Amazonian biotic data and conservation decisions

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We evaluate the utility of museum collections for conservation decisions by comparing recently assembled data sets on various taxa to an Amazonian indicator taxon, primates. Our data include one group of amphibians, two groups each of fishes and flowering plants, and four groups of terrestrial arthropods. In contrast to many other Amazonian groups, the taxa analyzed here and the primate indicator group are well-known taxonomically (few to no known undescribed species, no nomenclatural problems). We apply a suite of statistical and graphical methods designed to detect undersampling bias and nonrandom geographic patterns in the data. Our results indicate that: 1) Some of the taxa in our data set are adequately sampled at the species level, others are not; and 2) all geographic ranges appear to be undersampled, including those for the indicator group. Currently available data adequately determine species richness at the level of the Amazon basin for heliconias, the plant genus *Talisia*, heliconiine and ithomiine butterflies, certain fish genera from both large and small rivers, the frog genus *Leptodactylus*, birds, and primates. In contrast, present data are inadequate for the arthropod genera *Agra*, *Batesiana*, *Deinopis*, and *Hemiceras*. We recommend that similar suites of analytical techniques be used routinely to assess the adequacy of data prior to their use in making conservation decisions. We conclude that museum data are adequate to use for conservation purposes for certain Amazonian taxonomic groups, which is an encouraging finding. For taxonomic groups with data that fail the adequacy tests, we recommend a bottom-up approach of analysis using expert evaluation of the available data.

A utilidade de coleções de museu para decisões acerca da conservação ambiental foi avaliada por meio da comparação entre dados recentes de vários taxa e um taxon bem estudado de primatas da Amazônia. Os dados incluem um grupo de anfíbios, dois grupos de peixes, dois grupos de plantas fanerógamas, e quatro grupos de artrópodes terrestres. Ao contrário de muitos outros grupos amazônicos, os taxa analisados e o grupo de primatas são taxonomicamente bem entendidos (com poucas ou nenhuma espécie não-descrita e sem problemas de nomenclatura). Um conjunto de métodos estatísticos e gráficos foi aplicado aos dados para detectar desvios produzidos por amostras insuficientes e padrões geográficos não-aleatórios. Os resultados indicam que: 1) Alguns dos taxa do nosso conjunto de dados são adequadamente amostrados em nível de espécie, outros não; e 2) para todos os grupos as distribuições geográficas parecem incompletas, inclusive as do gru-

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po de referência (primatas). Os dados disponíveis no momento indi-
cam adequadamente, em nível da bacia do Amazonas, a riqueza de
espécies de helicônias, plantas do gênero **Talisia**, borboletas
(Heliconiinae e Ithoniinae), alguns gêneros de peixes tanto de grandes
como de pequenos rios, anfíbios do gênero **Leptodactylus**, pássaros e
primatas. Ao contrário, os dados disponíveis no momento não são
adequados para os gêneros de insetos e aranhas **Agra, Batesiana,
Deinopis**, e **Hemiceras**. Recomenda-se que conjuntos semelhantes de

técnicas de análise sejam usados rotineiramente para avaliar a ade-
quação dos dados antes de se fazer uso dos mesmos em decisões de
conservação. Conclui-se que para certos grupos taxonômicos da Ama-
zônia, as coleções de museu são adequadas para utilizar para fins de
conservação ambiental, o que é encorajador. Para os grupos taxonômi-
cos que se mostrarem inadequados nos testes, recomenda-se uma aná-
lise detalhada e cuidadosa da informação disponível usando-se avali-
ações de especialistas dos grupos.

The world's museums contain over two billion speci-
mens (1), the largest source of scientifically verifi-
able evidence on the Earth's biota. To an alarming
extent these data are all we reliably know about the
distribution and abundance of most species. Although each
specimen and its associated data are potentially useful for
conservation (and comprise all the data we are likely to have
in the short-term for many groups), museum data are gener-
ally assumed to be biased in various ways, even if those
biases are rarely quantified. Species lists are suspected to be
incomplete because most groups are undersampled, but to
an unknown extent. Apparent species ranges may be both
undersampled and biased by patchy, nonrandom collecting.
Even if collected, species may remain undescribed,
misidentified, erroneously synonymized, or inaccurately de-
limited from other closely related species. All these errors
prevent production of the accurate maps on which sound
conservation decisions depend. Such problems are legendarily
severe in the Amazon basin (e.g. References 2,3,4), the focus
of this paper.

One way around these problems is to use a theory that
predicts speciation and distributional patterns for all organ-
isms in the region of interest in hopes that its predictions
yield a realistic picture not obvious from the raw data them-
selves. For example, the forest refugia model (5) hypoth-
esized historical processes that should have affected all bi-
otic distributions in Amazonia. During peak glaciation
cycles, the climate in most of the Amazon basin is thought
to have been cooler and drier. The predicted consequence
was that the rain forest contracted to islands of habitat, or
refugia, within which differentiation of the isolated taxa took
place. Based originally on bird data, the model predicted
that the conservation of these refugia would be particularly
effective in conserving the forest-associated biota. How-
ever, refugia predicted from distributional data of other
groups did not coincide convincingly with the bird-predicted
refugia (6,7). Since the forest refugia hypothesis, other
equally plausible hypotheses have been invoked to account
for the historical and recent distributions of the Amazonian
biota (e.g. Reference 8). None of them are so convincing
that conservation decisions should be exclusively based
upon them.

A more common circumvention uses just those few
groups for which distributional data are thought to be rela-
tively complete and relatively unbiased to set priorities
(biodiversity indicator species as defined in Reference 9).
For Amazonia, primates, birds, and certain butterflies are
generally considered to meet these criteria. Like general theo-
ries about lineage diversification in the basin, this approach

also assumes that speciation and distribution patterns of
lesser known groups correlate well with the best known
groups. Others make the same kind of assumption on a glo-
bal basis (10). For purposes of this paper, we refer to this as
the indicator taxa approach, and the purportedly well-un-
derstood species that serve as proxies for the entire biota as
indicator species, taxa, or groups. The indicator taxa ap-
proach shares with the first approach the notion that groups
covary, although it does not specify why. Even absent evi-
dence of covariation, the indicator taxa approach may still
be justified simply because the indicator taxa data, by defi-
nition, are most complete and free from the biases discussed
above.

But how are such indicator taxa defined? What quanti-
tative criteria might place taxa (or, more exactly, our knowl-
edge of taxa) along a continuum from lesser-known to indica-
tor status so that more than just human favorites such as
primates, birds, and butterflies might support conservation
decisions?

Evaluating the completeness of inventories, lists, distri-
bution maps, and the like, whether for the species of a local
community or whole lineages at regional or global scales,
involves the same general statistical problem—estimating from
a sample the number of unknown classes in a statistical popu-
lation (11). The question is, how complete is the sample? This
problem has been the focus of increasing theoretical and em-
pirical research with encouraging results (12-24).

