CHAPTER

4

Biodiversity at Its Utmost: Tropical Forest Beetles

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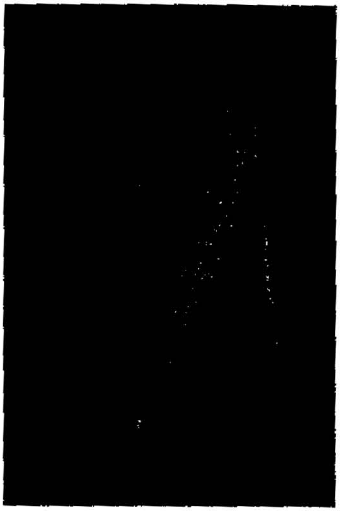
Life on Earth takes many forms and comes in all sizes, from microscopic one-celled plants to blue whales and human beings. Together these organisms and their interactions constitute our planet's biodiversity. Among this profusion of life are the beetles and their insect and arachnomorph relatives, which, taken together, constitute most of Earth's biodiversity (Erwin, 1982; Hammond, 1992; Robinson, 1986; Wilson, 1992). There are 1.4 million species of insects described in the scientific literature (Hammond, 1992), which is about 80% of all life currently recorded on Earth. Taxonomists, those who name and classify species, have been describing species of insects at about 4,400 per year for more than 235 years, and in the last 25 years, have described about 8,680 per year (±363). This written record is at best perhaps only 3.4% of the species actually living on the planet (Erwin, 1983a). Recent estimates of insect species, mostly in tropical forests, indicate that the descriptive process is woefully behind. These estimates indicate there may be as many as 30–50 million species of insects (Erwin, 1982, 1983b), making this pervasive terrestrial arthropod group 97% of global biodiversity. The familiar ants and grasshoppers, bees and beetles, houseflies and cockroaches, and spiders are but the tip of the iceberg of arthropod diversity; most species are small to very small tropical forest-dwelling forms that no one has seen or described on any adequate scale.

Insects and their relatives (spiders, ticks, centipedes, etc.) are the most dominant and important group of terrestrial organisms, besides humans, that affect life on Earth, often with an impact on human life. They affect human life in a multitude of ways—both for good and bad. Profound ignorance about insect life permeates most of human society, even among the highly educated. Insects



Weevils are a very diverse group of rainforest beetles.

and their relatives, in fact, are little credited for their beneficial environmental services and overblamed for their destructive activities. Despite lack of general human interest in insects, E. O. Wilson (1987:1) wrote that they are "the little things that run the world."

Insects and their relatives live on all continents and occupy microhabitats from deep in the soil and underground aquifers to the tops of trees and mountains, among the feathers of penguins on Antarctica, and even deep into caves and in our eyebrows. Many lineages have evolved adaptations for living on and under ice fields, others at the margins of hot springs, and still others on the open ocean. Land arthropods, by virtue of their pervasiveness, are incredibly important to the balance of life within ecosystems, e.g., pollination, nutrient recycling, and population control through vectoring diseases. Insects and their relatives eat virtually everything and compete even for the rocks under which they hide, mate, and rear their young. What would happen if all insects were removed from a habitat or natural community overnight? For one thing, most broadleaf trees and shrubs would not be pollinated, and there would be no fruits and seeds. For another, instead of penetrating dead matter, decomposers such as bacteria and fungi would live only on the surface, taking years or perhaps millennia to break the substrate down into recyclable nutrients for plants, and thus soils would be much less fertile. Many fish and birds, and even some mammals, would have no food and would cease to exist. In fact, insects seem to be one of nature's most important cornerstones on which most other types of life depend in one way or another.

Among the insects, the beetles are the most speciose, the most pervasive, and the most widespread across the face of the globe. During dry seasons in tropical forests, they are also the third most numerous individuals, after ants and termites, making up a full 12% of the total insect community (Erwin, 1989).

