

**Key words:** beetles, biodiversity, cloud forest, conservation, Curculionidae, Honduras, Staphylinidae, tropical forest

## Introduction

Throughout the world tropical montane cloud forests (TMCFs; Figure 1) are one of the most threatened and vulnerable habitats. Their rate of loss exceeds that of lowland rain forests, an issue that has received much recent public attention (Hamilton et al. 1995). While cutting for firewood or charcoal production, or for conversion to agriculture are the chief causes of habitat loss, the threats are many and varied (Hamilton et al. 1995). Increasingly, TMCFs are being fragmented, reduced, and disturbed at an alarming rate and steps must be taken to further knowledge of their biodiversity and to develop and implement sound conservation plans.

Unfortunately, the importance of TMCFs is poorly understood and underrated. Despite their recognized significance as water catchment sites, their topography is usually complex, access to them is difficult, and little is known of their biodiversity. They are generally considered less diverse than lowland forests but this is likely a misconception and certainly, when their high levels of regional endemism are considered, their collective species diversity probably exceeds that of any other forest type.

Clear definition of TMCF is difficult but can be summarised as follows (Hamilton et al. 1995; Webster 1995). The TMCF is composed of forest ecosystems with distinctive floristic and structural form which includes reduced tree stature and increased stem density. Trunks and limbs of canopy trees have a gnarled form, crowns are dense and compact and leaves are small, thick and hard (Figure 2). There is a high proportion of floral biomass as epiphytes (including bryophytes, lichens and ferns)



*Figure 1.* TMCF at Reserva Biología Güisayote, 2170 m, east of Ocotepeque, Honduras. Undisturbed TMCF is limited to the dark ridgetop forest at center. Most of the remaining forest is second growth.



*Figure 2.* TMCF at El Pital, 2650 m, El Salvador-Honduras border.

and a reduction in woody climbers (Figures 3 and 4). Soils are wet and highly organic. Biodiversity is relatively high (given the generally small size of TMCFs) and endemism is often very high. TMCF typically occurs as a narrow elevational band where the weather is characterized by persistent, frequent or seasonal cloud cover at the vegetation level. TMCF can occur at various elevations. In inland situations in large mountain systems, TMCF is typically found between 2000–3500 m, in coastal situations the zone may occur at 1000 m, and in insular situations under exceptional conditions TMCF may occur as low as 300–500 m.

TMCF's are found throughout the world although no detailed compilation of information on their location or extent is available. In Latin America TMCFs occur from northeastern Mexico south into southern Brazil and northern Argentina. Central America has an extensively developed network of TMCFs, the more extensive of which generally hold some sort of protected status, whereas the many less extensive areas do not. In most instances, these small areas are remnants of historically more extensive TMCF, but for some more isolated areas, they represent the full local extent of this habitat type.



*Figure 3.* TMCF at Reserve Biología Yuscaran, 1700 m, near Yuscaran, Honduras. Note extensive bryophytes.

Given the extent of Neotropical biodiversity and the pressing need to make informed decisions about regional conservation and management priorities, it is unlikely that such issues can be addressed in a timely manner using information from more than but a few taxonomic groups. A strategic approach that uses key indicator taxa emphasizing effective sampling procedures and employing techniques of estimation and extrapolation (Colwell and Coddington 1994) is required. Successful and efficient conservation of biodiversity requires robust quantitative assessments of the extent of regional biodiversity, the nature of spatial variation in biodiversity or endemism, and the extent of regional phylogenetic diversity. Priority-areas analysis provides a means of ranking the candidate areas in a manner that optimizes the variety of biodiversity conserved (Margules et al. 1988; Williams et al. 1993).

In Honduras, surprising documentation and legislation exists concerning recognition and protection of TMCFs (Cruz 1993). Since 1990 the CONSEFORH project,



*Figure 4.* TMCF-pine forest transition, Montaña Celaque, 1300 m, near Gracias, Honduras. Note extensive epiphytes.

which is a bilateral project between Honduras and Great Britain, has carried out the following principal activities:

- to identify the location and extent of TMCF in Honduras,
- to identify and catalog the primary forest tree, shrub and herbaceous species and where possible gather data about the distribution and conservation status of the forest fauna,
- to identify the major land uses in TMCF, determine the primary causes of forest loss and prepare estimates of the rate and magnitude of damage.

While more than 30 TMCFs are listed as ‘protected’ in Honduras (Figure 5), the nature of this status varies from Parque Nacional, to Reserva Biología or Reserva de Vida Silvestre. According to Cruz (1993) these are distinguished as follows.

- ‘Parque Nacional’ – Large area containing natural features of national interest. Their function is to conserve representative examples of principal natural

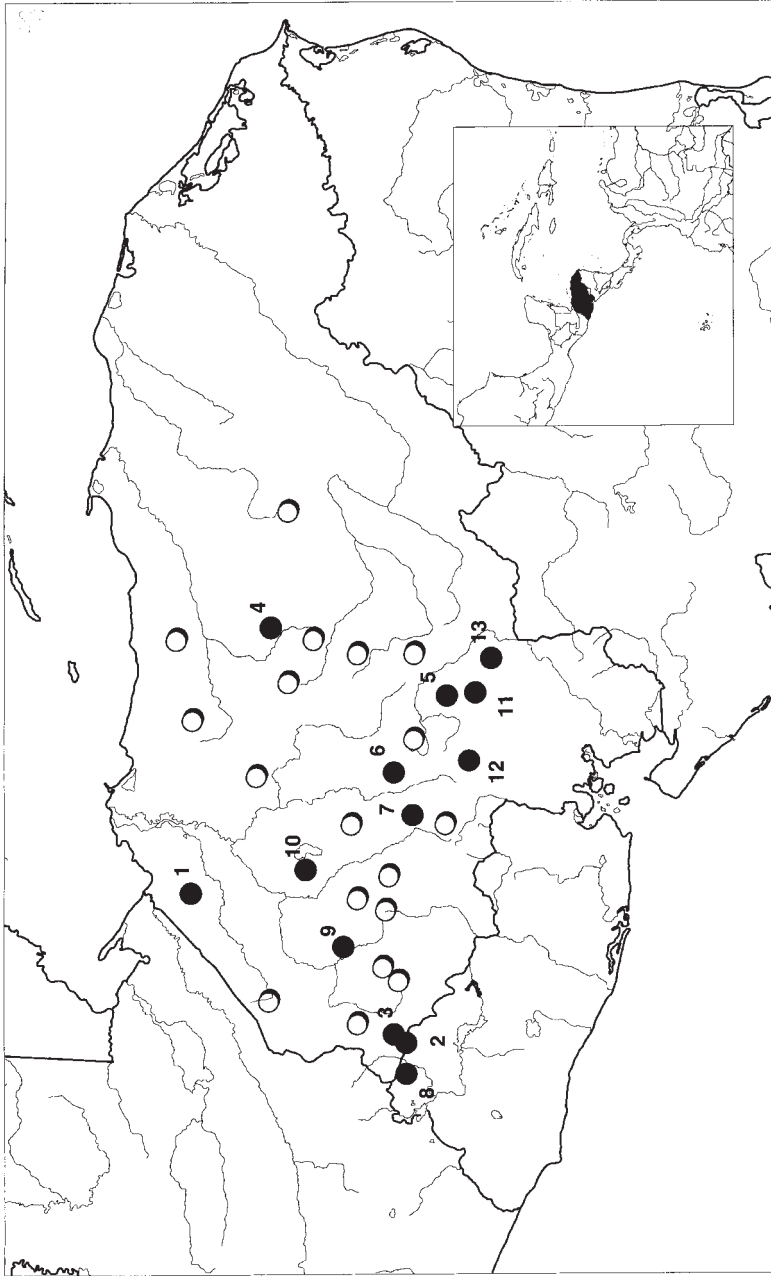


Figure 5. Map of Honduras and adjacent El Salvador showing location of 31 'protected' TMCs in Honduras. Sites sampled by us are noted by solid circles; other sites by open circles. Site numbers correspond to sites as listed in Table 1.

ecosystems and to serve as a location for scientific studies and environmental education.

- ‘Reserva Biología’ – Intact area which contains ecosystems, natural features or flora and fauna of scientific value. They function primarily to protect, conserve and maintain natural processes in an unaltered state for scientific study.
- ‘Refugio de Vida Silvestre’ – Area protecting species defined as ‘wildlife’. They function primarily to ensure the conservation of species, populations or habitat of wildlife and serve as locations for scientific study or recreational use.

In Honduras, TMCFs occur on mountains from 1800–2850 m in elevation and vary in extent from tens to hundreds of square kms. Despite this well-developed and documented network of reserves, many of which are relatively accessible, little is known of their biodiversity or of variation in biodiversity among them.

Taxa traditionally used as indicators or surrogates in studies of patterns in low-land biodiversity are generally not well-represented in TMCF or are not sufficiently diversified on a regional scale to adequately depict differences between local TMCFs. As is being increasingly recognized, various arthropod taxa are well-suited for use as surrogates for the development of land management and conservation strategies on regional scales (Kremen et al. 1993; Finnamore 1996). Leaf litter arthropod communities are exceptionally and surprisingly diverse and make excellent candidates for community characterization of TMCFs and as surrogates for general patterns in biodiversity among these forests. Among leaf litter inhabiting beetles, the families Curculionidae and Staphylinidae are the two most species rich and among the most numerically dominant taxa in the leaf litter community (Olson 1993; pers. obs.). Members of these families also possess a rich array of features facilitating species level identifications. For both weevils and staphylinids, the higher level taxonomic composition of the leaf litter community is relatively uniform throughout Central America from Mexico south into Honduras, and, with a few changes, also extending into Costa Rica and Panama. Most of the taxa found in leaf litter are found only in this habitat. Leaf litter inhabiting species are characterized by such features as lack of pigmentation, lack of wings, and lack of, or reduced eyes. As such, taxa not resident in the community (i.e., ‘tourists’) are generally easily recognized.

Consistent with the objectives of the CONSEFORH project, our investigation uses data about species diversity and distribution to characterize community structure for the leaf litter inhabiting Coleoptera in the families Curculionidae and Staphylinidae. Using these results, a priority-areas analysis of selected TMCFs in Honduras (including two sites from adjacent El Salvador) is conducted. Comparisons are made of the effectiveness of various measures and estimates of biodiversity in developing conservation priorities (selection of reserves) and of the applicability of leaf litter inhabiting curculionids and staphylinids as surrogates for general patterns of biodiversity in TMCF. The effectiveness of the present status of selected TMCF reserves in Honduras in achieving efficient conservation is also assessed. Following reserve selection, we also examine reserve design, specifically, the issue of whether to favor one large or

several small reserves (SLOSS debate; Simberloff 1986), especially in view of the extent of regional endemism projected in TMCF. We believe these Honduras results are applicable to TMCF in general in Central America and elsewhere.