We have been working with the neotropical lowland biota
and are interested in methods of objectively evaluating spe-
cies-level distributional data for use in making conservation
decisions. We are particularly concerned with assessing sam-
pling completeness for areas where most of the biota is still
poorly understood, such as Amazonia. For such areas, even
rough, heuristic methods that help to evaluate knowledge of
taxa would be useful.

In this paper we use statistical and graphical criteria to
evaluate the data assembled during our taxonomic revision-
ary work on ten Amazonian groups of vertebrates, plants,
and arthropods; we compare the results to those obtained
from Amazonian primates, a well-known indicator taxon. If
data on species richness (total number of species) are ad-
equate for conservation purposes at the scale of the entire
Amazon basin for the indicator taxon, and any of our data are
comparable, then our data should also be considered in con-
servation decisions. Our analyses indicate that at finer scales
(e.g. detailed distribution maps of small areas), even indicator
taxa data may be inadequate. Faced with the reality of having
partial data to make local conservation decisions in Amazonia,
we propose a protocol for resolving this dilemma.

A precise definition of "Amazonia" is to some extent arbitrary. For this study we defined Amazonia as the combination of the "Domínio equatorial amazônico" and the "Domínio Roraima-Guianense" on Ab'Saber's (25) map. We included any species with a significant portion of its distribution (> incidental) within Amazonia and below 350 m. Some of these Amazonian species are truly rare in collections (i.e. few records in total are known for a species), but others are rare only within Amazonia (i.e. many more records for the species outside Amazonia exist). In order to assess the impact of our definition of Amazonia, we also recorded all extra-Amazonian localities for the species in the dataset.

The taxa

We selected taxonomically well-understood groups (usually genera) from our own ongoing systematic revisions, based on collections from the entire geographic range of the taxon. It is worth emphasizing that our taxa are well understood taxonomically but are poorly to moderately sampled geographically.

Data were assembled for three genera of plants:

Phenakospermum (Zingiberales, Strelitziaceae), a monotypic neotropical genus, is an arborescent herb widespread in Amazonia (26). These distinctive palm-like plants grow to over ten meters in height and occur in transitional habitats between tall rain forests and open areas of savanna and cerrado (27). Data are from 27 specimens.

Heliconia (Zingiberales, Heliconiaceae) contains approximately 225 species, of which 95% occur from Central Mexico to northern Argentina (28). These often large herbaceous plants are a conspicuous component of the flora of lowland primary and secondary tropical forests. Thirty two species (including two undescribed taxa) known from Amazonia are included in this analysis (29,30,31,32), taken from 822 specimens. Although most of these species are restricted to this biogeographic area, the main distributions of several species occur elsewhere in the Neotropics. Amazonian *Heliconia* are relatively well-known taxonomically (31,33).

Talisia (Sapindaceae) in the Amazon contains 36 species, all of which are included in our analysis, based on 411 specimens. These species occur within the Amazon basin, with a few extending into surrounding non-Amazonian lowlands. *Talisia* are monocaulous shrubs to large trees mostly of nonflooded lowland forest (< 500 m elevation), but also occur in seasonally flooded varzea forests. They are scattered throughout the forest, never dominating the habitats in which they occur. About 70% of the taxa used for this analysis are taxonomically well understood, but 30% are incompletely known from fragmentary collections. Twelve taxa are currently known from more than ten collections, while the vast majority (30 species) are known from less than eight collections; seven are known from one collection only.

Data were assembled for Amazonian representatives of six arthropod taxa: Four beetle genera, one moth genus, and one spider genus.

Agra (Carabidae, Lebiini) to date contains 101 species with ranges within Amazonia. Distributional data extracted from 348 specimens were included in the data set (34-40). *Agra* extends from southern Texas to northern Argentina, and is estimated to contain more than 2,000 species, 464 of which are described. It is the largest known monophyletic generic-level lineage among predatory beetles. Possibly due to undersampling, very few species are known to have extensive ranges. Even where canopy fogging has been used in the western Amazon basin for more than two decades at nine scattered localities, most *Agra* species are known from single localities, implying high species turnover or beta diversity.

Batesiana-Geballusa-Gouleta (Carabidae, Bembidiini), a monophyletic lineage of three closely related genera, contains 65 species, of which 26 occur in Amazonia. Members of this lineage are associated with tree trunks, lianas, branches, and twigs, either standing or decaying on the forest floor. Co-occurrence of as many as eight species at a site is common in the western Amazon basin. Distributional data were extracted from 1,990 specimens.

Hemiceras (Lepidoptera: Notodontidae) is a large group of conspicuous, exclusively neotropical moths, containing 230 species. Amazonia to date has 106 species of *Hemiceras*. Species can be either widespread or restricted and, for an insect, are commonly collected. *Hemiceras* have been reared upon Leguminosae, the most important neotropical tree family, especially from *Inga* (41). Distributional data were extracted from 2,250 specimens.

Deinopis is a poorly known pantropical spider genus. Six of the 15 neotropical species are undescribed. *Deinopis* are stick mimics by day and web-spinning sit-and-wait predators by night. They are among the largest of web-spinning spiders, but appear to be comparatively rare both in nature and in collections, and are certainly difficult to collect. The six Amazonian *Deinopis* species are represented by only 69 specimens from 55 localities.

Data were assembled for Amazonian representatives of one genus of frogs, two groups of fishes (one typical of large rivers, the other of small river systems), and 37 species of platyrrine monkeys.

Leptodactylus is a neotropical frog genus with 14 well-defined species occurring in the Amazon basin. Data were extracted from Heyer (42,43,44), supplemented by museum data obtained after the respective revisions were published. A few other species of *Leptodactylus* occur in Amazonia, but neither their species limits nor distributions are well defined at present (e.g., *L. didymus* and *L. mystaceus* are diagnosable only by advertisement calls and have poorly understood distributional limits) (45). The 14 *Leptodactylus* species occur collectively in forests and open habitats. They are often common and easy to collect; their distributions are among the best understood for frogs in Amazonia. Data extracted from revisions are based on examination of more than 5,600 individuals.

