

## PRELIMINARY ESTIMATES OF LEPIDOPTERA DIVERSITY FROM SPECIFIC SITES IN THE NEOTROPICS USING COMPLEMENTARITY AND SPECIES RICHNESS ESTIMATORS

MICHAEL G. POGUE

Systematic Entomology Laboratory, P. S. I., Agricultural Research Service, U.S. Department of Agriculture,  
% Department of Entomology, National Museum of Natural History,  
Smithsonian Institution, Washington, D.C. 20560-0168, USA

**ABSTRACT.** Lepidoptera were collected and species richness and complementarity or uniqueness were compared between two rainforest sites: Pakitza, Peru and Beni, Bolivia. The total number of species collected from both sites was 1,879 of which 60 were shared resulting in a complementarity of 96.8%. Non-parametric equations and species accumulation curves of *Hemiceras* Guenée (Lepidoptera: Notodontidae) were used to compare species richness between three rainforest sites, Pakitza and Tambopata, Peru and Reserva Ethnica Waorani, Onkone Gare, Ecuador. Cluster analysis, using complementarity values for selected sites was used to determine altitudinal relationships between sites in Costa Rica; relationships between forest types in Brazil; and faunal differences among sites in western Amazonia using *Hemiceras*.

**Additional key words:** Biodiversity, Notodontidae, *Hemiceras*, Chao, jackknife.

Biodiversity as defined by E. O. Wilson (Reaka-Kudla et al. 1997) is “everything”. Biodiversity encompasses the genes within a single local population or species, the species within a local community, and communities comprising the diverse ecosystems of the world. Life on earth is supported by the interactions and products produced by all other life on earth. Without biodiversity there would be no life on earth as we know it. Therefore, it is essential that biologists begin to document and record biodiversity, whether it be how many species of insects are in your backyard to how many species of trees in a forest to how many forest types in the world.

Anyone with an interest in natural history can begin to study their local biodiversity and to document it. One basic element of biodiversity is to know how many species are present at a particular site. This paper will outline how anyone can begin to document local biodiversity by gathering data on species richness or the number of species present at a site at a particular point in time. Knowing what species are present at a site is essential because it is the first step in understanding the interactions between the species documented and their interactions within the local community and ecosystem.

Presently, no one has much of an idea exactly how many species are present today on earth. Estimates of the number of species worldwide range from 3 to 100 million (Erwin 1982, 1983, Stork 1988, Hodkinson & Casson 1991, May 1992, Raven and Wilson 1992). The study of species richness and complementarity, or how different species composition is between sites, is essential to assessing global biodiversity patterns.

To address the question of world insect diversity one must get accurate estimates of site-specific species richness for a variety of taxa (Colwell & Coddington 1994), and then to compare these species lists to measure relative levels of overlap and richness of these

taxa around the globe. After a site has been sampled, species richness estimates are used to predict how many species were missed during the sampling process, thus arriving at an estimated number of species based on the actual number observed plus the number missed. By using species lists, either generated by sampling at a site or from museum collections, species composition among sites can be compared. These comparisons can then be used in setting policy and making informed conservation and management decisions.

The goals of this paper are 1) to emphasize the importance of adequate sampling, 2) to assess whether inadequate sampling can still be useful in predicting species richness and complementarity between study sites, and 3) to provide a method of using complementarity to compare faunal relationships between sites. To accomplish these goals, I compared overall species richness and complementarity of Lepidoptera from two rainforest sites, one in Peru and the other in Bolivia. In addition, I estimated species richness from species accumulation curves and non-parametric estimators to compare the *Hemiceras* Guenée (Notodontidae) fauna between 2 sites in Peru and 1 in Ecuador. Finally, museum specimens of *Hemiceras* were used for faunal comparisons among sites in Costa Rica, Brazil, and western Amazonia, using complementarity and cluster analysis.

### MATERIALS AND METHODS

**Lepidoptera complementarity in SW Amazonia.** Lepidoptera were collected at two rainforest sites: Beni, Bolivia and Pakitza, Peru. The Beni study site at 14°49' S, 66°28' W is 40 km E of San Borja, at 250 meters elevation. Pakitza is located on the Río Manu at 11°56'47"S, 71°17'00"W within the large drainage basin of the Río Madre de Dios in southeastern Peru, at 356 m elevation, approximately 550 km NW of Beni.