## Methods

### *Field sampling and specimen processing*

A total of 13 TMCFs in Honduras and adjacent El Salvador were sampled for Coleoptera in the families Curculionidae and Staphylinidae (Table 1, Figure 5) inhabiting the leaf litter and other fallen plant material on the forest floor. Samples were taken by RSA in undisturbed TMCFs during the months of June and August, 1994. Selected TMCF sites were identified using Cruz (1993) on the basis of accessibility. Elevations at each site were determined by RSA using a Thommen hand held altimeter. Latitude and longitude measures were calculated from 1:50,000 topographic maps and verified with measures presented in Cruz (1993). Access to the sites was generally achieved with use of a 4WD vehicle until roads became impassable, followed by walking on footpaths until relatively undisturbed TMCF was reached. All samples from one site were taken within 100–200 m walking distance of each other. Sampling consisted of first vigorously sifting coarse organic debris (such as leaf litter [down to, but not including soil], twigs, smaller deadfall, litter underlying larger deadfall, patches of fungus, etc.) through 1 cm hardware cloth fixed in a ripstop nylon sifter (see Martin 1977; Figure 41 for design). Sampling continued in the immediate vicinity until approximately 4.5 l of sifted litter had accumulated in the bag of the sifter. This 4.5 l of litter constituted one sample and was emptied into a cotton bag (pillowcases are ideal) which was sealed and left by the trailside. Further samples were taken in the same manner in the general vicinity. Sampling continued until inclement weather or darkness. The bags were then collected and transported back to the laboratory where all arthropods were extracted. Care was taken to ensure samples were processed within 24 h and were not exposed to extreme heat, dryness or humidity. Weather was uniformly dry and sunny during all sampling; no unusually wet samples were processed. Number of replicate samples per site varied between 4 and 18 with an average of 13 samples per site. One sample consists of 4.5 l of processed leaf litter representing approximately 9 m<sup>2</sup> of undisturbed forest floor debris.

Beetles (along with other arthropods) were extracted from each sample by placing 1.5 l of litter poured from the sample bag in an evenly spread thin layer on cheesecloth placed on 1 cm hardware cloth in each of three circular metal berlese funnels (see Martin 1977; Figure 36 for design). A 60 W light bulb suspended 10 cm above the litter surface served as a heat source to dry out the litter. As the litter dries out, beetles burrow into the litter until they reach the cheesecloth, which they crawl through, falling into a jar of 90% alcohol placed under the apex of the funnel. Samples were each



Table 1. TCMCF sites in Honduras and El Salvador sampled in June and/or August of 1994. Measures of maximum elevation, area of buffer zone, area of nucleus and total area from Cruz (1993) except where noted with.\*

Site number	Category	Name	Latitude	Longitude	Maximum elevation (m)	Area of buffer zone (km <sup>2</sup> )	Area of nucleus (km <sup>2</sup> )	Total area (km <sup>2</sup> )	Elevation of sample (m)	Number of samples	Month
1	P.N.	Cusuco	15°31'	88°14'	2242	168.1	10.6	178.7	1650	6	August
2	R.B.	El Pital	14°23'30"	89°07'30"	2730	75.2*	18.7	93.9*	1960–2080	9	August
3	R.B.	Guísayote	14°27'15"	89°04'	2310	64.9	21.2	86.1	2050	4	June
4	P.N.	La Muralla	15°06'30"	86°41'30"	2064	136.6	13.4	150.0	2650	9	August
5	P.N.	La Tigra	14°10'45"	87°05'30"	2261	186.6*	142.6*	329.2*	2170	18	June
6	P.N.	Montaña de Comayagua	14°27'30"	87°32'30"	2407	118.8	66.0	184.8	1430–1450	15	June, August
7	R.B.	Montecillos	14°21'	87°47'30"	2459	76.7	54.5	131.2	1510–1550	5	August
8	P.N.	Montecristo	14°23'	89°18'	2419	84.0*	49.4*	133.4*	1950	5	June, August
9	R.V.S.	Puca	14°43'45"	88°33'	2234	38.4	9.6	48.0	2030–2100	18	June, August
10	P.N.	Santa Barbara	14°55'	88°06'30"	2744	67.6	53.7	121.3	2000	7	August
11	R.B.	Uyuca	14°01'30"	87°04'30"	1980	22.3*	5.8*	28.1*	1870	17	June, August
12	R.B.	Yerba Buena	14°03'30"	87°28'	2243	28.2	6.9	35.1	1840–1910	17	June
13	R.B.	Yuscaran	13°56'	86°52'	1980	20.9	1.5	22.4	1920	6	June
									1760	12	June

\* Unpublished data.

dried for 6 h. The results of the extractions from the three funnels were combined into one sample. All bags of litter were treated in a similar manner. In some instances a bag contained slightly more than 4.5 l of litter and this extra was discarded. Methods are essentially those of standard berlese funnel operation (Martin 1977) with the volume of litter processed and time of processing kept uniform.

Samples taken in June or August were considered within the same local season and were not retained as separate. On the other hand, samples taken from different elevations at P.N. La Tigra, P.N. La Muralla, P.N. Cusuco, R.B. El Pital were retained as separate in the analysis.

Specimens were extracted from samples and mounted, labelled and prepared for study. Sorting to morphospecies (read 'species' from here forward) for samples from each site was followed with comparisons between synoptic species sets from each site. Each distinct species then was assigned a unique combination of generic name (or other name) and identifying number. Specimens of Curculionidae were examined and sorted by RSA, and are deposited at the Canadian Museum of Nature, Ottawa; specimens of Staphylinidae were examined and sorted by JSA and are deposited at the Snow Entomological Museum, University of Kansas, Lawrence, KS. No attempt was made to assign formal specific names. Representative sets of the curculionid and staphylinid species are deposited in the arthropod collections of the Escuela Agricola Panamericana, El Zamorano, Honduras. The few specimens of both families collected in the samples but in taxa known or strongly suspected to be incidental in the litter habitat were not included in the analysis.

#### *Diversity measures and estimators*

Measures of diversity used are Sobs (number of observed species) and numbers of endemic species (species restricted to a single site although not necessarily having evolved *in situ*).

Estimators of diversity used were Chao 2, first order jackknife (Jack 1), second order jackknife (Jack 2) and bootstrap (SmitBel) (Colwell and Coddington 1994). All are non-parametric methods of estimating species diversity from samples. All estimates of diversity and variance measures were calculated using EstimateS 5.0 (Colwell 1997).

Chao 1 (Chao 1984), although not used here, is a simple estimator of the number of species represented based on the numbers of rare species in a sample,

$$\text{Chao 1} = \text{Sobs} + (a^2/2b)$$

where Sobs is the number of species observed in the sample,  $a$  is the number of species represented by single specimens, and  $b$  is the number of species represented by two specimens.

For Chao 2, the same approach can be applied to the distribution of species among samples as follows,

$$\text{Chao 2} = \text{Sobs} + (L^2/2M)$$

where Sobs is the number of species observed in all samples,  $L$  is the number of species represented in only one sample (but not found in any others), and  $M$  is the number of species represented in only two samples. The variance calculation for Chao 2 =  $M[(L/M)^4/4 + (L/M)^3 + (L/M)^2/2]$  provides a means of assessing the reliability of the estimation. The square root of the variance is equivalent to 1 standard deviation about the mean (1 SD).

It is generally accepted that Chao estimators perform well in instances where it is expected that relatively rare species predominate, such as in inventories of hyper-diverse arthropod groups (Colwell and Coddington 1994). As we think this is likely to be the case for litter inhabiting Curculionidae and Staphylinidae, our attention focuses on the applicability of Chao 2. Nevertheless, we present the results from other estimators as follows (see Colwell 1997):

$$\text{Jack 1} = \text{Sobs} + L(n - 1/n)$$

$$\text{Jack 2} = \text{Sobs} + [L(2n - 3)/n - M(n - 2)^2/n(n - 1)]$$

$$\text{Smitbel} = \text{Sobs} + \sum (1 - p_j)^n; \quad \text{Sobs, } j = 1$$

where  $n$  is the number of samples, and  $p$  is the proportion of quadrats containing each species  $j$ .

Simple linear regressions were employed to examine the relationships between measures and estimators for each of Curculionidae and Staphylinidae as well as to compare how each measure or estimator performed for Curculionidae versus Staphylinidae.

#### *Priority-areas analysis*

Ranking of sites for priority-areas analysis used measures of Sobs, number of endemic species, and the estimator Chao 2. For each of these measures or estimators, assignment of priorities is based on the individual measure of diversity for each site for each of Curculionidae and Staphylinidae. These values are taken from Tables 3–5.

In addition to the use of Sobs, number of endemics, and Chao 2, we also used the measure of Sobs but in a cumulative manner employing the ‘Greedy’ principle, in order to determine the optimum sequence and rate for which species could be conserved. In this method the first site selected is that with the highest Sobs; subsequent priorities are based upon maximizing the number of new species added by the addition of any one site. Thus a site with a high individual Sobs may be accorded a lower priority in this method than might be expected because many of its species are shared with site(s) already selected.

A measure of site complementarity (distinctness) which compared remaining sites with a list of already conserved sites was also used (see Colwell and Coddington 1994; but cf. Williams et al. 1993). The complementarity,  $C_{jk}$ , of any two lists is

$$C_{jk} = U_{jk}/S_{jk}$$

where

$$U_{jk} = S_j + S_k - 2V_{jk}$$

and

$$S_{jk} = S_j + S_k - V_{jk}$$

where  $S_j$  and  $S_k$  are the numbers of species represented on two lists  $j$  and  $k$  and  $V_{jk}$  is the number of species in common between the two lists.

Using this measure the first site selected is that with the highest Sobs. In contrast to priorities based on Sobs, Chao 2 and numbers of endemics, this method is cumulative. The second priority is the site with the maximum complementarity value to the first site. The third priority is the site with maximum complementarity to the two already conserved sites; the fourth priority is the site with maximum complementarity to the three already conserved sites, and so on.

Spearman Rank Correlation (SRC) procedures were used to compare priority-areas results based upon each of the various measures and estimators and to compare results for each of Curculionidae and Staphylinidae using the same measure or estimator. In all priority-areas analyses, if two sites had the same measure of diversity, measures of Chao 2 were used to break the tie and to establish priority.

#### *Taxonomic diversity*

Finally, a measure of taxonomic diversity based upon a hierarchical classification of the taxa present was used to assess representation of cladistic variation. Within Staphylinidae, assignment of many species to genus was not possible due to inadequate generic definitions (thus placement of species in most instances is to tribe only) and use of this measure is limited to Curculionidae. Percentage contribution (PC) to total diversity is calculated based upon the total number of taxa represented and the number of nodes between the terminal taxa and the base of the tree. Thus such taxa as *Dryophthorus*, with a single basal node, are assigned a PC of 6.74 as the only member of a higher taxon present in the study. On the other hand, taxa such as *Lymantini* new genus 1–4, each with three basal nodes, are each assigned lower values of 2.24 as one of many members of a higher taxon present. Vane-Wright et al. (1991) demonstrate in detail how this measure is calculated and discuss its applicability to selection of priorities for conservation. Modifications to this method have been discussed by Williams et al. (1993) but in view of the lack of more robust phylogenetic data are not employed here.

## Results

### *Curculionidae*

A total of 26,891 specimens of Curculionidae was collected. These specimens were sorted into 293 species representative of 33 genera (some of which are considered undescribed) (Table 2). Estimators of total number of genera present predict it unlikely that additional ones are expected (Chao 2  $\pm$  1 SD; 33.25  $\pm$  0.72). On the other hand, estimates of total expected species diversity of Curculionidae at the 13 sites predicted nearly 100 additional species remain to be found (Chao 2  $\pm$  1 SD; 389.18  $\pm$  21.83).