Steindachnerina and *Cyphocharax* (Curimatidae) (46,47), *Boulengerella* (Ctenoluciidae) (48), and *Caenotropus* (Chilodontidae) (49), are four fish genera characteristic of large rivers. Thirty-three species of *Steindachnerina* and *Cyphocharax* are distributed within the Amazon basin, but some range beyond the basin. These detritivorous curimatids

inhabit diverse habitats in lowlands and lower elevations. Amazonian *Boulengerella* comprises five species of large predatory characiforms, again typical of large rivers. *Caenotropus* is a lineage of herbivorous and sponge-eating fishes. The data for these three groups are among the most thorough for any broadly distributed Amazonian fishes. Data are based on 785 specimens of *Boulengerella,* 1,620 of *Caenotropus,* 4,101 of *Cyphocharax,* and 1,221 of *Steindachnerina.*

Nannostomus (Lebiasinidae, Nannostomina) is a genus of small river fishes with 15 well delimited species in the Amazon basin, six of which range either into the Rio Orinoco basin and/or into the Guianas. Data are based on 1,706 specimens. Distributional data are from published (50-55), and some previously unpublished records. Most *Nannostomus* species inhabit lowland forests, often slow moving blackwater or clearwater streams. Some species occur in lowland savannas and at least two can also be found in slow moving whitewater channels along the Rio Amazonas. Data are adequate to include 7 species from the lebiasinid tribes Lebiasinini and Pyrrhulinini. One species of Lebiasinini occurs in the Amazon basin along the eastern base of the Andes in Ecuador and Peru. The Pyrrhulinini are widely distributed throughout the Amazon with some species extending beyond the basin. All species in the group are small, primarily insectivorous fishes occurring mainly in quiet backwater portions of small forest streams in clear or blackwaters. A few inhabit lakes, close to shore, and swamps and small streams in savanna areas. Data for Lebiasinini and Pyrrhulinini are based on 3,318 specimens.

The final data set for this study includes neotropical primates, thus permitting direct comparison of the above taxa with an indicator group. Data from 37 primate species based on at least 4,500 specimens collected in 2,055 localities in Central and South America were extracted primarily from Hershkovitz's revisions (56-64).

The distributional data were assembled in final fashion on 27 June 1995. Few new locality records or taxonomic refinements have appeared since then, and these do not materially affect our results or conclusions.

Analysis

For mapping and other geographic purposes we chose the Plate Caree projection as a base map for three reasons. First, it minimizes distortion in the equatorial region. Second, it correlates precisely with the maps in Cartesian space produced by statistical programs. Third, it permits later grid- or raster-based analyses of the area. The coastlines, rivers and political borders were derived from the Digital Chart of the World, generalized to a scale of 1:25,000,000 using the MundoCart program (65).

To produce point maps of species or taxa we used museum locality data to determine longitude and latitude to the nearest minute, and converted these values to decimal degrees as used by the Arc/Info GIS program. A minute of either latitude or longitude at the equator is roughly 1.8 km.

Each distinct combination of latitude and longitude in the data was considered a distinct locality. Multiple collections or specimens of the same species (or subspecies, in some cases) with the same coordinates represent repeat collections from the same locality. The data set was thus a list of all observed localities for all taxa. From these data we calculated: *a)* The total species richness at a locality (again, to the nearest minute); *b)* the number of unique collecting localities (which might include various taxa); and *c)* the total number of distinct records (two species from the same locality represent two records).

As noted above, we included the extra-Amazonian localities for a species if part of its range fell in the Amazon basin, in order to assess the effect of our definition of the Amazon. The graphical criteria we wish to apply (19) require that point data be grouped in samples or quadrats. We chose one-degree on a side (latitude or longitude) cells as sample units. One degree at the equator of either latitude or longitude is roughly 111 km. As we have defined it, Ab'Saber's *Amazonian morphoclimatic domain* (25) contains all or part of 472 grid cells. If a grid straddled the domain boundary, all localities within the grid were included in the dataset.

We used EstimateS, version 5.0.1 (19) to assess the degree of undersampling and spatial aggregation (clumped collecting effort) in the data. This program computes randomized species accumulation curves, and reports the mean of various statistics based on those curves. It includes a variety of species richness estimators and graphical techniques to detect patchiness in data. For each estimator Pielou's (66,67) pooled quadrat method is used to depict graphically the behavior of the estimators and indicator of patchiness as sample size increases (20). In the ideal case of a complete inventory, the observed species accumulation curve climbs asymptotically to the true species richness in the area being sampled, but the estimators asymptote much sooner than the observed curve.

EstimateS includes richness estimators based either on relative abundance or incidence. Abundance-based estimators require relative abundance of species within and between samples. Incidence-based estimators require just presence/absence of taxa within quadrats or samples. While the number of times a species has been found at a particular locality is often viewed as a measure of its relative abundance, accurate measures of relative abundance are notoriously difficult to obtain and are more likely to be biased than incidence data (68,69). We prefer to be conservative and treat the data as a matrix of presence/absence scores of species by Amazonian localities. Therefore we used the incidence-based Chao2 estimator (13,20) and incidence-based coverage estimator ICE (13,16) to estimate species richness and to assess undersampling bias. Both estimators augment the negatively biased observed richness by a factor that depends on the presence of and distribution within samples of "rare" taxa. By definition, when all species in an inventory have been observed multiple times (i.e. are not "rare"), the inventory is complete. Conversely, inventories replete with "rare" species underestimate true richness. For the Chao2 estimator, "rare" species are those observed in only one or two samples; once all species are known from two samples or more, the estimate

will equal the observed richness. The ICE estimator is more complex and uses more information than just ones and twos, but the logic is basically the same. We used EstimateS, version 5.0.1's default values for number of randomizations and cutoff values for coverage-based estimators (50 and 10, respectively).

Although these richness estimators are nonparametric, they do assume random sampling. Unfortunately their sensitivity to departures from random sampling has not yet been studied, particularly as regards species accumulation curves and the like. Given the well-known difficulties in accessing the more remote regions in the Amazon basin, the random sampling assumption is unlikely to be valid, even for the primate data. In practice it is difficult to distinguish between real and artifactual spatial aggregation in data, because biological populations and species ranges are, in fact, very often spatially aggregated. This, of course, makes a truly random sample (equal probability of sampling each individual) difficult, if not impossible, to achieve (68,69,70,71). Furthermore, biologists in general, much less museum collections, do not usually track evidence of absence, which is thus difficult to distinguish from absence of evidence. Much sampling effort in the Amazon has not been recorded (see below, however). It does seem likely that museum data on rarer species is relatively less biased than for more common species, because collectors tend to skip common and concentrate on rare or unusual taxa. Museum collections do represent the sum total of a huge number of statistically independent events that vary in all kinds of ways. Perhaps a more practical question is how to measure the effects of spatial aggregation on species accumulation curves and estimates of species richness, rather than to what extent it is real or artifactual.

EstimateS 5.0.1 includes techniques to assess graphically the degree of spatial aggregation in data. A Coleman curve (17,18) randomly reassigns specimens to samples, and then recalculates the species accumulation curve. Any aggregated pattern in the data, real or artifactual, is destroyed, which thus yields a "null" curve based on random placement. If the empirical curve (mean of randomized accumulation curves without reassignment of specimens) differs substantially from the Coleman curve, then aggregated occurrences of species in particular and/or adjacent samples affects the shape of the accumulation curve, which in turn will affect estimates of species richness based on it. Conversely, if the empirical and Coleman curves are nearly the same, then aggregation in the data is less of a problem for statistics that depend on the empirical curve. We used Coleman curves to detect spatial aggregation in the data for all studied groups, including primates. We also calculated the Poisson index of dispersion to test for spatial aggregation (71), although, as noted above, this cannot distinguish between real and artifactual aggregation.