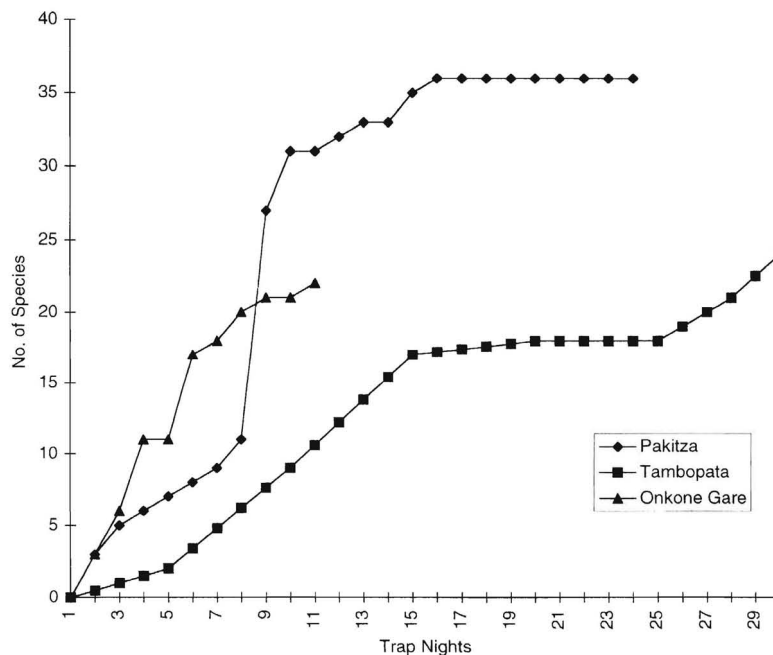


FIG. 1. Species accumulation curves of *Hemiceras* at Pakitza and Tambopata, Perú, and Onkone Gare, Ecuador.

Samples were collected between August 26–September 15, 1987 (Beni) and from September 27–October 5, 1987 (Pakitza). Adult moths were collected by UV light traps, spread, identified to family, sorted to morpho-species, and counted. Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Collecting effort was defined as the number of trap nights: 12 and 8 trap nights in Pakitza and Beni, respectively. Other studies have included the number of person-hours spent collecting (Coddington et al. 1991, Robbins et al. 1996), number of collecting days (Lounton et al. 1996), or trap nights (approximately 12 hours in length).

The Lepidoptera faunas of Pakitza and Beni were compared using complementarity (Colwell and Coddington 1994). In comparing two sites,  $j$  and  $k$ , the first site has a species richness of  $S_j$  and the second site has  $S_k$ . If the number of species in common between both sites is  $V_{jk}$ , then the total species richness for both sites is

$$S_{jk} = S_j + S_k - V_{jk}, \quad (1)$$

and the number of species unique to both sites ( $U_{jk}$ ) is

$$U_{jk} = S_j + S_k - 2V_{jk}. \quad (2)$$

The complementarity between the two sites is the proportion of the unique species to the pooled richness, or

$$C_{jk} = \frac{U_{jk}}{S_{jk}}. \quad (3)$$

***Hemiceras* species richness in western Amazonia.** The genus *Hemiceras* (Lepidoptera: Notodontidae), representing 245 species, was used as an indicator group for estimating species richness at three rainforest sites: Pakitza and Río Tambopata Research Station in southeastern Peru, and Onkone Gare, in Ecuador.

Río Tambopata Research Station, at 14°14'S, 69°11'W, is located on the Río Tambopata, 30 air km SE of Puerto Maldonado, Madre de Dios, Peru, at 290 m elevation. Onkone Gare, at 00°38'S, 76°36'W, is a research station within the Reserva Ethnica Waorani, Ecuador, at 220 m elevation. Tambopata had a total of 29 trap nights from November 2–25, 1979 and September 16–21, 1990. The 11 trap nights at Onkone Gare were January 10, 12, 13–18, 25; June 20; and July 16, 1994.