Measures (Sobs) and values for estimators of species diversity for each of the 13 TMC sites (and for different elevations at four sites) are given in Table 3. Parque Nacional Montecristo was the most diverse site with 62 species recorded and similarly, in terms of the estimators Chao 2 and Jack 1, was also the most diverse site. The second most diverse site was R.B. Güisayote with 49 recorded species. However, based on the estimator Chao 2, P.N. La Muralla (1430–1450 m) is expected to be more diverse (Chao 2  $\pm$  1 SD; 74.25  $\pm$  28.64) than R.B. Güisayote (Chao 2  $\pm$  1 SD; 61.25  $\pm$  8.59). Parque Nacional Santa Barbara with 48 species (Chao 2  $\pm$  1 SD; 53.78  $\pm$  5.04) was the third most diverse site. The least diverse site was R.B. Yerba Buena with only 19 species recorded (Chao 2  $\pm$  1 SD; 25.250  $\pm$  7.55).

Performance of Chao 2 with increasing numbers of samples is illustrated and compared with Sobs for each site in Figure 6. For all sites except P.N. Cusuco (1650 m), R.B. El Pital (2950 m), P.N. La Muralla (1430–1450 and 1510–1550 m), and R.B. Yuscaran, Chao 2 appears to be reaching a plateau and converging with Sobs. Greatest divergence between Chao 2 and Sobs is noted for P.N. La Muralla (1430–1450 m) with Chao 2 showing no indication of a plateau. In general, Chao 2 values average 26% higher than Sobs.

Distribution of endemics between sites is shown in Table 5. Endemism is high with 172 (138 + 34; 58.7% of total) species restricted to single sites. A further 65 species are known from only two sites. Numbers of endemics are greatest at P.N. Santa Barbara where 27 endemics were found. Another site with a large number of endemics is P.N. Montecristo with 23. Both P.N. La Muralla and P.N. Cusuco have 30 endemics if samples from both elevations at each site are considered together. Only R.B. Yerba Buena and R.B. Yuscaran have no endemic species.

Priority-areas sequences based on Sobs for both cumulative ('Greedy' principle) and non-cumulative processes are presented in Table 6 and Figure 7 (SRC;  $r_s = 0.846$ ,  $n = 17$ ,  $P < 0.001$ ). In both processes P.N. Montecristo is accorded the first priority but the selection of a second priority differs largely because of the high number of species shared between P.N. Montecristo and R.B. Güisayote, which ranks second in Sobs. If numbers of species added is to be maximized at each step, as it is when the 'Greedy' principle is employed, then P.N. Santa Barbara adds more species; 42 compared to 28 for Güisayote. In fact, the high number of species shared between

Table 2. Diversity measures and estimates for total numbers of species and genera of leaf litter inhabiting Curculionidae and Staphylinidae in selected TMCF sites in Honduras and El Salvador. See text for complete explanation.

Taxon	Level	<i>n</i>	Sobs	Ones <sup>a</sup>	Twos <sup>b</sup>	Chao 2	VChao 2	Jack 2	Jack 1	VJack 1	Jack 2	SmitBel
Curculionidae	Species	17	293	138	99 (34)	389.18	476.55	422.88	422.88	869.07	462.75	357.21
Staphylinidae	Species	17	224	119	37 (7)	415.36	241.79	336.00	336.00	419.43	410.39	272.01
Curculionidae	Genus	17	33	1	2	33.25	0.52	33.94	33.94	0.88	33.16	33.77
Staphylinidae	Genus	17	n/d <sup>c</sup>	—	—	—	—	—	—	—	—	—

<sup>a</sup> This number corresponds to the number of species endemic to a site.

<sup>b</sup> Number in parentheses corresponds to the number of species endemic to a site (exclusive of elevation).

<sup>c</sup> Assignment of many species to genus was not possible due to inadequate generic definitions (especially in Aleocharinae, Paederinae, Staphylininae [Xantholinini]).

Table 3. Diversity measures and estimates for leaf litter inhabiting Curculionidae in selected TMCFC sites in Honduras and El Salvador. See text for complete explanation.

Site number	Category	Name	s n	Sobs (Rank)	Ones (L) <sup>a</sup>	Twos (M) <sup>b</sup>	Chao 2 Genobs	Jack 1 VChao 2 (Rank)	Jack 1 VJack 1 (Rank)	Jack 2	SmitBel	Ranking <sup>c</sup>
1	P.N.	Cusuco (1650 m)	6	24 (13)	8	3	13	34.66 (12)	6.10	34.40	27.01	37 (12)
		Cusuco (1960–2080 m)	9	35 (7)	10	7	19	42.14 (7)	9.67	46.90	34.31	21 (6)
2	R.B.	El Pital (2050 m)	4	22 (14)	8	4	11	30.00 (14)	7.45	30.66	24.79	40 (13)
		El Pital (2650 m)	9	45 (4)	12	8	22	54.00 (5)	5.29	59.55	50.07	13 (4)
3	R.B.	Güisayote	18	49 (2)	14	8	22	61.25 (3)	19.89	67.97	55.20	7 (2)
4	P.N.	La Muralla (1430–1450 m)	15	44 (5)	11	2	19	74.25 (2)	8.29	62.19	49.27	12 (3)
		La Muralla (1510–1550 m)	5	28 (9)	8	3	13	38.66 (9)	2.56	37.85	30.90	27 (8)
5	P.N.	La Tigra (1950 m)	5	32 (8)	7	5	16	36.90 (10)	8.94	39.55	34.74	26 (7)
		La Tigra (2030–2100 m)	18	25 (12)	2	1	14	27.00 (15)	1.66	27.83	26.95	42 (14)
6	P.N.	Montaña de Comayagua	7	42 (6)	11	5	19	54.10 (4)	3.16	56.31	46.32	16 (5)
7	R.B.	Montecillos	6	27 (10)	8	4	14	35.00 (11)	2.75	36.86	30.09	31 (9)
8	P.N.	Montecristo	10	62 (1)	16	10	21	74.80 (1)	14.74	82.08	68.77	3 (1)
9	R.V.S.	Puca	5	26 (11)	8	6	12	31.33 (13)	4.12	34.50	29.14	35 (10)
10	P.N.	Santa Barbara	17	48 (3)	9	7	18	53.78 (6)	9.61	58.62	52.15	12 (3)
11	R.B.	Uyuca	17	21 (15)	5	2	16	27.25 (16)	3.31	28.46	23.04	47 (15)
12	R.B.	Yerba Buena	6	19 (16)	5	2	13	25.25 (17)	2.34	25.43	20.85	50 (16)
13	R.B.	Yúscaran	12	21 (15)	9	2	12	41.25 (8)	9.36	35.23	24.46	36 (11)

<sup>a</sup> Number of species represented in only one sample; total number of species represented by only one specimen in all samples at all sites is 38.

<sup>b</sup> Number of species represented in two samples; total number of species represented by only two specimens in all samples at all sites is 30.

<sup>c</sup> Number given is the sum of individual ranks for Sobs, Chao 2 and Jack 1. Cumulative rank is in parentheses.

Table 4. Diversity measures and estimates for leaf litter inhabiting Staphylinidae in selected TMCF sites in Honduras and El Salvador. See text for complete explanation.

Site number	Category	Name	<i>n</i>	Sobs (Rank)	Ones (L) <sup>a</sup>	Twos (M) <sup>b</sup>	Chao 2 (Rank)	VChao 2 (Rank)	Jack 1 (Rank)	VJack 1	Jack 2	SmitBel	Ranking <sup>c</sup>
1	P.N.	Cusuco (1650 m)	6	18 (11)	11	3	38.16 (13)	303.45	27.16 (15)	7.34	32.90	21.98	39 (10)
		Cusuco (1960–2080 m)	9	15 (12)	6	2	24.00 (16)	103.42	20.33 (16)	1.76	23.63	17.34	44 (11)
2	R.B.	El Pital (2050 m)	4	28 (7)	11	6	38.08 (14)	64.00	36.25 (10)	6.55	39.75	31.88	31 (8)
		El Pital (2650 m)	9	15 (12)	4	2	19.00 (17)	27.98	18.55 (17)	3.72	20.30	16.65	46 (12)
3	R.B.	Giüsayote	18	33 (6)	20	2	133.00 (1)	7099.74	51.88 (5)	26.21	67.99	40.53	12 (3)
4	P.N.	La Muralla (1430–1450 m)	15	61 (1)	23	11	85.04 (2)	177.15	82.46 (1)	27.66	93.54	70.81	4 (1)
		La Muralla (1510–1550 m)	5	23 (10)	11	5	35.10 (15)	94.47	31.80 (14)	7.02	36.15	27.04	39 (10)
5	P.N.	La Tigra (1950 m)	5	23 (10)	13	5	39.90 (12)	161.79	33.40 (12)	4.12	38.95	27.66	34 (9)
		La Tigra (2030–2100 m)	18	27 (8)	12	2	63.00 (6)	1115.56	38.33 (8)	9.42	47.32	31.79	22 (6)
6	P.N.	Montaña de Comayagua	7	36 (4)	19	5	72.10 (4)	565.96	52.28 (4)	13.17	62.88	43.06	12 (3)
7	R.B.	Montecillos	6	23 (10)	11	1	83.50 (3)	5050.94	32.16 (13)	9.00	38.96	26.81	26 (7)
8	P.N.	Montecristo	10	46 (2)	15	10	57.25 (7)	57.60	59.50 (2)	16.64	64.38	52.45	11 (2)
9	R.V.S.	Puca	5	25 (9)	13	5	41.90 (11)	161.79	35.40 (11)	24.90	40.95	29.67	31 (8)
10	P.N.	Santa Barbara	17	43 (3)	13	10	51.45 (9)	37.45	55.23 (3)	17.89	58.43	49.06	15 (4)
11	R.B.	Uyuca	17	35 (5)	16	6	56.33 (8)	210.83	50.05 (6)	17.80	59.21	41.50	19 (5)
12	R.B.	Yerba Buena	6	27 (8)	13	2	69.25 (5)	1483.79	37.83 (9)	17.30	45.43	31.58	22 (6)
13	R.B.	Yuscaran	12	35 (5)	12	6	47.00 (10)	83.90	46.00 (7)	9.12	51.45	40.02	22 (6)

<sup>a</sup> Number of species represented in only one sample; total number of species represented by only one specimen in all samples at all sites is 53.

<sup>b</sup> Number of species represented in two samples; total number of species represented by only two specimens in all samples at all sites is 24.

<sup>c</sup> Number given is the sum of individual ranks for Sobs, Chao 2 and Jack 1. Cumulative rank is in parentheses.



Güisayote and Montecristo relegates the former to a sixth level priority. The third level priority using the 'Greedy' principle is P.N. La Muralla (1430–1450 m) which adds an additional 37 species. It is significant to note that 141 species, or almost 50% of the total species diversity, are accounted for at these three sites.

