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Comment

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How many species are there? Today, this question transcends the discipline of taxonomy, where it was perhaps first asked by Westwood (1833) and more recently by Sabrosky (1952), reaching across science through conservation biology to the media, even to religion (Cobb 1988). Gaston's article in this volume (pp. 283–296) makes another attempt at trying to guess the near-imponderable. Determining the number of species is like reaching for the stars; there is no way with the data available today that we are even going to get reasonably close. Perhaps what is more important now is not so much the numbers, but how we go about data gathering and making analyses necessary to estimate the order of magnitude with a significant level of confidence.

Westwood (1833), in a pre-Darwinian approach to the results of creation, began with the number of species described by Linneaus and compared rates of new descriptions and those species known to be new in the collections. His estimates are thus based on the products of taxonomists doing their job rather than species living in nature. This approach continued to be perused until 1982, and it now has been resurrected in the present volume. Westwood also introduces the idea of relative abundance among groups as a source of data for biodiversity estimates; but with so few species known from so few areas in the year 1833, his conclusions are hopelessly naive. Metcalf (1940) also used the number of described species and the rates of new descriptions each year to arrive at an estimation of the number of species. Then he attempted to establish ratios of Homoptera to other insect taxa to arrive at an estimation of species numbers. Sabrosky (1953) relied too on published species descriptions for his estimates, much the same as Metcalf. White (1975) used taxonomists' products to generate species accumulation curves thinking he was obtaining an asymptote that reflected biodiversity estimates for beetle families.

On the other hand, as pointed out by May (1988), a totally different agenda was set up by me (see Erwin 1982) for asking pertinent questions in a scientific way, that is, hypothesis testing using data on how arthropod communities are assembled in nature and the numbers of species in these assemblies. I might add to May's insights here by *again* (Erwin 1988) pointing out that the estimate of 30 million species in my 1982 paper was set up as a testable hypothesis, not, as Gaston puts it, a "claim" that there are this many species. Each step of my process can be independently tested, weaknesses found and corrected, etc., and these tests (host specificity, relative species abundance between beetle families, canopy versus undercanopy species, etc.) are now underway in my laboratory at the Smithsonian Institution with enormous new collections gathered to ask the questions in the right way. There will be more on this in a subsequent article in this journal.

Gaston, however, takes another approach. He decided that, in addition to the literature approach of Westwood and others, the specialists in various taxonomic groups should be consulted to give their opinions on how many species remained to be described in their taxonomic specialties. He then added the number of species already described in the literature to arrive at a total number. The total of these figures is used to refute the number of species that was suggested by my field-gathered data and subsequent analysis. Gaston's Figure 2 summarizes his findings. What is wrong with this method?

The data base is nonscientific; it cannot be tested, therefore it cannot be used to test any other methods. Gaston's data base is an anecdotal one that rests on the experience and collections of various workers. How did his experts get their data to give him the estimates? We don't know. Since all those listed are good taxonomists, we can guess that they based their estimates on their own collections (mostly institutional), the collections they borrowed and visited in the past, and their own field experiences, but how they arrived at the numbers to give Gaston is unexplained. One source, P. Hammond of the BMNH, for example, told me in 1986 that he thought there were more than a million species of staphylinid beetles, but later told Gaston for this paper, 300,000 species. Another source, N. Stork, gave a number of 30,000 described carabid beetles, but all the literature for this family cites 40,000, except for one given by J. Lawrence who is not a carabid specialist. The point is, from where do all these numbers come? The answer is, from people, people who are guessing.

There are numerous problems with using published taxonomic information, opinions, and current collections as a data base. For example, as Gaston rightly points out, the literature is full of synonyms and these vary greatly between groups. Researchers differ in their opinions as to what constitutes a species. Adis (1990) and a host of mosquito taxonomists have shown that we "morphological" taxonomists may have significant problems with this. In forming opinions about our respective groups, we are limited by the collections we have studied, our methods of study, our reliance on past literature, which may or may not be anecdotal, taxonomic group bias (my group is bigger!), and lack of consistency between workers. Collections in museums today represent neither the incredible diversity found in tropical forest canopies nor the mosaic of forest types found in the Amazon Basin and its western foothills.