In summary, primates are an indicator taxon in the sense that they are generally considered to be well-known taxonomically and well-collected throughout the Amazon basin. The above criteria provide a means to evaluate objectively data of this sort for application to conservation decisions. When applied to the primate indicator taxon data, these statistical/graphical approaches provide a standard against which data on candidate groups can be compared.

The total data set contains 6,271 records, representing 422 distinct taxa among 3,930 unique localities. Of these, 4,455 records (2,618 unique) are within the 472 Amazonian one-degree grid cells (Table 1).

Our individual data sets vary considerably in terms of number of species included, number of localities known for the species involved, and the number of species known from a single locality in Amazonia (Table 1). As such, they are broadly representative of Amazonian biotic data.

Table 1 - Characterization of Amazonian species/distributional data broken down by taxonomic groupings.

Taxon	Total species	Total records	Mean records per species	Maximum records any species	Total unique localities	Total Amazonian records	Total unique Amazonian localities	# Of species known from one record	# Of species known from one grid cell
Arthropods									
Agra	101	155	1.5	9	85	148	85	70	71
Batesiana group	26	116	4.5	28	54	115	53	7	7
Deinopis	6	37	6.2	12	36	12	12	1	1
Hemiceras	106	888	8.4	37	319	374	81	22	22
Vertebrates									
Leptodactylus	14	942	67.3	202	756	615	455	1	1
Primates	37	2002	54.1	189	1372	1537	980	1	1
Large river fishes	41	719	17.5	64	489	628	414	1	1
Small river fishes	22	262	11.9	33	234	251	223	1	2
Plants									
Talisia	36	319	8.9	62	275	234	191	5	6
Zingiberales	33	831	25.2	58	643	541	403	1	1
Grand total	422	6271	11.8	202	3930	4455	2618	110	112

As expected, primates are known from many more localities than any other taxon (2,002 in all, 1,537 in Amazonia). The next most collected taxa are known from about half as many localities (Table 1). The collecting intensity for primates is high (54.1 localities per species). Despite only half as many localities as for primates, the frog genus *Leptodactylus* has been collected more intensely (67.3 localities per species (Table 1)). All primate species but one are known from two or more localities, but this is also true of six out of the ten other groups in the data set. By these measures the primate data are not markedly different from some of the other groups included here.

Amazonia is unevenly sampled. When nonprimate localities are plotted for all 385 taxa, the historical impact of primary access to Amazonia by major rivers is obvious (Fig. 1). Botanists do seem to have made a greater effort to collect between major rivers.

Undersampling bias

Statistical and graphical tests for undersampling bias conform to our a priori, intuitive expectations (Fig. 2). For ex-
ample, of all taxa treated here, the carabid genus *Agra* probably has the most species, and is relatively the most undersampled. The set of curves in Figure 2A has a number of characteristics that confirm this impression. First, the empirical species accumulation curve (Sobs) is nearly linear. Second, the gap between it and either richness estimate (ICE and Chao2) is so large that even the richness estimators, which attempt to correct for undersampling bias, are probably still, at best, lower bound estimates. Third, the curves for uniques and duplicates (species occurring in just one or two samples (19), respectively) increase monotonically. The vast majority of reasonably pristine species ranges include at least two distinct museum localities (i.e., latitudes or longitudes differing by one degree or more), so this is, again, good evidence of undersampling. The abundance of "rare" species (uniques and duplicates) in the sample suggests that many more species of *Agra* await discovery, and that the ranges of the known species are probably grossly underestimated.

In contrast the primates, zingibers (*Phenakospermum* and *Heliconia*), the frog genus *Leptodactylus*, and large river fishes show signs of being relatively well-known (Figure 2E,G,I,K). The richness estimates and the observed species curve essentially coincide and are nearly flat by the end of the sample.
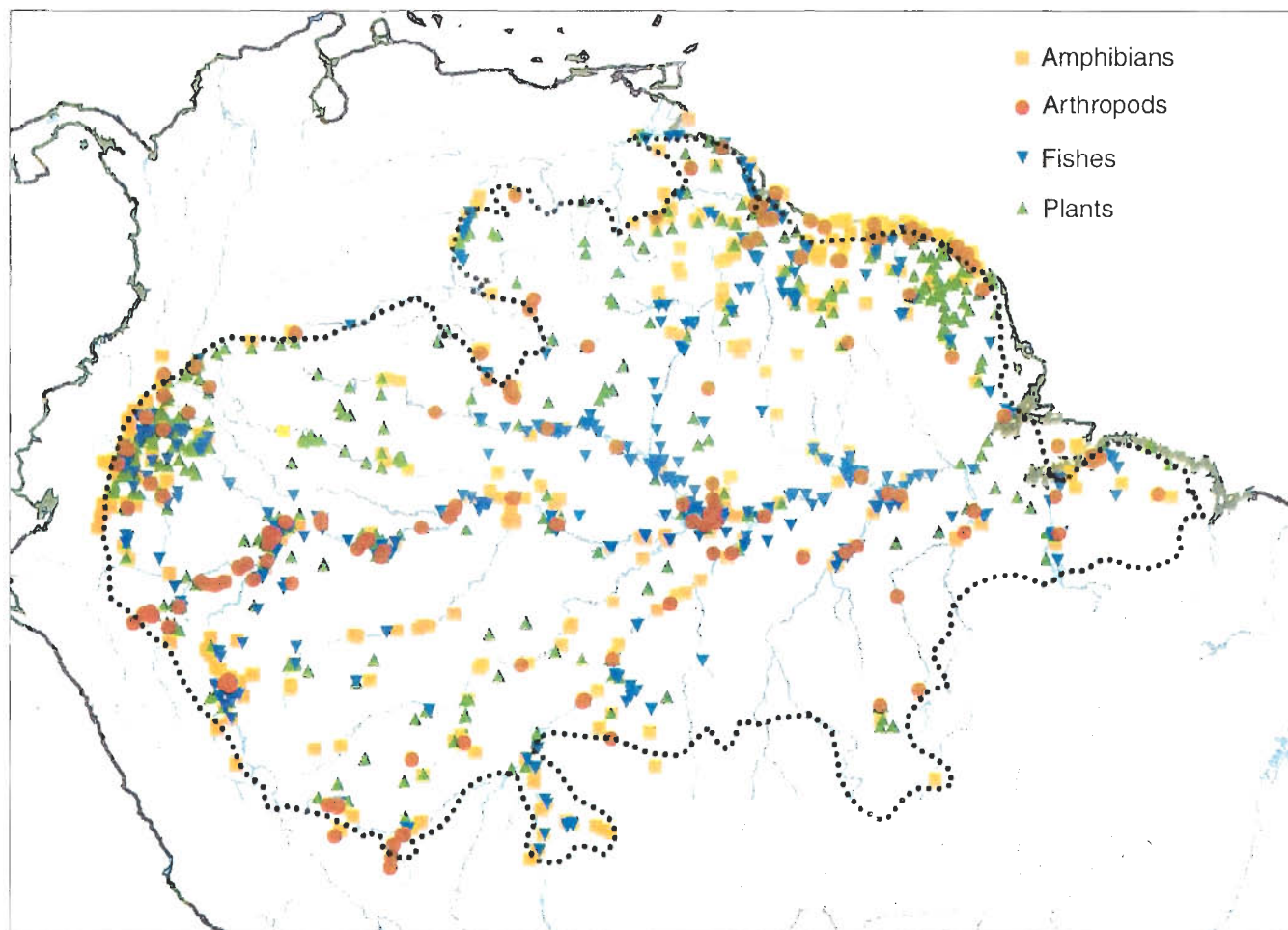