A priority-areas sequence based on Chao 2 also ranks P.N. Montecristo as the first priority area and P.N. La Muralla (1430–1450 m) at a second level priority, in general agreement with the 'Greedy' principle which placed the latter as a third level priority. The major difference between the rankings based on Chao 2 is for P.N. Santa Barbara, which although a second level priority using the 'Greedy' principle, is ranked as a sixth level priority using Chao 2 (SRC;  $r_s = 0.748$ ,  $n = 17$ ,  $P = 0.001$ ).

A priority-areas sequence based on number of endemics is in close agreement with the 'Greedy' principle (SRC;  $r_s = 0.892$ ,  $n = 17$ ,  $P < 0.001$ ), but ranks P.N. Montecristo as a second level priority behind P.N. Santa Barbara which has the greatest number of endemics at 27. Parque Nacional Comayagua and P.N. Cusuco (1960–2080 m) are ranked as third level priorities ahead of P.N. La Muralla (1430–1450 m) which is a fifth level priority using this method. If numbers of endemics at each site exclusive of elevation are considered, P.N. La Muralla (1430–1450 m) would be accorded the first priority with P.N. Santa Barbara second and P.N. Cusuco (1960–2080 m) third. It is of note that both P.N. La Muralla and P.N. Cusuco were sampled at two elevations thus adding additional endemics and moving them to a higher priority.

A final priority-areas sequence based on complementarity measures at the species level ranks P.N. Montecristo first (with the highest Sobs as the method dictates) but beyond that is in general disagreement with priorities based on other criteria, most notably Sobs ('Greedy') (SRC;  $r_s = -0.279$ ,  $n = 17$ ,  $P > 0.50$ ). Using this method such diverse sites as P.N. Santa Barbara and P.N. La Muralla (1430–1450 m) are ranked as ninth level and sixteenth level priorities respectively.

As a simple measure of taxonomic diversity, numbers of genera (Genobs) found at each site are given in Table 3. Sites with the greatest number of recorded genera are R.B. Güisayote and R.B. El Pital (2650 m elevation) with 22 recorded genera, and P.N. Montecristo with 21 recorded genera. However, a more detailed measure of taxonomic diversity (Vane-Wright et al. 1991) which considers phylogenetic relationships among the higher taxa represented (Figure 8) shows P.N. Montecristo to be most diverse with 69.1% of the total taxonomic diversity represented. This is marginally greater than either of R.B. El Pital (2650 m) at 68.1% and R.B. Güisayote at 65.8%. A priority areas sequence maximizing rate at which taxonomic diversity is represented ranks P.N. Montecristo first (69.1% of total diversity), followed by R.B. Güisayote (additional 21.6% of diversity represented), P.N. La Tigra (1950 m) (additional 8.0% of diversity), and finally one of P.N. Comayagua, P.N. Santa Barbara or P.N. Cusuco (either elevation). Only four sites are required to represent the total higher taxonomic diversity as measured using this method.

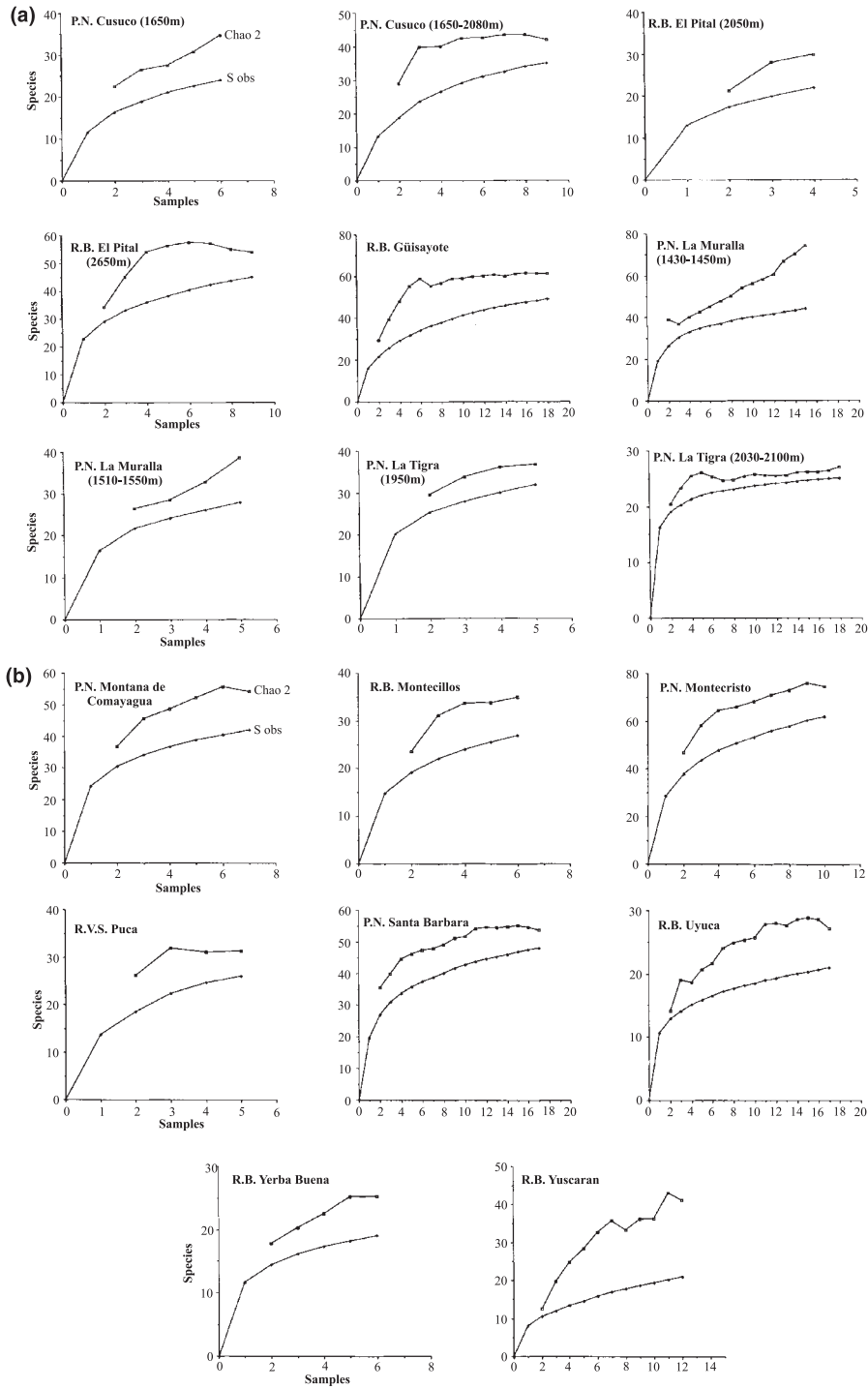


Table 5. Numbers of endemics for leaf litter inhabiting Curculionidae and Staphylinidae in selected TMCF sites in Honduras and El Salvador. See text for complete explanation.

Site number	Category	Name	<i>n</i>	Curc*	Ranking	Staph*	Ranking
1	P.N.	Cusuco (1650 m)	6	5 (11)	8	2 (0)	10
		Cusuco (1960–2080 m)	9	14 (11)	3	6 (0)	6
2	R.B.	El Pital (2050 m)	4	5 (0)	8	3 (0)	9
		El Pital (2650 m)	9	8 (0)	6	7 (0)	5
3	R.B.	Güisayote	18	7	7	10	3
4	P.N.	La Muralla (1430–1450 m)	15	9 (20)	5	24 (6)	1
		La Muralla (1510–1550 m)	5	1 (20)	11	1 (6)	11
5	P.N.	La Tigra (1950 m)	5	2 (3)	10	2 (1)	10
		La Tigra (2030–2100 m)	18	2 (3)	10	5 (1)	7
6	P.N.	Montaña de Comayagua	7	14	3	7	5
7	R.B.	Montecillos	6	8	6	4	8
8	P.N.	Montecristo	10	23	2	10	3
9	R.V.S.	Puca	5	11	4	5	7
10	P.N.	Santa Barbara	17	27	1	11	2
11	R.B.	Uyuca	17	3	9	8	4
12	R.B.	Yerba Buena	6	0	12	6	6
13	R.B.	Yuscaran	12	0	12	8	4

Total numbers of endemics. Curculionidae, 139 (34); Staphylinidae, 119 (7).

\* Numbers in parentheses are the number of endemics at that site exclusive of elevation.

### Staphylinidae

A total of 7349 specimens of Staphylinidae was collected. These specimens were sorted into 224 species (Table 2). Generic assignment was not possible for many Staphylinidae (especially in Aleocharinae, Paederinae, Staphylininae [Xantholinini]) and no estimate of total number of genera represented is given here. Estimates of total expected diversity of Staphylinidae at the 13 sites predicted almost 200 additional species remain to be found (Chao  $2 \pm 1$  SD;  $415.36 \pm 49.11$ ).

Measures (Sobs) and values for estimators of species numbers for each of the 13 TMCF sites (and for different elevations at four sites) are given in Table 4. Parque Nacional La Muralla (1430–1450 m) was the most diverse site with 61 species recorded (Chao  $2 \pm 1$  SD;  $85.04 \pm 13.31$ ). Other diverse sites were P.N. Montecristo with 46 recorded species (Chao  $2 \pm 1$  SD;  $57.25 \pm 7.59$ ) and P.N. Santa Barbara with 43 species (Chao  $2 \pm 1$  SD;  $51.45 \pm 6.12$ ). Both R.B. Güisayote and R.B. Montecillos sites (and to a lesser extent P.N. Comayagua) had surprisingly high values for Chao 2 (and associated variance measures) brought about by large numbers of ‘singletons’ (species represented by only one individual). For example, Güisayote

←

Figure 6 (a, b). Measure of species diversity (Sobs; lower curve) and performance of diversity estimator Chao 2 (upper curve) for all sites in relation to number of samples taken for Curculionidae. Data from EstimateS using 50 replications.

Table 6. Priority sequence for selection of TMCs in Honduras and El Salvador based on various criteria for Curculionidae. See text for complete explanation. Ties broken by ranking for Chao 2.