Further, an analysis of the distribution of Gaston's data sources shows that he consulted with 46 taxonomists of widely varying ages and experience, all of whom live and work in the North or South Temperate Zones, none in the tropics. Although several of these taxonomists perhaps have visited the tropics on one or more occasions, only five are known to me who have visited the Amazon Basin, and only one of these has been there repeatedly (but to only one site). The others have no first-hand appreciation of biodiversity in and across the Basin, let alone how that diversity is distributed across the myriad of soil types and microhabitats in even a small sector. Thus, Gaston's anecdotal data is overwhelmingly skewed by taxonomists of temperate faunas who know tropical groups mostly through collections made in the past century or more recently from collections made on two or three small Indonesian Islands, or perhaps at a locality or two in Africa, all of which are depauperate compared with the Neotropical Realm (Erwin, in preparation). Another interesting point is that Gaston wrote letters to many taxonomists requesting information. We see he received at least 46 responses. But, how many responses from taxonomists were not used and how many said there is no way to estimate how many more species were in their group? I believe Gaston's approach here needs no further comment. It is anecdotal; it is a measure of human activity, thus it is simply not a scientifically valid method either to arrive at a sound estimate or to test estimations based on field data.

What else might we glean from Gaston's paper that would lie in the realm of science? His discussion, following that of Westwood, of relative abundance of species in the major orders might offer something that could be used in a scientific/statistical approach to the question, if we knew enough about one major order and used it to compare relative abundance of species in other orders in our samples. Unfortunately, we still do not have a base in even one order and are not even close. More to the point however, is that the variation between sites in relative abundance would require a tremendous data base of site-inventories to appreciate the variation. In my neotropical canopy samples, Diptera are *often* more numerous in individuals in wetter forest than dry ones (but not always) and sometimes "overwhelm" the visual aspect of the sample, but in terms of species present they do not even approach the Coleoptera. Ants always constitute 50% or more of the individuals in the samples, but about 60 species is maximum for any one tree canopy, while 500 to 1,000 beetle species will share the same tree. Relative species abundance might lead to more reasonable estimates if enough measurable samples from enough microhabitats were available. Unfortunately, they are not.

Gaston feels that the contribution of canopy specialists to global biodiversity may be less than suggested, but destroys his own case by showing that his data set (actually Peter Hammond's) was collected in ecotonal areas. Actually, the contribution of canopy to non-canopy is significant in the neotropics, as will be amply demonstrated (Erwin, in preparation). For now, let us look at only one family, the Carabidae, well known to be common "ground beetles." At the latitude of Washington, D.C. 7% of the species are arboreal; in Panama, 49%; and at Pakitza, Peru, 40% are already known to be arbicolus and that definitely will increase when more fogging is done. Arbicolus adaptations are derived in this predaceous beetle family. Why are so many tropical species canopy specialists? One hypothesis is that there is plenty of food (i.e., other insects).

Gaston's "taxonomist approach" leads him to the conclusion that the proportion of undescribed species encountered by his taxonomists is insufficient to support high richness estimates. Unfortunately none of his experts have studied Neotropical canopy samples. Let us look at just the Carabidae from one Peruvian site (Erwin, in press). This is a well known family relative to others; H. W. Bates lived on the Amazon for 11 years collecting, and spent many more describing what he got, or sending material to Chaudoir and Putzeys who also vigorously described new species. My survey at Pakitza, Peru (17 manweeks collecting), only 1,200 km from Bates' favorite site at Tefé (Ega), has turned up 569 species in 118 genera. At least 55% are undescribed.

Another point made by Gaston is that of distribution of tropical species. Of course there are widespread species, but the question is what percent are widespread and what is the nature of the species that are not widespread. Various large data sets suggest that larger species have broader geographical ranges than small ones (Pogue, pers. comm.). For example, of the 1,939 species of moths sampled by Pogue at Beni, Bolivia, and Pakitza, Peru (500 km apart but both in the Amazon Basin), 3.2% of the species are shared (Table 1). Of the 1,080 species of beetles sampled at Manaus, Brazil, in four forest types, only 1% was found in all four sampling sites a mere 67 km (or less) apart (Erwin 1983*a*). Further, small species, which are more geographically restricted (Table 1), are vastly more numerous in canopies of tropical trees than large ones (Erwin 1983*a*, 1983*b*), and small species is where the major part of biodiversity lies. Gaston's conclusions in this regard are the result of not looking at the available data rigorously and of not looking at neotropical canopy samples personally.