Beetles are found everywhere on our planet except in the deep sea. However, they do occur commonly in the sea's intertidal zone and estuarine salt flats (Erwin and Kavanaugh, 1980; Kavanaugh and Erwin, 1992; Lindroth, 1980). Beetles even occurred on Antarctica not long ago (Ashworth, personal communication, 1994). Most families of beetles, about 140 of them, are world-wide in distribution, and their species provide equivalent ecological services wherever they occur. The "play" is generally the same everywhere, only the "actors" themselves change from place to place.

We know of beetles from the Permian Period to the present (Arnol'di et al., 1992), a recorded history of some 250 million years. This history shows that two major faunal changes took place, the first in the mid-Jurassic Period when primitive lineages of beetles lost their dominance, and the second in the mid-Cretaceous Period, at which time modern forms acquired dominance over all other terrestrial arthropods. In terms of species and number of guilds (groups of species that fill similar ecological roles), they still have this dominance in nearly every biotope. By any broad measure, beetles are the most successful lineage of complex organisms ever to have evolved.

The *described* species of beetles, about 400,000+ (Hammond, 1992), comprise about 25% of all described species on Earth. This dominance of beetle taxa (any systematic category, such as species, genus, family, etc.) in the literature has resulted in Coleoptera being perceived as Earth's most speciose taxon. Thus, it has garnered further taxonomic attention from young taxonomists which in turn has resulted in more species of beetles being described than in other groups. Beetles are relatively easy to collect, prepare, and describe, significantly adding to their popularity. Such unevenness in taxonomic effort may or may not give us a false picture of true relative insect diversities. Nevertheless, the dominance of beetles has been used to arrive at an estimate of 30 million insects overall (Erwin, 1982), and even to designate the group most endeared to God (Gould, 1993). While this dominance may be arguable either scientifically or philosophically, it is certainly interesting. However, it does not address the real power that a knowledge of this extraordinary taxon might allow in evolutionary biology and conservation. What is neglected in the science of "coleopterology" is nearly everything except collecting, taxonomy, systematics, and a little autecology. Given that nearly everyone from naturalists, including Darwin and Bates to Edgar Allen Poe has or had "an inordinate fondness" (see Gould, 1993) for beetles, it seems strange that more attention is not given to them for use in interpreting environmental perturbations (Ashworth et al., 1991; Ashworth and Hoganson, 1993; Halffter and Favila, 1993), in understanding the rules (or nonrules) of assembly in tropical communities and biotopes (Erwin, 1985), and in environmental monitoring (Kremen, 1992; Kremen et al., 1993).

The reasons probably lie in the overwhelming numbers of species, individuals, and the ever-plodding course of traditional taxonomy. Potential users of data on beetles simply have to wait too long to get names; taxonomists have to wait too long to receive money to visit museums in which name-bearing type specimens are held; monographers take too long to produce documents with which users might identify their specimens by themselves; and specialists are reluctant to take on a large identification load for other scientists, such as ecologists and conservation biologists.

Given that millions of data points can be gathered in a very short time by sampling beetles (Table 4-1), far more than in any other group of diverse organisms (Adis et al., 1984; Allison et al., 1993; Basset, 1990, 1991; Erwin, 1982,

TABLE 4-1 Species Level Studies of Tropical/Subtropical Canopy/Subcanopy Beetles Using Insecticidal Fogging Techniques

	Est. vol. of foliage (m^3)	No. of species	No. of specimens	Familes	Density	Species/m^3/m	Specimen/ species ratio	% Singletons
Allison/Miller (New Guinea)	2150	633	4840	54	2.25	0.29	7.65	50.7
Basset (Australia)[a]	4040	68	863	48	4.68	0.02	12.69	est. 19
Erwin (Panama)	1065	1250	8500	60	7.99	1.17	6.8	?
Erwin (Peru)[b]	2283	3429	15869	83	6.95	1.5	4.63	50.4
Stork (Brunei)	2690	859	4000	61	0.42	0.32	4.66	?
Stork (Sulawesi)	56550	1176	9158	?	0.16	0.02	7.79	?