Priority	Sobs (Greedy) Cumulative	Sobs Non-cumulative	Chao 2 Non-cumulative	Endemics Non-cumulative	Complementarity Cumulative	Taxonomic diversity
1	Montecristo (62; 21.1%)	Montecristo (62; 21.1%)	Montecristo (62; 21.1%)	Santa Barbara (48; 16.4%)	Montecristo (62; 21.1%)	Montecristo (69.1%)
2	Santa Barbara (42; 35.5%)	Güisayote (28; 30.7%)	La Muralla (1430–1450 m) (41; 35.2%)	Montecristo (56; 35.5%)	Uyuca; 1,000 (21; 28.3%)	Güisayote (90.7%)
3	La Muralla (1430–1450 m) (37; 48.1%)	Santa Barbara (40; 44.4%)	Güisayote (25; 43.7%)	Comayagua (34; 47.1%)	Cusuco (1650 m); 0.971 (21; 35.5%)	La Tigra (1950 m) (98.7%)
4	Comayagua (33; 59.4%)	El Pital (2650 m) (9; 47.4%)	Comayagua (37; 56.3%)	Cusuco (1960–2080 m) (27; 56.3%)	La Muralla (1510–1550 m); 0.957 (23; 43.3%)	Choice of: Cusuco (1960–2080 m), Cusuco (1650 m), Comayagua, Santa Barbara (100%)
5	Cusuco (1960–2080 m) (27; 68.6%)	La Muralla (1430–1450 m) (35; 59.4%)	El Pital (2650 m) (9; 59.4%)	Puca (17; 62.1%)	Montecillos; 0.952 (20; 50.1%)	
6	Güisayote (24; 76.8%)	Comayagua (32; 70.3%)	Santa Barbara (32; 70.3%)	La Muralla (1430–1450 m) (33; 73.4%)	Puca; 0.945 (18; 56.3%)	
7	La Tigra (1950 m) (19; 83.3%)	Cusuco (1960–2080 m) (27; 79.5%)	Cusuco (1960–2080 m) (27; 79.5%)	El Pital (2650 m) (20; 80.2%)	Yuscaran; 0.917 (8; 59.0%)	
8	Puca (14; 88.1%)	La Tigra (1950 m) (19; 86.0%)	Yuscaran (10; 82.9%)	Montecillos (14; 85.0%)	El Pital (2050 m); 0.914 (9; 62.1%)	

9	Montecillos (9; 91.1%)	La Muralla (1510–1550 m) (1; 86.3%)	La Muralla (1510–1550 m) (1; 83.3%)	Güisayote (12; 89.1%)	Santa Barbara; 0.912 (33; 73.4%)
10	El Pital (2650 m) (8; 93.9%)	Montecillos (9; 89.4%)	La Tigra (1950 m) (11; 87.0%)	El Pital (2050 m) (5; 90.8%)	Yerba Buena; 0.923 (6; 75.4%)
11	Cusuco (1650 m) (5; 95.6%)	Puca (14; 94.2%)	Montecillos (9; 90.1%)	Cusuco (1650 m) (5; 92.5%)	Cusuco (1960–2080 m); 0.905 (14; 80.2%)
12	El Pital (2050 m) (5; 97.3%)	La Tigra (2030–2100 m) (5; 95.6%)	Cusuco (1650 m) (6; 92.2%)	Yyuca (10; 95.9)	La Tigra (2030–2100 m); 0.897 (5; 81.9%)
13	La Tigra (2030–2100 m) (4; 98.6%)	Cusuco (1650 m) (5; 97.3%)	Puca (12; 96.2%)	La Tigra (1950 m) (8; 98.6%)	El Pital (2650 m); 0.893 (19; 88.4%)
14	Yyuca (3; 99.7%)	El Pital (2050 m) (5; 99.0%)	El Pital (2050 m) (5; 98.0%)	La Tigra (2030–2100 m) (3; 99.7%)	Comayagua; 0.891 (14; 93.1%)
15	La Muralla (1510–1550 m) (1; 100%)	Yuscaran (0; 99.0%)	La Tigra (2030–2100 m) (3; 99.0%)	La Muralla (1510–1550 m) (1; 100%)	La Tigra (1950 m); 0.884 (4; 94.5%)
16	Yuscaran (0; 100%)	Yyuca (3; 100%)	Yyuca (3; 100.0%)	Yuscaran (0; 100%)	La Muralla (1430–1450 m); 0.868 (9; 97.6%)
17	Yerba Buena (0; 100%)	Yerba Buena (0; 100%)	Yerba Buena (0; 100%)	Yerba Buena (0; 100%)	Güisayote; 0.841 (7; 100%)

Numbers in parentheses are the number of species added to the cumulative species total by the addition of that site and the percentage accumulation of the total species known from all sites selected to this point.

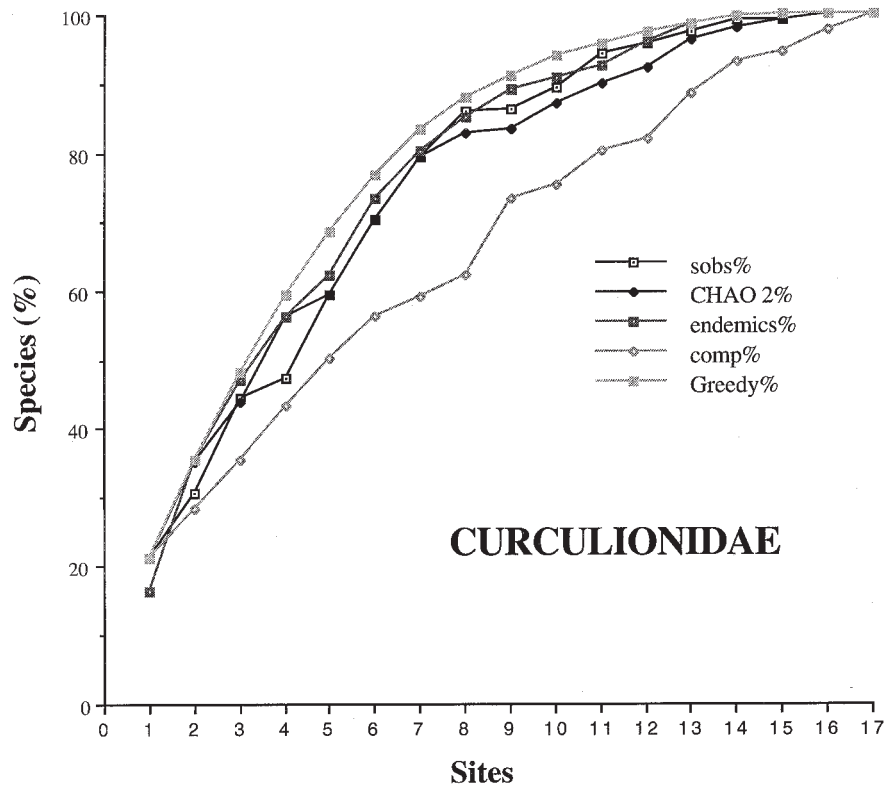
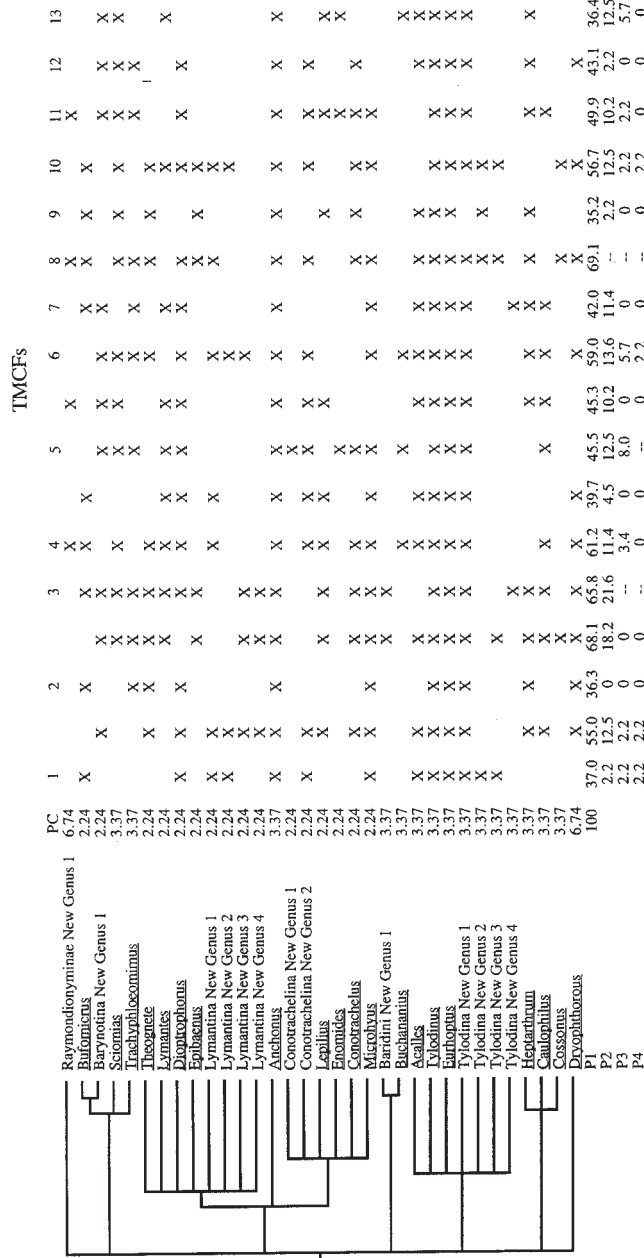


Figure 7. Priority-areas sequences for Curculionidae based on Sobs ('Greedy' and non-cumulative), Chao 2, number of endemics and complementarity.

which ranks fifth in terms of Sobs, ranks first in terms of Chao 2 ( $133.00 \pm 84.26$ ). The least diverse sites were P.N. Cusuco (1960–2080 m) and R.B. El Pital (2650 m) each with only 15 species recorded (Chao 2  $\pm 1$  SD;  $24.00 \pm 10.17$ ,  $19.000 \pm 5.29$  respectively).

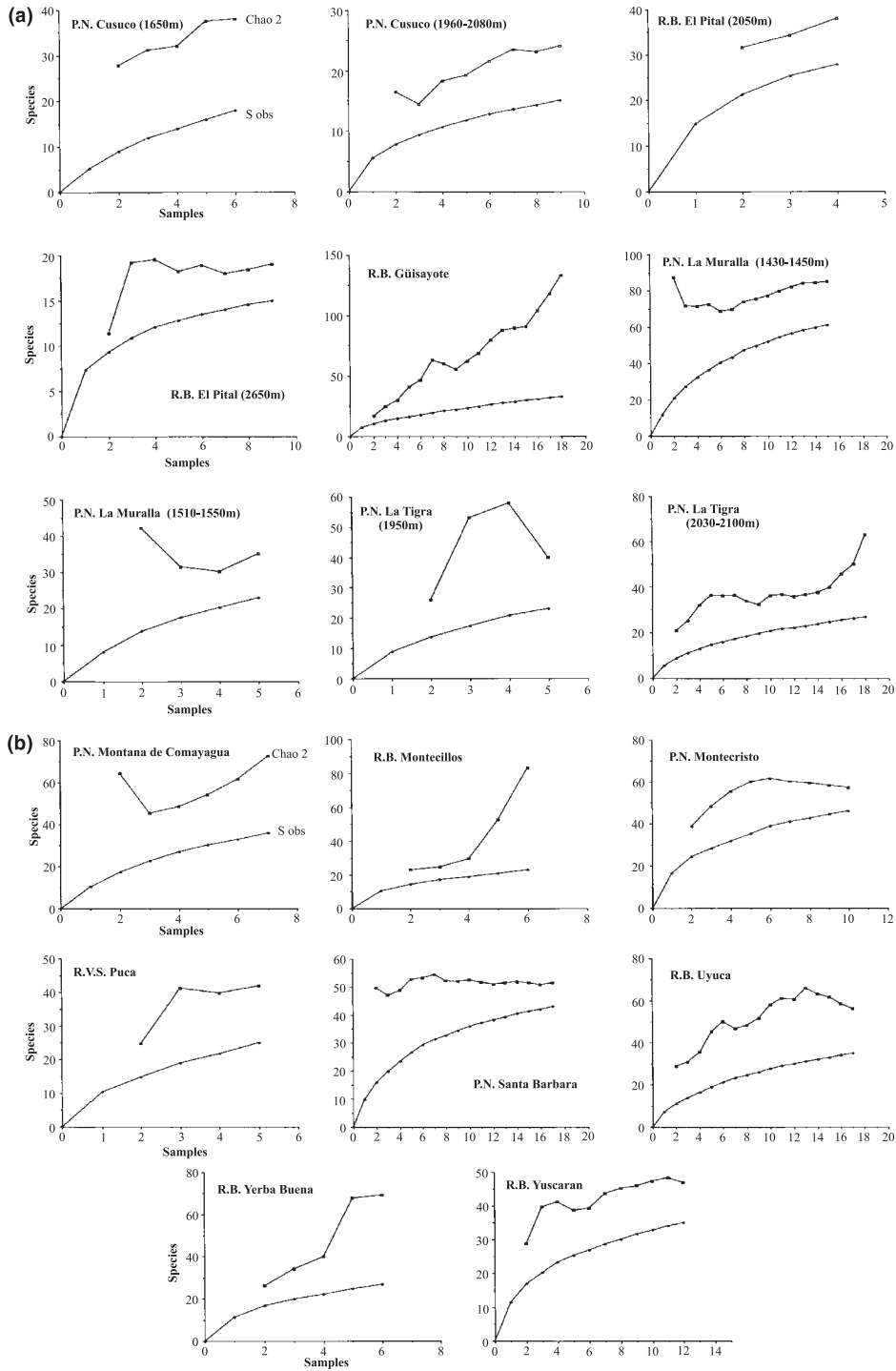
Performance of Chao 2 with increasing numbers of samples is illustrated and compared with Sobs for each site in Figure 9. For Staphylinidae, Chao 2 appears to be reaching a plateau and converging with Sobs only at R.B. El Pital (2650 m), P.N. La Muralla (1430–1450 m), P.N. Montecristo, R.V.S. Puca, P.N. Santa Barbara, R.B. Uyuca, and R.B. Yuscaran. Greatest divergence between Chao 2 and Sobs is noted for R.B. Güisayote with Chao 2 showing no indication of a plateau. In general, Chao 2 values average 92% higher than Sobs.