Since "biodiversity—what are we losing?" seems to be a burning issue in political and scientific circles and the answer is critical to conservation strategy (Erwin 1991*a*), it is incumbent on taxonomists and field biologists to supply the underpinning data base. How might we go about this and obtain scientifically valid results within a reasonable timeframe?

Data must be obtained from the field directly and it must be in a context that allows appropriate questions to be asked. It does not matter if species are named; what matters is that they exist. Samples must be comparable across the globe and they must be tied to specific measurable environments (habitats and microhabitats) in the context of co-occurrence (Erwin 1991*b*). For the most part, vertebrates are easily inventoried and do not contribute much to total biodiversity. Insects, their allies, and perhaps nematodes and fungi constitute most of the biodiversity of earth exclusive of bacteria, etc. Insects and their allies are incredibly speciose everywhere, especially in the tropics; the others, at this point in time, are questionably so in the tropics. A sound estimation of the number of insect species likely will provide the order of magnitude of all earth's biodiversity. How, then, do we sample the insects and their allies?

Table 1. Shared species of moths between Beni, Bolivia, and Pakitza, Peru (data courtesy of Michael G. Pogue).

Beni: 933 species, 1748 individuals prepared.
Pakitza: 1006 species, 1731 individuals prepared.
60 species (3.2%) shared.

Selected Families

MICROLEPIDOPTERA	MACROLEPIDOPTERA
Gelechiidae: 1.4% shared.	Noctuidae: 1.4%
Cosmopterygidae: 0 shared.	Arctiidae (all): 10.8%
Oecophoridae: 2.2% shared	Arctiidae, Lithosiinae: 18.8%
Tineidae: 0 shared	Notodontidae: 5.2%
Pyralidae: 3.2% shared	Geometridae: 6.6%

Before inventorying, we must know the physical parameters of the sampling environment and the distribution of these locally and across each biome. For example, one important guild of insects uses the clumps of suspended dry leaves clinging to a fallen tree branch that didn't fully reach the ground when it broke off the tree. Microhabitats (Erwin 1991*b*) such as this can be repeatedly sampled, and accumulation curves established for each family-level or other appropriate taxonomic category and for trophic groups. Sampling can continue until the target taxa have reached an asymptote on the curve. All microhabitats in each habitat can be sampled at the area of study and the behavior of the curves watched. Pairing of microhabitat data sets across habitats measures utilization of the environmental grain by a taxon or trophic group. When one site is well enough known, a second site can be sampled, etc., and data sets paired and compared until a regional grid of collection sites is well known. Of course, at each site seasonal samples are required too. Sampling procedures must extract *all* individuals from the microhabitat so that the sample can be compared with similar samples from other habitats, seasons, and areas. Insecticidal fogging (Erwin 1990), berlese funnels, and photoeclectors are appropriate as they take everything in the targeted microhabitat, although berlese is destructive to microhabitat architecture. Use of this strategy allows comparability, tracking of species accumulation, and testing of results at any point in the sampling regime. Collection and analysis of beetle samples and preparation of voucher specimens requires 48 manhours per thousand species; at a site near Iquitos, Peru, 25 m^3 of suspended dry leaf-clump material contained 1,300+ species.

On the other hand, air is not a "habitat," therefore malaise traps, nets, and UV lights are methods of sampling that are difficult to use for biodiversity estimates because in order to reach the asymptote for any locality, nearly all species at the general locality using airspace would need to be recorded and one would still not know if the species captured actually lived in the area.

Finally, and it is the first point with which I fully agree with Kevin Gaston, perhaps it does not really make any difference exactly how many species there are. The world is losing them at an astounding rate along with their habitats, and we humans are responsible. Now that the problem has been recognized and a bleak future forecast if policy changes are not made, we must all do our part in changing policies and stopping the carnage. In terms of potential extinctions, if the weight of higher species numbers is greater on the collective human conscience, then so be it. For this reason, I'd rather err on the high side.

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We will publish a concluding response to Dr. Erwin by Dr. Gaston in our December 1991 issue.—Editor