Species accumulation curves (Fig. 1) were used to plot the cumulative number of new species collected over unit effort (number of trap nights) at each of the

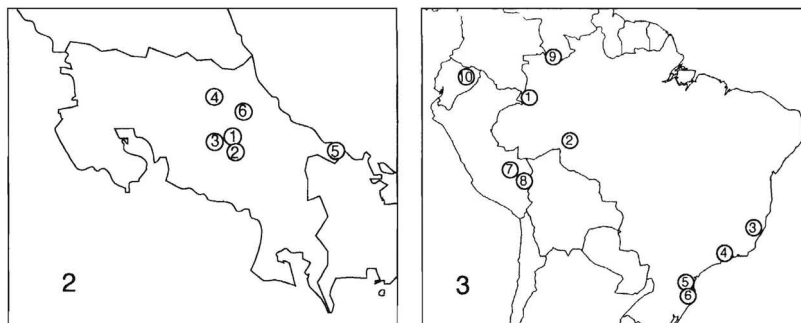


FIG. 2. Localities of Costa Rican sites used in cluster analysis of dissimilarity matrix in Table 3.

FIG. 3. Localities of South American sites used in cluster analyses of dissimilarity matrices in Tables 4 and 5.

three sites. To extrapolate total species richness from the species accumulation curves at each site, four different nonparametric equations were compared: 1) Chao 1, 2) Chao 2, 3) first-order jackknife, and 4) second-order jackknife.

Chao (1984) developed a simple estimator of the true number of species at a given site based on the number of rare species in the pooled sample  $j$ . This is considered an abundance-based estimator because it is based on the number of species that are only represented by only 1 or 2 individuals to estimate overall species richness. Colwell and Coddington (1994) called this Chao 1,

$$\text{Chao 1} = S_{\text{obs}} + a^2/2b, \quad (4)$$

where  $S_{\text{obs}}$  is the observed number of species in a sample,  $a$  is the number of species that are only represented by one specimen in the pooled sample (singletons), and  $b$  is the number of species represented by two specimens in the pooled sample (doubletons). This estimator works well when the samples contain a large number of rare species (Chao 1984), which frequently occurs when sampling diverse groups such as insects.

A related estimator is Chao 2 (Colwell & Coddington 1994), which is based on the incidence of rare species among samples,

$$\text{Chao 2} = S_{\text{obs}} + L^2/2M, \quad (5)$$

where  $L$  is the number of species that occur in only one sample, and  $M$  is the number of species that occur in exactly two samples.

Jackknife estimators (Burnham & Overton 1978, 1979) also use the distribution of species among samples (Colwell & Coddington 1994). The first-order

jackknife estimator of species richness is based on the number of species that occur in only one sample  $L$ ,

$$1 \text{ jackknife} = S_{\text{obs}} + L(n - 1/n), \quad (6)$$

where  $n$  is the number of samples.

The second-order jackknife (Burnham & Overton 1978, 1979) is like the Chao 2 estimator where  $L$  is the number of species that occur in only one sample and  $M$  is the number of species that occur in exactly two samples,

$$2 \text{ jackknife} = S_{\text{obs}} + 1/2 [L(2n - 3)/n - M(n - 2)^2/n(n - 1)], \quad (7)$$

where  $n$  is the number of samples.

***Hemiceras* faunal comparisons between three tropical regions.** Species lists of *Hemiceras* were compiled from specimens in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and were used to examine faunal relationships among sites in Costa Rica, Brazil, and western Amazonia. In Costa Rica, six sites were chosen to see how altitude affected species composition. The sites chosen were Juan Vinas (1500 m), Tuis (732 m), Turrialba (634 m), Guapiles (259 m), La Selva (40 m) and Sixaola River (0 m) (Fig. 2). Six sites in Brazil were chosen to examine the effect of forest type: the lowland Amazonia forest included the sites of São Paulo de Olivença (Amazonas) and Porto Velho (Rondonia), and the Atlantic coast forest sites were Baixo Guandu (Espírito Santo), Campo Bello (Rio de Janeiro), Hansa Humboldt (Santa Catarina), and Santa Catherines (Santa Catarina) (Fig. 3, sites 1–6). Six sites were chosen to determine faunal relationships in western Amazonia. They included Neblina, Venezuela; Onkone Gare, Ecuador; São Paulo