Distribution of endemics between sites is shown in Table 5. Site endemism is high with 126 ( $119 + 7$ ; 56.3% of total) species restricted to a single site. A further 30 species are known from only two sites. Numbers of endemics are greatest at P.N. La Muralla where 31 endemics were found when both elevations are pooled. Other sites have substantially smaller numbers of endemics. Highest numbers of endemics



PC - percentage contribution by each genus to total diversity; P1, percentage diversity score for each region at step 1 indicating P.N. Montecristo as top-priority site; P2, percentage diversity score for each region at step 2 indicating R.B. Guisayote as second priority site; P3, percentage diversity score for each region at step 3 indicating P.N. La Tigra (1950m) as third priority site; P4, percentage diversity score for each region at step 4 indicating any of four sites of equal priority.

Figure 8. Priority-areas analysis based on topology and taxonomic weights derived from unresolved classification of genera of Curculionidae (Appendix 1) represented in selected TMCFs in Honduras and El Salvador (see Table 1 for site names).





among these other sites are found at P.N. Santa Barbara with 11 and P.N. Montecristo with 10. All sites possess endemic species of staphylinids.

Priority-areas sequences based on Sobs for both cumulative ('Greedy' principle) and non-cumulative processes are presented in Table 7 and Figure 10 (SRC;  $r_s = 0.779$ ,  $n = 17$ ,  $P < 0.001$ ). In both processes P.N. La Muralla (1430–1450 m) is accorded the first priority and P.N. Montecristo the second priority. When the 'Greedy' principle is employed, R.B. Yuscaran ranks as the third level priority (sixth level in terms of Sobs) and P.N. Santa Barbara as the fourth level priority (third level in terms of Sobs). It is significant to note that 122 species, or slightly more than 50% of the total species diversity, are accounted for at these three sites.

A priority-areas sequence based on Chao 2 ranks R.B. Güisayote as the first priority area and P.N. La Muralla (1430–1450 m) at a second level priority. For P.N. La Muralla (1430–1450 m) this is in general agreement with results based on the 'Greedy' principle which placed it as the first level priority. In contrast, R.B. Güisayote is accorded a substantially lower fifth level priority using the 'Greedy' principle. The major differences between the rankings based on Chao 2 is for P.N. Montecristo, which although a second level priority using both the 'Greedy' principle and Sobs is ranked as a seventh level priority using Chao 2. Also, R.B. Yuscaran, a third level priority using the 'Greedy' principle is a tenth level priority using Chao 2 (SRC;  $r_s = 0.583$ ,  $n = 17$ ,  $P < 0.002$ ,  $> 0.001$ ).

A priority-areas sequence based on number of endemics is in close agreement with the 'Greedy' principle (SRC;  $r_s = 0.912$ ,  $n = 17$ ,  $P < 0.001$ ), but ranks P.N. La Muralla (1430–1450 m), with 24 endemics, as the first level priority ahead of P.N. Santa Barbara which has only 11 endemics. Parque Nacional Montecristo is ranked as a third level priority along with R.B. Güisayote, each of which have 10 endemic species. If numbers of endemics at each site exclusive of elevation are considered, unlike for Curculionidae, the order of priorities would not change.

A final priority-areas sequence based on complementarity measures at the species level ranks P.N. La Muralla (1430–1450 m) first (with the highest Sobs as the method dictates) but, as for Curculionidae, beyond that is in general disagreement with priorities based on other criteria, most notably Sobs ('Greedy') (SRC;  $r_s = -0.059$ ,  $n = 17$ ,  $P > 0.50$ ). Using this method P.N. Montecristo is ranked as the tenth level priority, R.B. Yuscaran as fifteenth level priority and P.N. Santa Barbara as the seventeenth, or lowest level priority.

No priority-areas sequence was based on a measure of taxonomic diversity for Staphylinidae.

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Figure 9 (a, b). Measure of species diversity (Sobs; lower curve) and performance of diversity estimator Chao 2 (upper curve) for all sites in relation to number of samples taken for Staphylinidae. Data from EstimateS using 50 replications.

Table 7. Priority sequence for selection of TMCs in Honduras and El Salvador based on various criteria for Staphylinidae. See text for complete explanation. Ties broken by ranking for Chao 2.

Priority	Sobs (Greedy) Cumulative	Sobs Non-cumulative	Chao 2 Non-cumulative	Endemics Non-cumulative	Complementarity Cumulative
1	La Muralla (1430–1450 m) (61; 27.2%)	La Muralla (1430–1450 m) (61; 27.2%)	Güisayote (33; 14.7%)	La Muralla (1430–1450 m) (61; 27.2%)	La Muralla (1430–1450 m) (61; 27.2%)
2	Montecristo (35; 42.4%)	Montecristo (35; 42.4%)	La Muralla (1430–1450 m) (54; 38.8%)	Santa Barbara (34; 42.4%)	El Pital (2650 m); 0.986 (12; 32.6%)
3	Yuscaran (26; 54.4%)	Santa Barbara (24; 53.1%)	Montecillos (13; 44.6%)	Montecristo (24; 53.1%)	La Tigra (2030–2100 m); 0.968 (23; 42.7%)
4	Santa Barbara (20; 63.4%)	Comayagua (12; 58.5%)	Comayagua (16; 51.8%)	Güisayote (14; 59.4%)	Cusuco (1960–2080 m); 0.963 (11; 47.8%)
5	Güisayote (14; 69.6%)	Uyuca (19; 67.0%)	Yerba Buena (14; 58.0%)	Uyuca (20; 68.3%)	Yerba Buena; 0.912 (14; 54.0%)
6	La Tigra (2030–2100 m) (12; 75.0%)	Yuscaran (13; 72.8%)	La Tigra (2030–2100 m) (13; 63.8%)	Yuscaran (14; 74.6%)	El Pital (2050 m); 0.899 (13; 59.8%)
7	Uyuca (9; 79.0%)	Güisayote (14; 79.0%)	Montecristo (17; 71.4%)	Comayagua (9; 78.6%)	Cusuco (1650 m); 0.902 (4; 61.6%)
8	Yerba Buena (8; 82.6%)	El Pital (2050 m) (5; 81.3%)	Uyuca (12; 76.8%)	El Pital (2650 m) (7; 81.7%)	Puca; 0.884 (8; 65.2%)
9	Puca (7; 85.7%)	Yerba Buena (7; 84.1%)	Santa Barbara (13; 82.6%)	Yerba Buena (8; 85.3%)	Montecillos; 0.885 (5; 67.4%)
10	Comayagua (7; 88.8%)	La Tigra (2030–2100 m) (6; 87.1%)	Yuscaran (10; 87.1%)	La Tigra (2030–2100 m) (7; 88.8%)	Montecristo; 0.884 (17; 75.0%)
11	Cusuco (1960–2080 m) (6; 91.5%)	Puca (6; 89.7%)	Puca (7; 90.2%)	Cusuco (1960–2080 m) (6; 91.1%)	La Tigra (1950 m); 0.897 (4; 76.3%)
12	El Pital (2650 m) (7; 94.6%)	Montecillos (4; 91.5%)	La Tigra (1950 m) (3; 91.5%)	Puca (7; 94.2%)	Güisayote; 0.892 (12; 81.7%)
13	Montecillos (4; 96.4%)	La Tigra (1950 m) (3; 92.9%)	Cusuco (1650 m) (2; 92.4%)	Montecillos (4; 96.0%)	La Muralla (1510–1550 m); 0.894 (1; 82.1%)
14	El Pital (2050 m) (3; 97.8%)	La Muralla (1510–1550 m) (1; 93.3%)	El Pital (2050 m) (3; 93.8%)	El Pital (2050 m) (3; 97.4%)	Uyuca; 0.885 (10; 86.6%)
15	Cusuco (1650 m) (2; 98.6%)	Cusuco (1650 m) (2; 94.2%)	La Muralla (1510–1550 m) (1; 94.2%)	La Tigra (1950 m) (3; 98.7%)	Yuscaran; 0.885 (9; 90.6%)
16	La Tigra (1950 m) (2; 99.6%)	Cusuco (1960–2080 m) (6; 96.9%)	Cusuco (1960–2080 m) (6; 96.9%)	Cusuco (1650 m) (2; 99.6%)	Comayagua; 0.875 (8; 94.2%)
17	La Muralla (1510–1550 m) (1; 100%)	El Pital (2650 m) (7; 100%)	El Pital (2650 m) (7; 100%)	La Muralla (1510–1550 m) (1; 100%)	Santa Barbara (13; 100%)

Numbers in parentheses are the number of species added to the cumulative species total by the addition of that site and the percentage accumulation of the total species known from all sites selected to this point.