[a]Restricted canopy fogging method.

[b]Includes six specific microhabitats, while others are predominately canopy rims with perhaps epiphytic growth.

1983a,b, 1988, 1989, 1991; Erwin and Scott, 1981; Farrell and Erwin, 1988; Kitching et al., 1993; Stork, 1991), how might we digest those data, turn them around to discern patterns that, once recognized and interpreted, can give us powers of prediction about the environment. With such an understanding, we could discern rich sites from slightly less rich sites for conservation (Rapid Assessment Program Team approach), or monitor life (environmental health) at those sites at a much finer resolution than is possible with vertebrates; and we could test much ecological theory also on a fine scale.

Neotropical beetles are second only to ants and flies (the latter in the wet season only) in numbers of free-ranging individuals of arthropods in the canopies and subcanopies of neotropical trees (termites are not usually free-ranging); Psocoptera are a distant third (Erwin, 1989). However, per species, beetles are not abundant (Figure 4–1). Beetles participate in virtually all aspects of ecosystem processes; they are predators, herbivores, folivores, detritivores, scavengers, fungivores, wood-eaters, and grazers, and they tunnel, mine, and chew nearly every substrate. Some are ectoparasites, others are nest parasites, some even live in the fur of vertebrates. Still others are subsocial, with adults participating in the raising of young. Knowledge of beetles, because they are *the* hyperdiverse group on the planet, offers direct insights into total biodiversity and the evolution of that biodiversity, as well as how this diversity is distributed in time and space across microenvironments, habitats, biomes, and seasons. A global perspective based on beetles could provide a much more fine-grained view of biodiversity than the coarse-grained one we get from less speciose groups such as jaguars, birds, and monkeys, which heretofore have garnered most of the attention.

The publication resulting from the National Forum on BioDiversity (Wilson

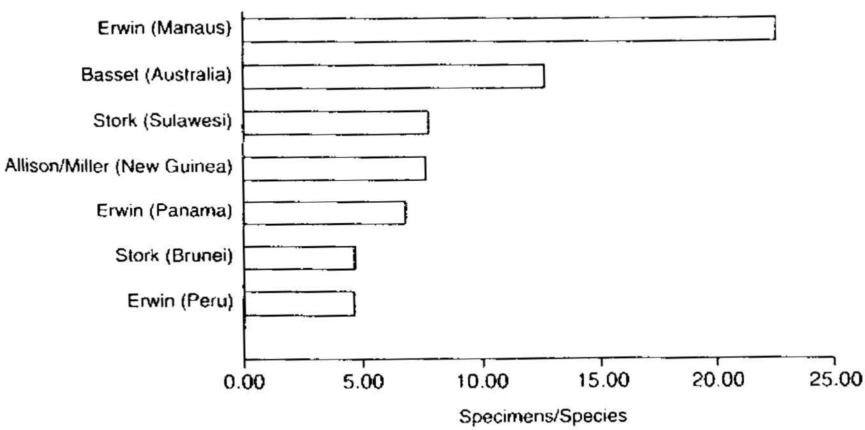


FIGURE 4–1 Relative abundance of species (large beetle-sampling programs).

and Peter, 1988), held in Washington, D.C. in 1986, included only 7 out of 521 pages devoted to insects (and only one speaker at the forum). At the most recent Biodiversity Forum (the Inaugural Symposium of the Consortium of Systematics and Biodiversity which formed the basis for this volume), there were six speakers on insects and three others whose contributions were at least partially based on insects (23%), a substantial realization in a mere 8 years within the biological community that biodiversity and the environment are insect dominated! If we are to understand the environment, which we must do if we are to successfully manage it, then we must have a better picture of the processes that brought about and maintained insect dominance since the Mesozoic Era.