TABLE 1. Comparison of % complementarity and number of species of Lepidoptera between Beni, Bolivia and Pakitza, Peru.

| Family              | % Complementarity | Number shared species |
|---------------------|-------------------|-----------------------|
| Microlepidoptera    |                   |                       |
| Cosmopterygidae     | 100.0             | 50 (0)                |
| Tineidae            | 100.0             | 113 (0)               |
| Celechiidae         | 98.8              | 167 (2)               |
| Oecophoridae        | 97.8              | 324 (7)               |
| Pyralidae/Crambidae | 96.8              | 281 (9)               |
| Macrolepidoptera    |                   |                       |
| Noctuidae           | 98.6              | 296 (4)               |
| Notodontidae        | 95.2              | 63 (3)                |
| Geometridae         | 93.3              | 213 (14)              |
| Arctiidae           | 91.5              | 189 (16)              |

de Olivença and Porto Velho in Brazil; and Pakitza and Tambopata in Peru (Fig. 3, sites 1–2, 7–10).

Complementarity was calculated between sites. These values were used to produce dissimilarity matrices which were converted, for easier interpretation, into dendrograms using cluster analysis (SYSTAT 1992).

## RESULTS

### Lepidoptera complementarity in SW Amazonia.

Some 38 families of Lepidoptera were collected from both sites, although only nine families had numbers of species sufficient to illustrate trends in complementarity. Five of these families were Microlepidoptera and the remaining four were Macrolepidoptera. A total of 1748 specimens representing 933 species were collected at Beni and 1731 specimens representing 1006 species from were collected at Pakitza. The pooled species richness for both sites ( $S_{jk}$ ) was 1879, the total number of unique species ( $U_{jk}$ ) was 1819, resulting in a complementarity of 96.8%. The Microlepidoptera families had higher complementarity values (100–96.8%), than the Macrolepidoptera families (95.2–91.5%), with the exception of the Noctuidae (98.6%) (Table 1).

**Hemiceras species richness in western Amazonia.** Comparing the four nonparametric equations for estimating species richness of *Hemiceras* at Pakitza and Tambopata, Peru, and at Onkone Gare, Ecuador resulted in Chao 1 estimating the highest number of species. The incidence-based estimators (Chao 2 and the Jackknives) consistently estimated total richness

TABLE 2. Estimated total species richness of *Hemiceras* species for 4 nonparametric estimators.

| Species richness estimator | Pakitza Peru | Tambopata Peru | Onkone Gare Ecuador |
|----------------------------|--------------|----------------|---------------------|
| Observed                   | 36           | 24             | 22                  |
| Chao 1                     | 43           | 29             | 40                  |
| Chao 2                     | 39           | 25             | 24                  |
| 1 Jackknife                | 41           | 24             | 24                  |
| 2 Jackknife                | 39           | 25             | 23                  |

closer to the observed values than did Chao 1, on abundance-based estimates (Table 2).

**Hemiceras faunal comparisons between three tropical regions.** Costa Rica: The high altitude sites of Juan Vinas and Tuis (1500 m and 732 m) were clustered at a dissimilarity value of 0.389, and the low altitude sites (0 m and 40 m) of Sixaola River and La Selva were clustered at a dissimilarity value of 0.571. Guapiles (259 m) was clustered with the low sites at a dissimilarity value of 0.667. The high altitude and low altitude sites were clustered at a dissimilarity value of 0.718. Turrialba (634 m) showed the greatest faunal dissimilarity between all other sites at 0.758 (Table 3; Fig. 4).

Brazil: The two Amazonian sites of São Paulo de Olivença and Porto Velho were clustered at a dissimilarity value of 0.883. Within the Atlantic Coast sites Hansa Humboldt and Santa Catherines were least dissimilar (0.600), Campo Bello was most similar to Hansa Humboldt + Santa Catherines (0.724), and Baixo Guandu was most dissimilar to the previous Atlantic Coast Forest sites (0.833). Dissimilarity between the Amazonia and Atlantic Coast Forests was 0.951 (Table 4; Fig. 5).