Figure 1. Localities of nonprimate taxa in Amazonia: (squares) all fishes; (triangles) all plants, (circles) amphibians, (stars) all arthropods.
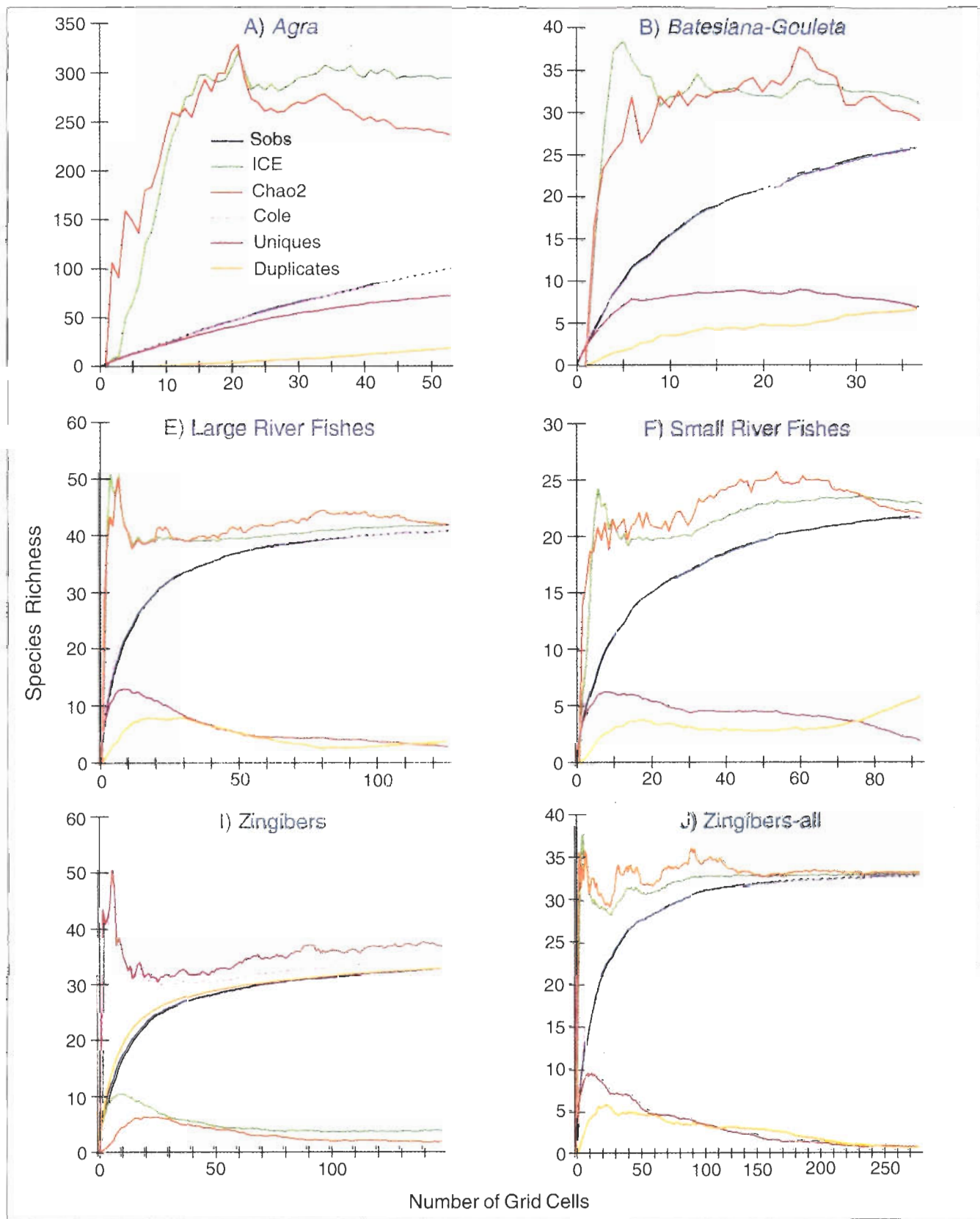
Figure 2. Species richness estimators and patchiness indicators for (A) species of the canopy beetle genus Agra, (B) species of terrestrial beetles of the **Batesiana** group, (C) moths of the genus **Hemiceras**, (D) spiders of the genus **Deinopis**, (E) species of large river fishes, (F) species of small river fishes, (G) species of the frog genus **Leptodactylus**, (H) species of the plant genus **Talisia**, (I) Zingiberales based on localities of species delimited within Amazonia, (J) all Amazonian and extra-Amazonian localities for Zingiberales that occur in Amazonia, (K) primates
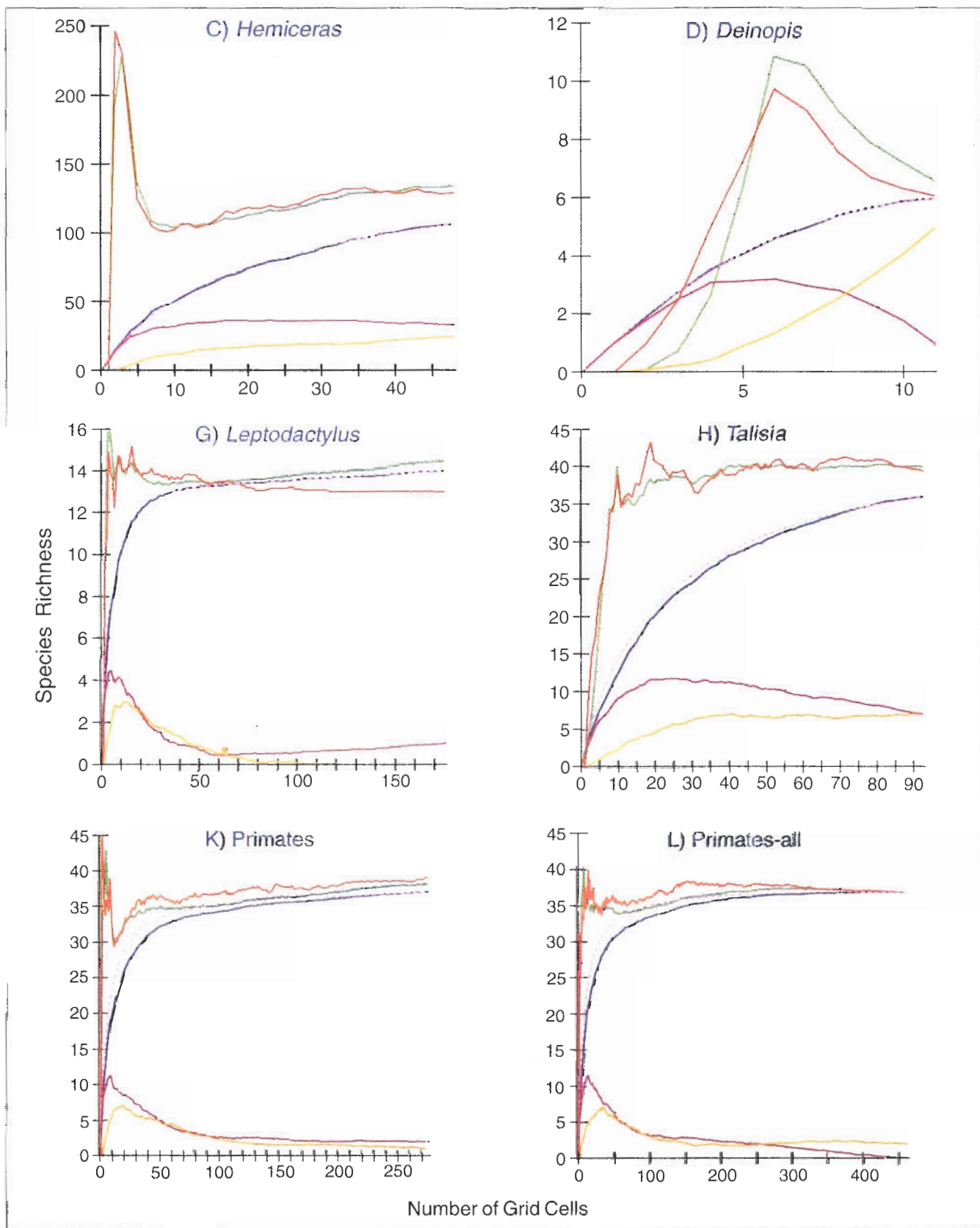
based on localities delimited within Amazonia, (L) all Amazonian and extra-Amazonian localities that occur in Amazonia. Sobs = empirical species accumulation curve; ICE = coverage estimator of Chao and Lee (14); Chao2 = incidence-based estimator of Chao (13); Cole = Coleman curve, a patchiness indicator, of Coleman (17); uniques = number of species occurring in just one grid cell; duplicates = number of species occurring in just two grid cells.