Whether or not there are 30 million species (and, of that, 7.5 million species of beetles) or only a little more than the 1.4 million species that are already described, current human activity and that of the immediate future will exterminate a large percentage of these species (Erwin, 1988; Wilson, 1988). Attention must focus on the underlying evolutionary processes that have resulted in such diversity and evaluate these in terms of present human activities.

COLLECTION OF DATA

Because the interface between insects and their environment is at a small resolution, information they provide may well be critical for ecological restoration. Management will depend on what we really know rather than what we surmise. Conservation cannot now deal with insect information, but will be compelled to do so in the not-too-distant future. We will need a system for data gathering that is just now becoming available.

In Chapter 27 of this volume, Daniel Janzen describes his concept of an All Taxa Biodiversity Inventory (ATBI) for a 110,000 hectare site in Costa Rica. Such an undertaking, even in such a small area, will require methods other than those now employed for inventory, because the beetles alone are so pervasive and speciose anywhere in the tropics (along with all the other insects and their relatives) that completing an inventory would require generations of investigators.

One goal of Janzen's ATBI is to inventory *all* the taxa within a given area. A biotic inventory includes finding the area's species, classifying them, making voucher collections, and storing these data in a way that they are easily retrievable. Additional information about the species, either gathered during the process of inventorying or added later from literature or follow-up studies, can be piled on top of the four basic elements in a growing database.

The first ATBI area is destined to be at the Guanacaste Conservation Area (GCA), Costa Rica, a site with dry forest in lower elevations ascending through cloud forest and containing intermediaries between these levels. Based on my experience in (and data from) nearby Panama with a similar range of habitats, I estimate that GCA should have about 50,000 species of beetles. Since this estimate can be only a first approximation (but certainly within an order of magnitude), it is used for purposes of designing a sampling regime for the project: budget and time must be considered to be modifiable as the project narrows to better estimates.

Given GCA's latitude and altitudinal gradient, there are a minimum of 24 distinctive communities (forested and open habitats), each forest with a set of 15 or so microhabitats and each open area with 5 or so microhabitats (Erwin, 1991), all of which may contain different beetle faunules with perhaps as little as 20% species overlap, as was observed in my studies of 6 forest microhabitats at Pakitza, Peru. Each species of tree, shrub, and herb/grass may have its own host-specific species of beetles. Riparian strands in various watersheds will have different types of substrates, water quality, vegetation, etc., contributing to their distinctive biodiversities. In addition, the GCA is distinctly seasonal, hence both dry and wet seasons need to be sampled for each microhabitat (Erwin and Scott, 1981).

The sampling regime must consider the above in its attempt to record as many species as possible in the shortest amount of time. The guiding principles are as follows:

- Phase 1: mass co-occurrence sampling; rapid processing with bulk cold storage (dry and wet specimens, depending on Order); identification process using matching specimens; interim naming with alphanumerics; accumulation of data using linked spreadsheets, including curves showing sampling progress; and character filing with the Quick Taxonomic Assessment System (QTES).
- Phase 2: send target taxa and QTES data into the taxasphere (formal systematic literature) for formal species names;
- Phase 3: replace EXCEL 4.0 spreadsheet and QTES interim names with formal ones, transfer these data to the database at Instituto Nacional de Biodiversidad (INBio).
- Phase 4: generate illustrations and three-dimensional laser images; produce documents (lists, brochures, field guides, revisions, monographs, other analyses).

AN AGENDA FOR SAMPLING BEETLES IN AN ATBI

Sampling

The following criteria must be met for acquiring samples of beetles that can provide a reasonable inventory and serve both immediate and future needs of research, as well as determine to an order of magnitude the species present in the target area for use in subsequent sampling projects:

(1) Sampling assumes the use of a fogger and 3% Resmethrin (biodegradable with an LD50[1] better than aspirin, gone in 2 hours) for all microhabitats

[1]Dosage at which 50% of the organisms fail to survive.