Western Amazonia: Pakitza and Tambopata in southeastern Peru were clustered at a dissimilarity value of 0.766. Neblina, Venezuela and Onkone Gare, Ecuador were clustered at a dissimilarity value of 0.793. These four sites were clustered at a dissimilarity value of 0.806. The fauna of São Paulo de Olivença had a dissimilarity value of 0.815 compared to the previous four sites and Porto Velho's fauna was the most dissimilar (0.833) (Table 5; Fig. 6).

TABLE 3. Dissimilarity matrix of Costa Rican altitudinal sites.

|                     | Juan Vinas (1500 m) | Tuis  | Turrialba | Guapiles | La Selva |
|---------------------|---------------------|-------|-----------|----------|----------|
| Tuis (732 m)        | 0.389               |       |           |          |          |
| Turrialba (634 m)   | 0.771               | 0.758 |           |          |          |
| Guapiles (259 m)    | 0.897               | 0.829 | 0.960     |          |          |
| La Selva (40 m)     | 0.718               | 0.730 | 0.897     | 0.769    |          |
| Sixaola River (0 m) | 0.794               | 0.781 | 0.909     | 0.667    | 0.571    |

TABLE 4. Dissimilarity matrix of comparison of Brazilian Amazonia and Atlantic Coast Forest.

|                | São Paulo de Olivença | Porto Velho | Baixo Guandu | Campo Bello | St. Catherines |
|----------------|-----------------------|-------------|--------------|-------------|----------------|
| Porto Velho    | 0.883                 |             |              |             |                |
| Baixo Guandu   | 0.982                 | 0.951       |              |             |                |
| Campo Bello    | 0.927                 | 0.930       | 0.833        |             |                |
| St. Catherines | 0.945                 | 1.000       | 0.867        | 0.724       |                |
| Hansa Humboldt | 0.958                 | 1.000       | 0.870        | 0.792       | 0.600          |

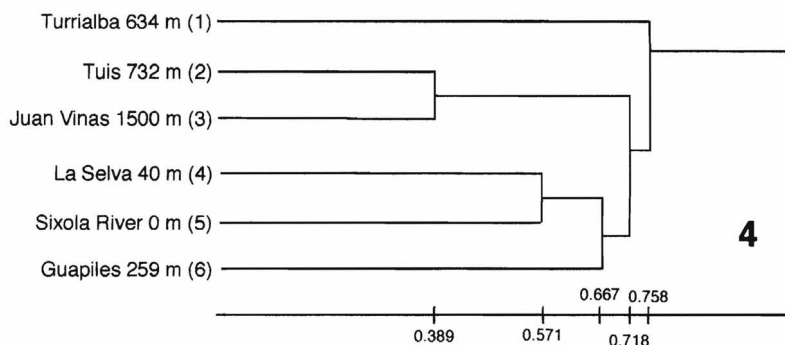


FIG. 4. Dendrogram for cluster analysis of dissimilarity matrix (Table 3) of Costa Rican sites. Numbers refer to localities on Fig. 2. Altitudes are indicated for each site. The scale indicates dissimilarity value.

## DISCUSSION

**Lepidoptera complementarity in SW Amazonia.** The lower complementarity found in most Macrolepidoptera, compared to the Microlepidoptera, may be due to sampling bias; because the collecting was done by UV light, larger moths may be coming from a larger collecting universe than the smaller moths, because the larger species are better able to disperse than the smaller ones. The relatively high complementarity of the Noctuidae is curious given that they are generally strong fliers, medium to large moths, and many species are known for their migration and wide ranging dispersal abilities. The answer may lie in their diversity; because these moths are the most speciose lepidopteran family, the sampling time possible in this preliminary study may be inadequate to accurately assess the ranges of many noctuid species, resulting in a higher complementarity value.