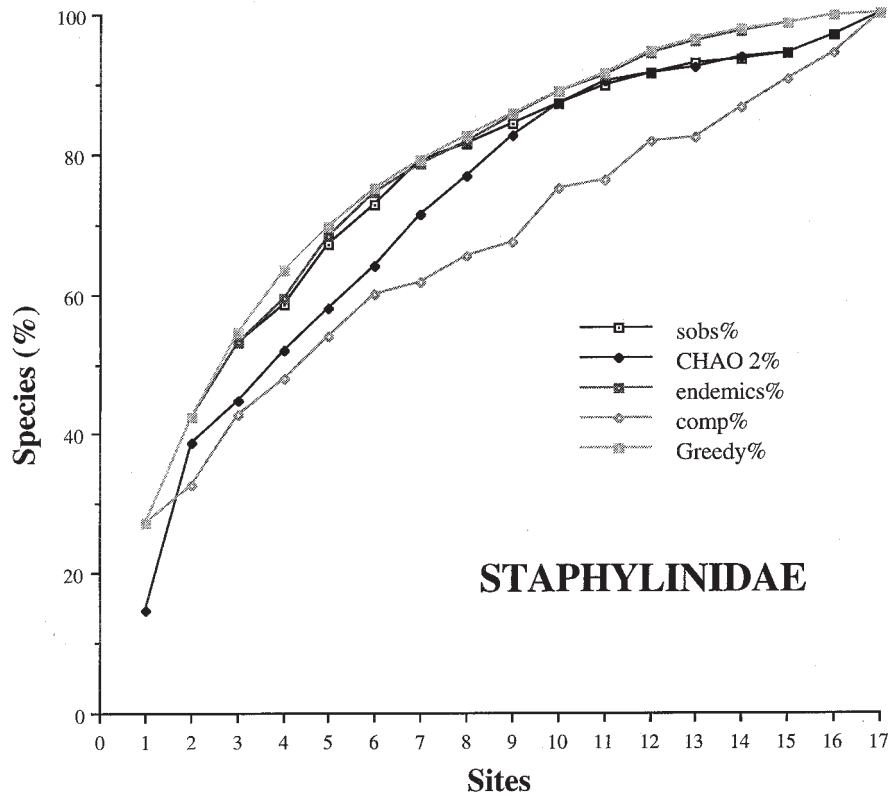


Figure 10. Priority-areas sequences for Staphylinidae based on Sobs ('Greedy' and non-cumulative), Chao 2, number of endemics and complementarity.

#### Combined analysis

As a means of comparing the results obtained from Curculionidae and those obtained from Staphylinidae, relationships between Sobs, number of endemics, numbers of rare species (number of species represented at a site by one or two individuals; data from Table 3), the estimator Chao 2 and area ( $\text{km}^2$ ) for each site for Curculionidae and Staphylinidae, are examined. As well, numbers of endemic versus non-endemic, rare versus non-rare, and measures of Sobs versus Chao 2, for curculionids and staphylinids at each site are examined to see how well various variables act as predictors of others. Results for Curculionidae show that as Sobs increases, so generally does the number of endemics ( $R^2 = 0.441$ ); however, the number of endemics at a site is seemingly not related to the number of non-endemics ( $R^2 = 0.024$ ). On the other hand, for staphylinids, there is a weak positive relationship ( $R^2 = 0.250$ ), which would otherwise have been much stronger ( $R^2 = 0.534$ ) with the exclusion of P.N. La Muralla which is the only site with a large number (31) of staphylinid endemics.

Other than at this site, number of endemics for staphylinids is relatively low, more so than for curculionids. For rare versus non-rare curculionids and staphylinids there is a weak positive relationship (Curculionidae;  $R^2 = 0.535$ , Staphylinidae;  $R^2 = 0.620$ ). The relationship between Chao 2 and Sobs also was examined. Whereas Chao 2 shows a strong positive association with Sobs for Curculionidae ( $R^2 = 0.818$ ), the association is surprisingly poor for Staphylinidae ( $R^2 = 0.054$ ).

Plots of Sobs, Chao 2 and number of endemics for Curculionidae versus Staphylinidae were examined to investigate how results obtained for one taxon relate to those obtained for the other. All show weak to very weak positive relationships (respectively  $R^2 = 0.250$ ,  $R^2 = 0.090$ ,  $R^2 = 0.314$ ) indicating little concordance between results for the two taxa. Outlying sites are P.N. La Muralla for Sobs and number of endemics, and R.B. Güisayote for Chao 2. Similarly, Spearman Rank Correlation procedures indicated poor relationships between priority-areas sequences based upon Sobs (SRC;  $r_s = -0.319$ ,  $n = 17$ ,  $P < 0.50$ ,  $>0.20$ ), Chao 2 (SRC;  $r_s = -0.172$ ,  $n = 17$ ,  $P > 0.50$ ) and number of endemics (SRC;  $r_s = -0.417$ ,  $n = 17$ ,  $P < 0.10$ ,  $>0.05$ ).

Lastly, Sobs for each of Curculionidae and Staphylinidae were compared with area ( $\text{km}^2$ ) of each site. The relationship between Sobs for curculionids versus area is very weakly positive ( $R^2 = 0.105$ ) but for staphylinids is zero ( $R^2 = 0.000$ ).

## Discussion

Few studies have attempted to address spatial patterns in TMCF biodiversity in the quantifiable manner necessary for the purpose of developing management and conservation strategies. Most of the focus on tropical biodiversity inventory, management and conservation has been directed at lowland rain forests (Peterson et al. 1993). While it is widely accepted that lowland rain forests have very high levels of species diversity, there is accumulating evidence that there are many wide-ranging species in the lowlands. Certainly, this is true for the Curculionidae (Anderson and O'Brien 1996) and likely also for Staphylinidae (Navarette-Heredia and Newton 1996). In addition, the general lack of knowledge about biodiversity in TMCF leads to the misconception that TMCF is substantially less diverse. Yet our experience with various arthropods (especially beetles) indicates surprisingly high levels of diversity. We argue that TMCFs are the home of the better part of Neotropical biodiversity (Balslev 1993) and conservation efforts should focus on the biota of highland habitats and less so on that of the lowlands (Peterson et al. 1993).

Within Honduras, 13 of the more than 30 'protected' TMCFs were sampled for leaf litter Curculionidae and Staphylinidae. Based on the combined results of the priority-areas analyses four sites rank highly and each should be considered a conservation priority (Tables 6 and 7). These sites and their cumulative rankings for Curculionidae and Staphylinidae respectively (Tables 6 and 7) are P.N. Montecristo (1, 2), P.N. La Muralla (3, 1), P.N. Santa Barbara (3, 4) and P.N. Comayagua (5, 3). A

second level of priority would include R.B. Güisayote, P.N. La Tigra and P.N. Cusuco. Upon first examination based on Sobs and Chao 2 (Tables 3 and 4), R.B. Güisayote may appear to rank more highly than P.N. Santa Barbara and P.N. Comayagua; however, while diverse, R.B. Güisayote is geographically close to P.N. Montecristo and shares a substantial proportion of its species with that site.

If one considers only the results of the weevil analyses, P.N. Montecristo is clearly the highest priority. Aside from having the highest ranking in all categories except number of endemics (where it is the second priority after P.N. Santa Barbara), this site also ranks first in terms of higher taxonomic diversity represented. This site accounted for 69.1% of the total taxonomic diversity of weevils represented in the selected TM-CFs. Aside from P.N. La Muralla, P.N. Santa Barbara and P.N. Comayagua, another site which ranks highly in the priority-areas analysis for weevils is P.N. Cusuco. This site ranked fifth in terms of Sobs (cumulative) and fourth in numbers of endemics.

In slight contrast to the weevil results, the results from the staphylinid analyses support the selection of P.N. La Muralla (1430–1450 m) as the highest priority. This site ranks first in all categories with the exception of Chao 2 where it ranks second, behind R.B. Güisayote. Parque Nacional Montecristo ranks second in terms of Sobs (Greedy) and third in number of endemics; however, it ranks seventh in terms of Chao 2. Also, in contrast to the weevil results are the rankings of P.N. Cusuco and R.B. Yuscaran. For Staphylinidae, P.N. Cusuco is ranked eleventh or lower for all measures compared with higher rankings for Curculionidae. On the other hand, R.B. Yuscaran, with an eighth or lower ranking for all measures for Curculionidae, ranks third for Sobs (cumulative) and sixth for each of Sobs (non-cumulative) and number of endemics for Staphylinidae.

It is clear from the data available in this study that not all TMCF sites are equivalent. Regional differences, even within the same general habitat can be pronounced. These differences are not easy to determine in the absence of biological inventories of at least a few taxa. Given that we do not have the time or resources to inventory all or even a substantial number of taxa, selection of taxa to act as surrogates for a complete inventory must be carried out carefully. Prendergast et al. (1993) in a study of rare species and the coincidence of diversity hotspots in England noted that effective use of surrogate taxa depended upon two things; 1, habitats (or sites) that are species-rich for one taxon are also species-rich for others; and 2, rare species (we would add endemic as well) occur in, and thus benefit from the conservation of species-rich habitats (or sites). Our data demonstrate that despite our comparison of two higher taxa of Coleoptera, occupying the same habitat within the same sites, differences in regional patterns in the diversity of weevils and staphylinids are evident. While there is general agreement in that a site 'species-rich' for weevils is similarly 'species-rich' for staphylinids, regressions of diversity measures (Sobs, number of endemics) or estimates (Chao 2) for Curculionidae versus Staphylinidae show at best only weak significance (Sobs;  $R^2 = 0.250$ , Chao 2;  $R^2 = 0.090$ , number of endemics;  $R^2 = 0.314$ ). Similarly, although sites species-rich for either Curculionidae

or Staphylinidae tend to have a greater number of endemics or rare curculionids or staphylinids, respectively, these relationships are not particularly strong. Furthermore, when the number of endemics versus number of non-endemics are compared for either taxon, weak negative (Curculionidae;  $R^2 = 0.024$ ) and weak positive (Staphylinidae;  $R^2 = 0.250$ ) relationships are evident demonstrating that sites with larger numbers of endemics do not necessarily have larger numbers of non-endemics. Similar, but stronger, relationships exist for rare versus non-rare species (Curculionidae;  $R^2 = 0.535$ , Staphylinidae;  $R^2 = 0.620$ ). Considering the generally poor adherence to the criteria for effective surrogates listed previously, one could argue that the utility of one of either Curculionidae or Staphylinidae as surrogates for patterns in TMCF biodiversity is equivocal. Site species diversity for curculionids is at best weakly correlated with species diversity for staphylinids. Similarly, numbers of rare and of endemic species also are only weakly correlated with site species diversity. Nevertheless, these relationships are positive, and at present we have no measures or estimates of diversity, endemism or rarity in other arthropod taxa with which to assess results. Ultimately, one of either curculionids or staphylinids may prove to be the better surrogate.

Clearly, given unlimited resources for conservation, all sites have merits warranting their preservation; however, such resources are rarely unlimited, or even adequate, to deal with most conservation plans and a strategy for assigning priorities for reserve selection must be established. If the goal is to conserve all species then all sites (with the exception of R.B. Yuscaran and R.B. Yerba Buena [based on weevil data]) should be selected as all harbor endemic species. On the other hand, it is important from a managerial perspective to note that even though individual site endemism is relatively high (more so for Curculionidae), selection of only three sites, namely P.N. Montecristo, P.N. La Muralla and P.N. Santa Barbara, conserves 48.1% and 53.1% of the species diversity of both weevils and staphylinids respectively, and over 90% of the higher taxonomic diversity of weevils represented at all sites. Since higher taxonomic composition of the TMCF litter weevil fauna is quite uniform throughout most of Central America, selection of the P.N. Montecristo site ensures conservation of a significant portion of weevil higher taxonomic diversity (and likely higher taxonomic diversity for staphylinids) in this habitat for all of Central America.