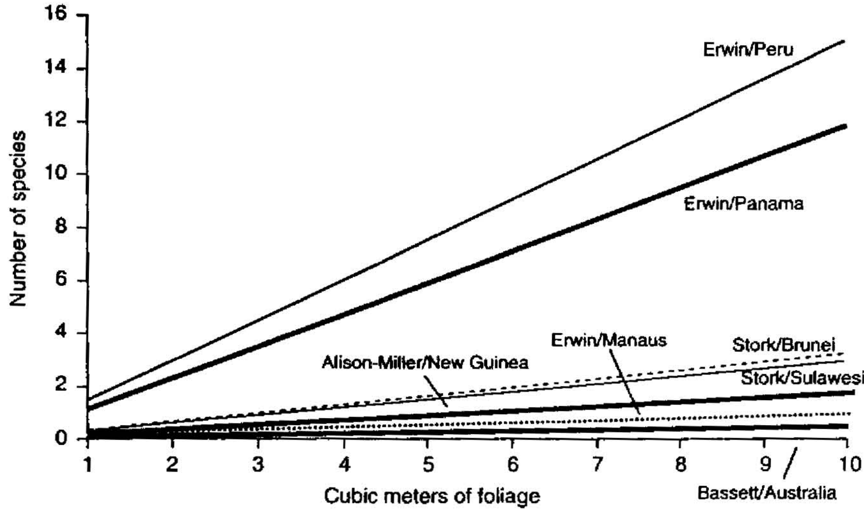


FIGURE 4–2 Accumulation of species (per m³ of foliage).

from 1 m above ground through the canopy rim (Erwin, 1982, 1983b, 1989, 1991); this should capture 1.7 species per m³ of foliage (see Figure 4–2) and much more in compacted microhabitats such as suspended dry leaves, vine tangles, and complex canopies. Leaf litter and soil layers are sampled by photoeclectors (Adis, 1984; Adis and Schubart, 1984) and sifting/Tolgren extractor techniques. Berlese banks can substitute for Tolgren, if electricity is available. The stratum of herbs and grasses is sweep-sampled by sweep-netting.

Methods of trapping by attraction and even passive traps that catch flying insects produce catch without biocontext, i.e., specimens that are not tied to any microhabitat, substrate, host plant, etc. Much time and effort goes into preparing, identifying, and storing such bulk lots, yet the quality of data is at the lowest level. These methods of collecting simply are not worth the effort, unless one is interested solely in recording presence of species in the general area or in building collections. However, these techniques can be used as a test of the methods that incorporate biocontext to determine if microhabitats exist that are not being sampled with the other techniques.

(2) A standard set of field data includes precise locality (latitude/longitude to seconds, and notes on permanent trail markers and topographic features if available; a Global Positioning System [GPS] device provides data on position and elevation); type of forest; type of microhabitat and its volume or surface area; information on species of plants (or other host); date; and collector(s). Lot numbers are assigned to each individual fogging collection, sifting series, photoeclector sample, sweep series, etc. Thus, all specimens taken from the same

microhabitat or plant or trap at the same time get the same lot number so that the set of species, including nonbeetles, can be reassembled at a later date if desired (this faunule reassembly may be only a computer construct). Nonbeetle specimens will be directed to another Taxonomic Working Group (TWIG), along with appropriate sets of data.

(3) Specimens of beetles are preserved in 70% alcohol in the field. Alcohol must be changed the same day at the lab and subsequently each time the specimens undergo processing (see below). If specialists for nonbeetle groups are available at the time of fogging, dry specimens may be extracted by hand before the general sample goes into alcohol, so long as this does not delay the routine of the inventory for beetles and appropriate lot numbers are defined. Egg carton inserts are placed in funnels or on suspended sheets to catch specimens dry. After these are selected from the carton surface, the remaining specimens are dumped into the alcohol bottle.