***Hemiceras* species richness in western Amazonia.** To accurately estimate the total number of species of a target taxon (such as *Hemiceras*) at a particular site the species accumulation curve (or the curve of a

suitable richness estimator) should reach an asymptote or remain constant over time with additional sampling. Of the three sites, the species accumulation curve reached an asymptote, only at Pakitza (Fig. 1), suggesting that the species estimate there should be the most accurate. Although Tambopata is known for the high species richness of various insect groups (Fisher 1985, Paulson 1985, Pearson 1985, Wilkerson & Fairchild 1985, Robbins et al. 1996). The *Hemiceras* fauna there is poor, considering that there are 245 species in the neotropics. Although samples taken at Tambopata and Onkone Gare were insufficient to accurately estimate richness, as shown by the non-asymptotic species accumulation curves (Fig. 1), it appears from all the nonparametric estimates, and the steeper accumulation curve, that Pakitza is even richer in *Hemiceras* than is Tambopata. That contrasts with a study of the faunal relationships between the Cicadoidea (Homoptera) (Pogue 1996) and Odonata (Louton et al. 1996) at Pakitza and Tambopata, in which the species richness was greater at Tambopata. Thus, either the preliminary estimate for *Hemiceras* at Tambopata is inaccurate, or this study demonstrates

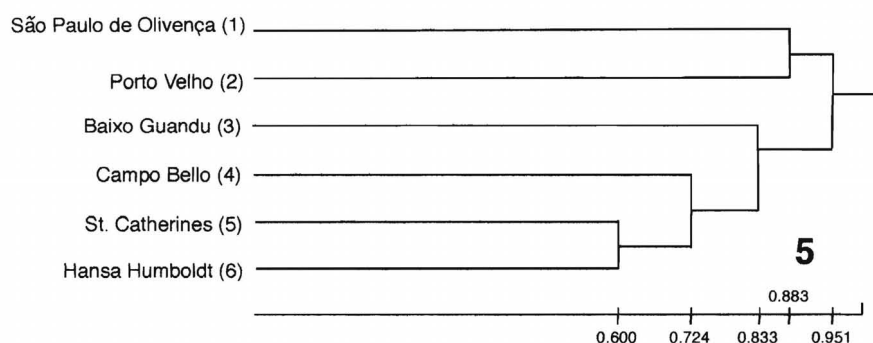


FIG. 5. Dendrogram for cluster analysis of dissimilarity matrix (Table 4) of Brazilian Amazonian and Atlantic Coast Forest sites. Numbers refer to localities on Fig. 3. The scale indicates dissimilarity value.

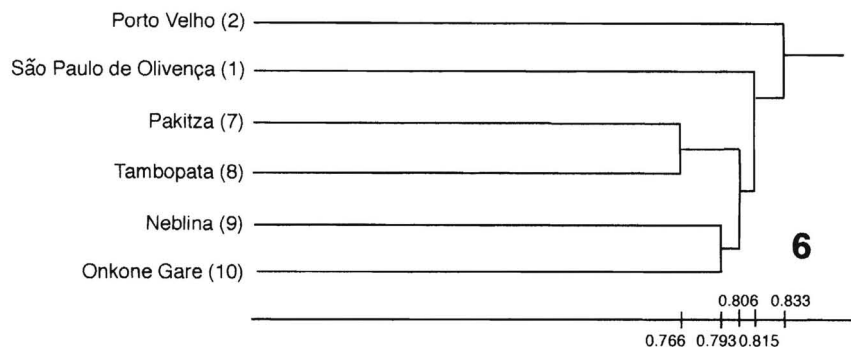


FIG. 6. Dendrogram for cluster analysis of dissimilarity matrix (Table 5) of western Amazonian sites. Numbers refer to localities on Fig. 3. The scale indicates dissimilarity value.

that different taxa, with divergent biologies, have different centers of diversity.

At the Onkone Gare site in Ecuador it is not clear whether the species accumulation curve is approaching an asymptote (Fig. 1) and there are more rare species (12 singletons) than at the other sites, so the prediction of 40 species by Chao 1 (Table 3) may be accurate. Based on the species richness data of *Hemiceras*, the following are recommended for follow-up studies: 1) collecting effort must be adequate for the species accumulation curve, or the estimate curve, to reach an asymptote, 2) if there is a preponderance of rare species, (singletons) Chao 1 should give the highest, and perhaps best estimate, and 3) if the number of rare species is low, Chao 2 or the second-order jackknife may give a better estimate. It is also important to choose your target taxon carefully.