In fact, these Amazonian groups are arguably oversampled as far as a rough estimate of the species richness is concerned. The behaviors of the "rare" species curves (uniques and duplicates) are typical of putatively complete inventories. Early on, the uniques curve rises faster than the duplicates curve. Additional sampling eventually converts uniques into duplicates, and duplicates into triples or higher frequencies. The uniques curve thus declines faster than the duplicates curves and may even cross it, but both tend towards zero when no species remain to be discovered and almost all species are known from two or more localities. The other taxa in the study fell between these two extremes. Among arthropods, the *Batesiana* group and *Hemiceras* (Fig. 2B,C) seem much better known than *Agra* (note the different Y-axis scales). The curves for *Deinopis* illustrate the very earliest stages in knowledge of a taxon, when sample data are so sparse that statistics based on accumulation curves vary widely.

The curves for zingibers and primates illustrate how a strict geographic definition of Amazonia can distort interpretation of biological patterns. Zingibers are fairly well collected (25.2 localities per species; 403 Amazonian localities for 33 species), but the observed and estimator curves (Fig. 2I) are still rising by the end of the sample, and the uniques curve is level rather than declining. Primates (Fig. 2K) show the same symptoms. If all extra-Amazonian records are added, however, the curves show the typical signature of nearly complete inventories (Fig. 2J, L). Some *Heliconia* and primate species are primarily non-Amazonian taxa, at least as we define it, though they do occur in Amazonia. When records outside "Amazonia" and above 350 m are deleted, these species are artifactually rare; additional random sampling in Amazonia would be quite unlikely to encounter them. Limiting the analysis to just Amazonian records distorts the results for these taxa in a characteristic and logical way.

While apparently not as complete as the primate, large river fishes, *Leptodactylus,* and Zingiberales inventories, the inventories of *Talisia* (Fig. 2H) and small river fishes (Fig. 2F) are much more complete than for any of the arthropods (Fig. 2A-D). By the end of the samples, the Chao2 and ICE estimator curves for arthropod taxa are still an average of 65% above the observed curves. The similar figures for vertebrates (Fig. 2E-G) and plants (Fig. 2H,I) are 3% and 9%, respectively.

Another way to approach sampling intensity is to plot the number of species per grid cell against the number of localities per grid cell. For our data (excluding primates, Figure 3), the Spearman r for the 364 grid cells with data is 0.928 and significant ($p < 0.001$), with a r^2 of 0.86. Thus more than four-fifths of the variation in local species-per-grid cell richness can be explained

by collecting effort (number of localities/grid cell). In summary, the vertebrate and plant data probably reflect biological reality much more faithfully than the arthropod data. Primates are well-known and well-collected, but our plant and vertebrate groups are known nearly as well. In contrast the patterns shown by poorly known and undercollected groups (arthropods) differ in consistent, sensible ways. Patterns shown by such taxa may not be spurious, but they should be used carefully and critically.

Spatial aggregation

When tested using classical statistical techniques (Poisson index of dispersion *I*), collections for all of these Amazonian taxa, either separately or together are highly clumped ($p < 0.000$). This result is not surprising, but it is difficult to specify how much is due to biased sampling versus biological reality. The Coleman curves (which provide a picture of the data as if individuals were distributed and had been sampled at random) in all cases closely follow the observed (Sobs) curves (Fig. 2). Because EstimateS repeatedly randomizes sample order as it computes statistics (here 50 times), it provides a standard deviation for each statistic as each sample is added to the curve. If twice the standard deviation of the Coleman curve is taken as a rough confidence interval, in all cases the observed curves fall within these limits. Hence, the estimator curves for species richness seem little affected, despite the obvious spatial aggregation in the data (Fig. 1).