Unfortunately, no measure or estimator of diversity matched the optimum sequence or rate for which species could be conserved (Sobs using 'Greedy' principle). Despite closely approximating the performance of the latter, Sobs, number of endemics, Chao 2, and complementarity give consistently sub-optimal results for both curculionids (Figure 7) and staphylinids (Figure 10). Thus in general, we feel the best method of establishing priorities, and the one incorporating the fewest assumptions, is comparison of the number of species observed at that site (Sobs). Using the 'Greedy' principle, sites can be prioritized to maximize the number of additional species added with the addition of each successive site. This is essentially the method of Williams et al. (1993) which seeks to maximize the 'faunal complement' at each step in the

analysis. Such a method takes levels of endemism into account such that while two sites may each be individually species-rich, a combined species list for the two may not be maximally diverse due to the presence of the same species on both lists. This method may at first appear similar to one based on a measure of faunal complementarity that represents the proportion of all species on two lists that occurs on only one of the other of them (Colwell and Coddington 1994). However, the latter is not sensitive to measures of species diversity and does not perform well in an attempt to maximize accumulated species numbers (Figures 7 and 10; Tables 6 and 7, column 5). Rather than adding the maximum number of new species, it appears to favor less diverse sites which share the fewest number of species with the site(s) already selected.

The generally close approximation of the performance of Sobs, number of endemics and Chao 2 in TCMF (Figures 7 and 10) is likely due to the relatively high numbers of endemic species. Consider the extreme case when all species at a site are endemic. In such a situation, priority-areas analyses based on Sobs (Greedy), Sobs, and numbers of endemics would be identical, determined solely by the numbers of species at each site. As sites share increasingly larger proportions of their faunas, we would not expect such a correlation to exist.

As an alternative to measures of diversity, various biodiversity estimators are becoming increasingly popular (Colwell 1997). Use of the estimator Chao 2 attempts to account for possible sampling bias by considering the numbers of rare species in the samples. For Curculionidae, Chao 2 gives similar results to those based on Sobs. For Staphylinidae on the other hand, Chao 2 gives less similar results to those for Sobs. This is especially evident for R.B. Güisayote for which Chao 2 considers the site as a first level ranking (Chao 2 = 133.00) compared with a seventh level ranking based on Sobs (Sobs = 33) (Tables 4 and 7). Similarly for R.B. Montecillos, this site moves from a twelfth level ranking based on Sobs (Sobs = 23) to a third level ranking based on Chao 2 (Chao 2 = 83.50) (Tables 4 and 7). For staphylinids, Chao 2 performs poorer than Sobs or number of endemic species in its attempt to establish priorities (Figure 10; Table 7). Whether the high numbers of apparently rare staphylinid species at these sites (and thus marked differences between Sobs and Chao 2 values) are indicative of incomplete sampling, a higher number of non-litter resident species, or variation within the habitat is not known. Interestingly, weevils far outnumber staphylinids in their numbers collected during the study, and outnumber them in numbers of species observed; however, Chao 2 estimates of predicted diversity indicate that staphylinid diversity would surpass weevil diversity if more sampling was conducted. We suspect that the higher number of species of staphylinids represented in the entire data set by singletons (53 compared to 38 for weevils) indicates either unrecognized tourism, or, that staphylinid species are more unevenly distributed within the habitat than are weevils, perhaps due to the ephemeral and localized nature of their food resources (e.g., fruiting fungi, dung, carrion, etc.) or aspects of their natural history (e.g., predators). Density of rare larger staphylinid predators may be sufficiently low that the litter sample size (9 m<sup>2</sup>) is too small to adequately sample them. This may

not be so for curculionids which tend to be smaller and likely more evenly distributed in the leaf litter habitat.

Once a list of priorities for reserve selection has been established, attention should then turn to aspects of reserve design. A central debate in selection of reserve design is the size of the reserve, particularly whether to favor a single large or several small reserves (SLOSS; Simberloff and Abele 1976; Boecklin and Gotelli 1984; Simberloff 1986). Our data are particularly relevant to this debate. Diamond (1975) proposed six somewhat controversial features to be favored in reserve design based on island biogeography theory. Of particular concern here are two issues; 1, that a single large reserve is preferable to several small (given they represent the same habitat type); and, 2, that if it is necessary to have several small reserves, that they be close to each other to minimize isolation. Certainly as far as TMCF is concerned, both proposals appear to counter the goal of optimizing diversity in the conserved areas. Assuming that viability of populations among the sites (be they large or small) is equivalent, high levels of local endemism in both weevils and staphylinids argue in favor of as many areas as is possible, regardless of size. The preference for a single large reserve is based on the idea that sites of greater area are likely to possess a greater diversity than are smaller sites. Our data on local species diversity and data from Cruz (1993) on land area do not support this contention. While smaller TMCFs generally have lower levels of diversity, when all TMCF sites are considered, measures or estimates of biodiversity for both weevils and staphylinids do not appear to correlate significantly with size of the area (Curculionidae;  $R^2 = 0.105$ , Staphylinidae;  $R^2 = 0.000$ ). Not only should there be as many reserves as possible, there is no support for the idea that they should be proximal. Our data indicate this would appear to result in lower overall diversity. For example, each of the geographically adjacent R.B. El Pital (2650 m), P.N. Montecristo and R.B. Güisayote have high Sobs or Chao 2 values (especially for weevils; Table 3); however, they share a substantial portion of their diversity with one or more of the other two sites. Based on Sobs, P.N. Montecristo ranks first, R.B. Güisayote second, and R.B. El Pital (2650 m) fourth (Table 3). Yet, in the priority-areas analyses based on Sobs ('Greedy'), R.B. Güisayote moves from a second priority to sixth, and R.B. El Pital (2650 m) moves from fourth to tenth (Table 6).

The implications of these results as far as developing TMCF management plans are concerned is significant as it would appear to emphasize the importance of the preservation of many small regional preserves rather than fewer, larger preserves. These results may be complicated by another factor of potential importance, the extent of disturbance within the site. Unfortunately, we have no data to address this issue.

## Conclusions

Emerging predictions about the extent of global biodiversity have made it unlikely that contemporary issues in biodiversity management, such as establishing conser-



vation priorities, can be addressed in a timely manner using information from more than but a few 'surrogate' or indicator taxa. In addition, financial resources and taxonomic expertise available for such activities are limited and these must be deployed as effectively and effectively as possible (Pressey et al. 1993; Vane-Wright 1996).

The data presented here are presently the only available quantitative data on spatial patterns in arthropod biodiversity in Neotropical TMCF that we are aware of. They provide a general measure of the extent of diversity in the leaf litter habitat in these forests and the extent to which species are limited in their geographic distributions. Endemism has generally been regarded as substantial in TMCF and, at least for litter inhabiting weevils and staphylinids, quantitative data are now available to support this contention. Just over 50% of all weevil and staphylinid species sampled are restricted to single sites. Diversity is also substantial in these habitats with a combined total of slightly over 500 species of leaf litter inhabiting species of weevils and staphylinids collected during the course of this study.

These data are valuable for establishing regional priorities for conservation of TMCF based solely on the biodiversity these sites contain. Although closely approximating the performance of Sobs ('Greedy'), no one of Sobs, Chao 2, number of endemic species, or complementarity, perform in a manner sufficient for them to replace the former. Thus, for the purposes of establishing priorities, we argue that use of Sobs ('Greedy') is to be preferred. Sobs and number of endemic species are simple to obtain measures, and a priority-areas analysis based on Sobs using the 'Greedy' method is a relatively easy and rapid analysis to conduct. With additional sampling, Chao 2 may actually prove a better performer than Sobs ('Greedy') in representing the true, but not yet observed, local diversity. Larger numbers of samples from each site than those obtained here will indicate if this is so.

Unfortunately, our data do not provide a clear indication of the utility of either leaf litter inhabiting curculionids or staphylinids as surrogates for general patterns of biodiversity in TMCF. Correlations between measures and estimators of diversity based on either curculionids or staphylinids are at best weak. Similarly, species diversity measures are only weakly (but at least positively) correlated with numbers of endemic or rare species. Obviously, part of the problem is assessing the value of these curculionids or staphylinids lies in the paucity of quantitative data from additional taxa about TMCF biodiversity. More taxa need to be sampled, but often these choices are limited by ease of sampling, extent of financial resources, and especially, availability of taxonomic expertise and knowledge. Information from inventories of additional surrogate taxa can not only be used to assess the efficacy of potential surrogates but results from all taxa can be integrated with social and cultural issues to formulate a comprehensive regional development or management plan for the TMCF habitat.

As far as Honduras is concerned, presently, and fortunately, this country has legislation concerning the status of many regional TMCFs. This status varies from Parque Nacional, to Reserva Biología or Reserva de Vida Silvestre (Cruz 1993). Of the thirteen sites sampled, six are Parques Nacionales, six are Reservas Biológicas,

and one is a Reserva de Vida Silvestre (Table 1). Our priority-areas analysis supports the status of sites designated as Parques Nacionales by selecting them as high level priorities and thus recognizing the stated goal that Parques Nacionales “conserve representative examples of principal natural ecosystems” (Cruz 1993). Of the four sites with high priority for conservation all are Parques Nacionales. Reserva Biología Güisayote and two additional Parques Nacionales, La Tigra and Cusuco, could be considered second level priorities.

Finally, and perhaps most importantly, if conservation efforts within Middle America are to focus on the preservation of taxa unique to particular regions, then the focus should be on the endemic biota of highland habitats and not the apparently more diverse but generally wide-ranging biota of the lowlands. Unfortunately, in practice this continues not to be so. “Smaller, carefully planned reserves may be very effective in preserving the most unique parts of the biological diversity of Middle America” (Peterson et al. 1993).

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## Appendix 1

Classification of litter Curculionidae collected  
in Honduras and El Salvador TMCf.

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### Curculionidae

Raymondionyminae  
New Genus 1

### Brachycerinae

#### Polydrosini

#### Barynotina

*Bufomicrus* Sharp  
New Genus 1

#### Brachyderina

*Sciomias* Sharp

#### Trachyphloeina

*Trachyphloeomimus* Champion

### Curculioninae

#### Molytini

#### Lymantina

*Theognete* Champion

*Lymantes* Schoenherr

*Dioprophorus* Faust

*Epibaenus* Kuschel

New Genus 1

New Genus 2

New Genus 3

New Genus 4

#### Anchonina

*Anchonus* Schoenherr

#### Conotrachelina

*Conotrachelus* Dejean

*Microhyus* LeConte

*Enomides* Champion

*Lepilius* Champion

New Genus 1

New Genus 2

#### Baridini

#### Centrinina

*Buchananius* Kissinger

#### Incertae sedis

New Genus 1

#### Cryptorhynchini

#### Tylodina

*Tylodinus* Champion

*Acalles* Schoenherr

*Eurhoptus* LeConte

New Genus 1

New Genus 2

New Genus 3

New Genus 4

New Genus 5

**Appendix 1.** Continued.

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Cossoninae

Cotasternini

*Caulophilus* Wollaston

Rhyncholini

*Heptarthrum* Champion

Cossonini

*Cossonus* Clairville & Schellenberg

Rhynchophorinae

Dryophorini

*Dryophthorus* Germar

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