To assess taxon richness, target taxa can be any category, an order, family, subfamily, tribe, or genus. The taxon should be chosen with care. For example, one that is too speciose requires too much time to process and extrapolate the needed data, one with too few species could result in insufficient data. I have found in the Neotropics that a target taxon of 200–400 species seems to be large enough so that the species accumulation curve reached an asymptote after 20–30 samples (trap nights, in this case). The data for the target

taxon can come from collecting, or from using museum collections to obtain faunistic data from specific sites. An advantage of using museum collections are the data available from sites that are no longer pristine, such as those in Amazonia that were collected more than 50 to 100 years ago. Today, with the destruction of the rain forest, these sights will no longer have the same biota. The target taxon has to be common throughout the study area so it can be easily sampled and there should not be a dominance of rare species.

***Hemiceras* faunal comparisons between three tropical regions.** The six sites in Costa Rica show a broad altitudinal range from 0–1500 meters. Altitude seems to influence species composition among sites in Costa Rica more than distance between sites. Juan Vinas (1500 m) and Tuis (732 m) are the highest sites and are clustered at a dissimilarity value of 0.389, the lowest of any pair. If distance was the significant limiting factor of faunal composition, one would expect that Tuis and Turrialba would be clustered. The same is true for the lower altitudinal sites, with La Selva (40 m) and Sixaola River (0 m) having the lower dissimilarity value (0.571), even though La Selva is closer to Guapiles than the Sixaola River site (Table 3) (Fig. 4).

Analysis of the six sites within Brazil were used to show if there was a faunal difference between Amazonia and the Atlantic Coast forest. The Atlantic Coast sites were clustered (Baixo Guandu to Hansa Humboldt) and were quite distinct from the Amazonian fauna (São Paulo de Olivença and Porto Velho) which were also clustered. Within the Atlantic Coast Forest distance seems to be influencing the faunal relationships. Hansa Humboldt and Santa Catherines were most faunistically similar and closest in distance. Campo Bello shows similarity with Hansa Humboldt + Santa Catherines and is closer than Baixo Guandu, which is the most dissimilar and furthest from these

TABLE 5. Dissimilarity matrix of Amazonian sites.

|                   | Neblina | Onkone Gare | São Paulo de Olivença | Porto Velho | Pakitza |
|-------------------|---------|-------------|-----------------------|-------------|---------|
| Onkone Gare       | 0.793   |             |                       |             |         |
| S. P. De Olivença | 0.918   | 0.873       |                       |             |         |
| Porto Velho       | 0.947   | 0.886       | 0.883                 |             |         |
| Pakitza           | 0.860   | 0.863       | 0.831                 | 0.833       |         |
| Tambopata         | 0.806   | 0.821       | 0.815                 | 0.915       | 0.766   |



two sites. Cluster analysis indicates that there is a faunal difference between Amazonia and the Atlantic Coast Forest (Table 4) (Fig. 5).

Amazonia is often treated as one large biogeographical area, but just how different are sites within Amazonia? Among the six Amazonian localities dissimilarities (Table 5) seemed strongly affected by distance and habitat. Pakitza and Tambopata, both in south-eastern Peru clustered, as did Onkone Gare, Ecuador and Neblina, Venezuela which are similar in habitat despite being approximately 1160 km distant from each other. Taken together these western Amazonia sites appear to form a region (Fig. 3), perhaps because they lie along the eastern edge of the Andes. Porto Velho was less faunistically similar to São Paulo de Olivença than to Pakitza.

These studies from Costa Rica to Bolivia demonstrate that site-specific data analysis is a prerequisite to a thorough understanding of regional biodiversity patterns. The methods presented above were useful in assessing biodiversity on a site by site basis, and once similar data from other studies and other organisms are pooled, it may be possible to predict complementarity between and among sites and to predict species numbers at other sites. Complementarity, or distinctness of species assemblages among sites can be used with cluster analysis to predict complementarity between a wide variety of parameters such as biogeographic, habitat differences, or host plant specificity. Using species richness estimates, complementarity values, and species lists generated from biodiversity inventories can be useful for biologists and conservationists to make more informed decisions about land use and conservation.

#### ACKNOWLEDGMENTS

I would like to thank Terry L. Erwin for his support of this project and for providing time in the field for collecting and processing material. For critically reviewing a draft of this paper, I thank Marc E. Epstein and Jerry A. Louton, Smithsonian Institution, Washington, D.C., and M. Alma Solis, Stuart H. McKamey and David R. Smith, Systematic Entomology Laboratory, Washington, D.C., Eric H. Metzler, Columbus, Ohio, and Deane Bowers, University of Colorado, Boulder, Colorado. Funding was provided by the Smithsonian Institution's BIOLAT Program.