The Coleman curves do show evidence of patchiness, however, even if the effect is slight. For all the plant and vertebrate data (except large river fishes) the observed curves fall below the Coleman curves. This is because the relatively rare species occur in disproportionately few samples (i.e. are aggregated). When randomly dispersed among samples in the Coleman curves, the probability of encountering these
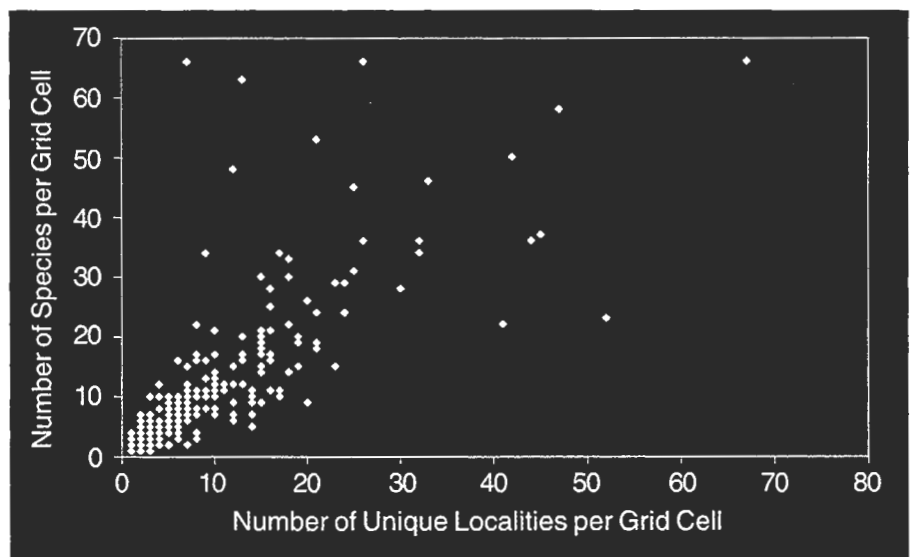

Figure 3. Plot of number of species (excluding primates) against unique localities for one degree grid cells within Amazonia. Individual symbols may represent more than one data point.

species earlier in the accumulation increases so that the Coleman curve tends to rise a bit faster than the observed curves.

Spatial aggregation does affect estimates of species ranges however. Taxonomically undersampled groups are inevitably undersampled geographically. The detailed ranges for all species analyzed herein are unknown. Some of the groups included here included common species, which almost certainly occur in many more grid cells than Figure 1 shows. About one fourth of the Amazonian grid cells (113 of 472) contain no localities for any of the groups investigated here. This is due to lack of sampling within those grid cells, not lack of species within them. These results suggest that for the grid cells that have been sampled, patchiness of collections seems not to be a severe problem. However, the presence of unsampled grid cells does pose problems in understanding individual species distributions and contributes to geographic undersampling for all of our individual data sets.

These results show that museum collection data (or other such inventory data) can be analyzed quantitatively to gauge the relative completeness of taxonomic inventories. As expected for the indicator group of primates, the curves suggest that nearly all Amazonian primate species are known. Evidence for this is the asymptotic behavior of the species accumulation and richness estimation curves, their near equality when all data are included, and the predictable behavior of

accumulation curves for "rare" species. These quantitative criteria can be used to judge the quality of other taxonomic inventories, and thus to rank taxa along a continuum of knowledge. For the groups considered here, zingibers, the frog genus *Leptodactylus*, and the fish genera typical of large rivers seem about as well known as primates. The same criteria indicate that the arthropod taxa analyzed here are much less well-known, although among those the *Batesiana* group of carabids and the noctuid genus *Hemiceras* are better known than the others. The sapindaceous genus *Talisia*, and fish genera typical of small rivers are intermediate. The statistical estimator results are best for the data sets with the most localities per species and worst for the data sets with the fewest localities per species.

The initial concern that collecting records for the Amazon basin are so biased geographically as to invalidate the sort of analysis attempted here is mitigated by the close agreement between observed curves and the Coleman curves from which all traces of aggregation have been removed. While it is possible that the Amazon still harbors new species of groups as well sampled as primates, the percentage of new species should be small. At a more general level, the Amazon basin has been and remains one of the largest and most inaccessible land areas in the world. Museum collection data in other areas should be much less patchy, and thus the methods used here to assess indicator status should work even better if applied elsewhere. Of course the analyses used here depend on new statistical techniques which themselves re-

Figure 4. Map of neotropical lowland primate collecting sites.

quire more testing before their strengths and weaknesses are really understood, in particular their robustness when assumptions are strained or violated.

Amazonian indicator groups

Amazonian bird, heliconiine and ithomiine butterfly, and primate data are generally considered more robust than data for other Amazonian groups and one might argue that these groups should be used preferentially to make conservation recommendations. Two critical aspects contribute to the utility of distributional data for making scientifically based inferences: *1)* The species-level taxonomy must be accurate; and *2)* geographic distributions must be correct.

Amazonian birds, heliconiine and ithomiine butterflies, and primates are well-known taxonomically. The suggestion that distributions for these groups are equally well understood is doubtful, however. Raymond A Paynter Jr and associates have recently published a series of ornithological gazetteers for Latin America. Their maps of collecting localities show that Amazonian bird locality data are as dominated by river access as ours. For example, Brazilian Amazonian collecting localities are sparse (72) and, as expected, most of those are near the major rivers. The butterfly data are similar, except that the road transect from southeast Brazil to Porto Velho has been well-sampled (73). The primate data are marginally better than our nonprimate data, but again with essentially all collecting localities restricted to the major rivers (Fig. 4). The richness estimator and the Coleman curve results for primates (Fig. 2K,L) are similar to those for *Leptodactylus* and Zingiberales (Fig. 2G,I,J), and large river fishes (Fig. 2E). Taxonomically the latter groups are just as well-known as any of the indicator taxa.

Historically rivers provided about the only access within Amazonia. As a result, all Amazonian taxa suffer from geographic undersampling. Only recently has it been practical to consider alternatives, and thus to ask if the classical strategy via rivers is an adequate way to sample Amazonian biota. The rivers do provide a vast network overlaid on the entire basin. Therefore, adequate sampling (as illustrated above) of taxa throughout Amazonia via the rivers may nevertheless provide reasonably complete pictures of species richness. This conjecture presumes that the effect of rivers diminishes rapidly with distance for most taxa – that is, all major ecosystem types in Amazonia occur within walking distance of accessible riverbanks. With satellite imagery it should be possible to determine how many, if any, ecosystem types between rivers (which might harbor new species) do not also occur along them.

Other robustly sampled groups certainly exist. Some of them are adequately understood taxonomically and are thus ready to be used. Others, such as bufonid and hylid frogs are probably adequately sampled, but poor taxonomic understanding diminishes their utility in this context. Focussed research to bring such groups to an acceptable taxonomic understanding would be a very cost-effective way to improve the scientific knowledge base of Amazonian conservation.