#### LITERATURE CITED

- BURNHAM, K. P. & W. S. OVERTON. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65:623–633.
- . 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936.
- CHAO, A. 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Statistics* 11:265–270.
- CODDINGTON, J. A., C. E. GRISWOLD, D. SILVA DAVILA, E. PENARANDA & S. F. LARCHER. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems, pp. 44–60. *In* E. C. Dudley (ed.), *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*. Dioscorides Press, Portland, Oregon. 1048 pp.
- COLWELL, R. K. & J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. London* 345:101–118.
- ERWIN, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36:74–75.
- . 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, samples by insecticidal fogging, pp. 59–75. *In* S. L. Sutton, T. C. Whitmore & A. C. Chadwick (eds.), *Tropical rain forest ecology and management*. Oxford, Blackwell Scientific Publications. 498 pp.
- FISHER, E. M. 1985. A preliminary list of the robber flies (Diptera: Asilidae) of the Tambopata Reserved Zone, Madre de Dios, Perú. *Rev. Peru. Entomol.* 27:25–36.
- HODKINSON, I. D. & D. CASSON. 1991. A lesser predilection for bugs; Hemiptera (Insecta) diversity in tropical rain forests. *Biol. J. Linn. Soc.* 43:101–109.
- LOUTON, J. A., R. W. GARRISON & O. S. FLINT. 1996. The Odonata of Parque Nacional Manu, Madre de Dios, Peru; natural history, species richness and comparisons with other Peruvian sites, pp. 431–449. *In* D. E. Wilson & A. Sandoval (eds.), *La biodiversidad del sureste del Peru: Manu (Biodiversity of Southeastern Peru)*. Editorial Horizonte, Lima, Peru. 679 pp.
- MAY, R. M. 1992. How many species inhabit the Earth? *Sci. Am.* 267(4):42–48.
- PAULSON, D. R. 1985. Odonata of the Tambopata Reserved Zone, Madre de Dios, Perú. *Rev. Peru. Entomol.* 27:9–14.
- PEARSON, D. L. 1985. The tiger beetles (Coleoptera: Cicindelidae) of the Tambopata Reserved Zone, Madre de Dios, Perú. *Rev. Peru. Entomol.* 27:15–24.
- POGUE, M. G. 1996. Biodiversity of Cicadoidea (Homoptera) of Pakitza, Manu Reserved Zone and Tambopata Reserved Zone, Perú: a faunal comparison, pp. 313–325. *In* D. E. Wilson & A. Sandoval (eds.), *La biodiversidad del sureste del Peru: Manu (Biodiversity of Southeastern Peru)*. Editorial Horizonte, Lima, Peru. 679 pp.
- RAVEN, P. H. & E. O. WILSON. 1992. A fifty-year plan for biodiversity surveys. *Science* 258:1099–1100.
- REAKA-KUDLA, M. L., D. E. WILSON & E. O. WILSON. 1997. Biodiversity II: understanding and protecting our biological resources. The National Academy of Sciences. John Henry Press, Washington, D.C. 551 pp.
- ROBBINS, R. K., G. LAMAS, O. H. H. MIELKE, D. J. HARVEY & M. M. CASAGRANDE. 1996. Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Perú, pp. 217–252. *In* D. E. Wilson & A. Sandoval (eds.), *La biodiversidad del sureste del Peru: Manu (Biodiversity of Southeastern Peru)*. Editorial Horizonte, Lima, Peru. 679 pp.
- STORK, N. E. 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* 35:321–337.
- SYSTAT. 1992. Statistics, version 5.2 edition. SYSTAT Inc., Evanston, Illinois. 724 pp.
- WILKERSON, R. C. & G. B. FAIRCHILD. 1985. A checklist and generic key to the Tabanidae (Diptera) of Perú with special reference to the Tambopata Reserved Zone, Madre de Dios, Perú. *Rev. Peru. Entomol.* 27:37–53.

*Received for publication 24 July 1998; revised and accepted 9 April 1999.*