In summary, conservation decisions in Amazonia should be based on more than one or two well-known and collected (indicator) taxa, because the data for a number of other taxa are just as good, at least at the level of the entire Amazon basin. In addition to birds, heliconiine and ithomiine butterflies, and primates, we can use several fish genera from large rivers, *Leptodactylus*, heliconias, probably aquatic beetles (74), scarab beetles (75), tiger beetles (76), mosquitoes (77,78,79), lizards (80,81), the plant families Chrysobalanaceae (see references in Reference 4), Lecythidaceae (see references in Reference 4), and Palmae (82). The data for certain fish genera from small rivers and the plant genus *Talisia* can be used with some caution. By contrast, taxa such as *Agra* and *Deinopis* are too seriously undersampled taxonomically and geographically over the entire basin to support conservation decisions, at least on their own. An additional point is that the graphical methods of analysis demonstrated here can be applied at any geographic scale to test for adequate taxonomic sampling and the effect of spatially aggregated samples on patterns in species richness.

We emphasize that the most significant finding of this paper is that there are several taxonomic groups with adequate museum-associated data to use for species richness analyses at the level of the Amazon basin. Species richness is an important piece of information in making informed conservation decisions. There are many groups in Amazonia that remain undersampled, as is true also for other relatively unknown geographic areas. In the following section, we discuss how incomplete data can be used to make conservation decisions.

Local Amazonian conservation

Increasing ecosystem degradation or loss within the Amazon basin means that conservation will be applied at increasingly finer scales, whereas problems of geographic undersampling worsen at finer and finer geographic scales in Amazonia. To formulate local conservation recommendations in the absence of adequate geographic data, we recommend a protocol that follows the philosophy laid out by Shrader-Frechette and McCoy (83). They argue that top-down, theoretically inspired solutions to ecologically based conservation problems have not worked, and in many cases should not be expected to work. Rather, the bottom-up case study approach has been much more successful and is likely to be more productive. We recommend that localized conservation decisions for Amazonian areas be made on a case-by-case basis, with knowledgeable experts evaluating the available data. A scientific rationale for this approach can be shown with frog and primate examples.

Suppose that a discrete area (1,000 – 10,000 km²) within Amazonia is being evaluated for possible protection and that the distributional data for frogs are incomplete (nearly always the case at present). Almost any list of frog species from such an area could erroneously suggest high levels of endemism, because frogs as a whole, unlike *Leptodactylus*, are still poorly sampled. However, an expert Amazonian her-

petologist should be able to make some reasonable inferences from a species list and associated information. For example, it should be obvious whether night collecting occurred, and how thoroughly forest habitats had been sampled (versus open river edge habitats etc). The frog fauna is reasonably well-known at roughly eight to ten scattered localities across Amazonia (most of these coincide with the highest species richness grid cells identified in a companion paper (84) (see Fig. 1). Comparison of the target area list with the nearest completely censused site should indicate if the target site is really different or unusual, or if the differences are due to undersampling. About 18 widespread frog species occur throughout Amazonia. Complete inventories at any site should probably contain all 18 species. Knowledge of the collectors and the weather conditions can help to assess the quality of the list. Transects through alternate regions can provide information on appropriate breeding habitats under suitable climatic conditions. Zimmerman and Bierregaard (85) have shown that elements of the Amazonian forest frog fauna depend on patchily distributed breeding habitats that are readily recognizable by humans. Finally, even if available data are misleading or unreliable, a knowledgeable herpetologist, given the available data, should be able to specify what fieldwork will most quickly provide the data required to make recommendations.

A knowledgeable specialist can also use a probabilistic approach to assess distributional limits and lacunae using taxon-specific locality data. For example, the original primate data set from which the Amazonia taxa data were extracted for this study includes 140 subspecies and 51 species from 2,100 localities in Central and South America. For each species throughout its expected range we counted the number of localities where it was collected and where it was not collected, but where other species of primates occur. From these counts, we calculated the frequency of sites (p) at which each species was collected within its range. Thus, the probability that it would not be collected at such a site is (1 - p). These probabilities can then be applied to an area in which a species is apparently absent to infer whether the absence is real or due to undersampling. If the number of collecting sites is (n), then the probability that the species occurs there but has not yet been collected is $(1 - p)^n$.

This approach assumes that collecting effort has been approximately the same in all areas. If some sites were intensively collected and others casually, the computed probabilities will be biased. However, this bias can be measured by comparing the number of specimens collected per site in various areas. Also, known associations between primate species can reveal bias due to differential collecting effort in two areas. For example, if squirrel monkeys (*Saimiri*) and spider monkeys (*Ateles*) were collected with equal frequency in both areas, then it is likely that the habitats do not differ greatly. Specialist expertise is required to recognize and evaluate these assumptions adequately.

In the case of the tamarin, *Saguinus midas*, Hershkovitz (58) shows the Rio Xingu as the western boundary of the range of this species. Is the Xingu really the western edge of the range of this tamarin? The subspecies that lives in the western portion of the range, *S. m. niger*, has been collected at only 19 of 75 localities within its putative range. The probability, p, of collecting it at a randomly selected site is then 19/75, or 0.25. The probability of not collecting it is 1 – p, or 0.75. The latter value is the probability of not finding this species at a locality within its western range, even though it occurs there. In the one-degree wide strip west of the rio Xingu, primates have been collected at seven localities. The probability of not finding this tamarin west of the Xingu, even if it were to occur there, is thus $(1 - p)^n = 0.75^7 = 0.13$. The rio Xingu may be a barrier for this species, but the evidence is not compelling.

The bottom-up approach to conservation using expert evaluation of many independent cases has an important limitation. Different Amazonian groups show different biotic patterns. Therefore, the more taxonomic groups (and experts) that contribute to the analysis, the more robust the conservation recommendations are likely to be (see also References 86,87, for non-Amazonian examples demonstrating that the distributional data for one taxon does not predict patterns in other groups). Taxonomic expertise on Amazonian groups is very limited. Given the amount of time and resources it would take to improve the Amazonian distributional database versus training more experts to evaluate the available data, one short-term solution seems to lie in training more experts.

In conclusion, we suggest that species and geographic undersampling can be detected graphically, and that such assessment should be routinely applied whenever the scientific data underpinning conservation decisions might suffer from such problems. Further, we suggest that to rely on a few so-called indicator taxa is both scientifically indefensible and unnecessary. We identify several taxonomic groups that have as robust data as Amazonian indicator taxa. Data from all of these groups should be used to make conservation decisions in Amazonia. Finally, we suggest that even when data are imperfect, as they are likely to be at more local scales, several critical approaches can still assess the quality of species lists and maps in order to optimize the allocation of scarce conservation resources. ∎

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