(4) Sampling design involves taking replicate microhabitat samples in sets of 10 throughout each type of forest and open area. During preparation and data entry of the 10 samples, species accumulation curves and Chao's estimator (Colwell and Coddington, 1994) track the progress of the inventory. A complete inventory for smaller families will require fewer replicates, but the leaf-beetles and weevils will require many more than 10 replicates, based on data from over 5,000 species acquired at Pakitza, Peru, from 1988-1992. A decision needs to be made at the outset as to when to stop, because it will not be "humanly" possible, given today's resources, to get the "last" species on the list in the larger families. However, 100% likely will be reached in smaller families.

Preparation

All tropical forest samples are replete with beetles. The object of preparation should be to make the species and their whereabouts and abundance known in the shortest amount of time possible. Traditional preparation of all collected specimens, therefore, is not feasible. The following method leads to one prepared specimen per species per sample, with cold storage of the bulk lots (other specimens of the species) that easily can be accessed later by taxonomists and other workers who need series.

(1) Each sample lot is sorted to families using a 6.2 cm white ceramic dish with 70% alcohol. Families are gathered in small plastic lids set inside the bottom of a petri dish, the top of which is ringed with vaseline to create a seal when the specimens are sitting unworked. Parataxonomists and beginning graduate students can be trained to sort at this level quickly.

(2) Each family then is sorted in sequence to species, with one good specimen selected for pinning/pointing. The specimen is placed on damp filter paper inside another petri dish. On the filter paper, numbers 1 to 20 are written and the chosen specimen is placed next to a number according to its abundance in

A collection of rainforest insects.

the sample. If over 20 specimens of a species are in a sample (which is rare), a small label is written with the number, and this label is affixed to the pin to be removed later in the process (see below). The rest of the counted but unprepared specimens are returned to the lot vial of 70% alcohol, bar-coded, and sent to cold storage. Sorting to species across the Coleoptera can be done only by a highly trained taxonomist with long experience, and this person becomes the key to the entire project. Preparation and storage procedures can be handled by a technically trained person.

(3) Each specimen from the filter paper is pinned or pointed with Elmer's glue to pins or preprepared points in the traditional manner and placed in a unit tray with strips of numbers sequenced from 1 to 20. Each specimen is aligned next to one of these numbers according to its abundance in the sample.

(4) Preprinted labels are attached to each specimen as it is "identified-by-matching" using the synoptic collection. The name of the species is an alphanumeric in the form of "family coden + number" and lot number. All families of Coleoptera have a standard coden of four letters. The margin of the label is color-coded with pencil for instant recognition of microhabitat, although the lot number references this too. Once a family is represented by more than 100 species, "identifying-by-matching" becomes less and less efficient. For very large families, such as weevils, staphylinids, and chrysomelids, use of QTES is recommended.

Interim Identification

Each prepared specimen from a sample is compared with its corresponding family-level synoptic collection. Smaller families are easy to keep in one or a few units. Larger families may be subdivided by subfamily so that the amount of matching necessary for recognizing the specimen's status is kept to a minimum. As a specimen is identified or recognized as a species new to the synoptic collection, it is placed either in an interim unit tray awaiting entry of the data before going to the duplicate collection (those identified previously) or added to the synoptic collection (those determined as new), from where its data are entered. All species of a family that are sorted from the sample are labeled, then the data are entered in EXCEL before preparing the next family.

Data Storage

My EXCEL linked spreadsheet templates for families of beetles contain about 13 Kilobytes of forms that are based on microhabitats. Entry of data from a sample involves simply number of specimens per species per lot. The program automatically computes all basic information and accumulates the data on summary sheets for easy viewing. The program is exceedingly user-friendly.

Building Collections

The resulting synoptic-unit trays of families of beetles are ready for specialists at any time during the process if the specialist is on-site to make formal identifications. The duplicate collection—built from second through *n* occurrences of a species across samples (hence, it will not contain "uniques" [species known from single specimens] found only in the synoptic trays)—can be sent through the taxasphere regularly and results can be fed back into the EXCEL data system, making it easy to move the information to the INBio standard data files. As additional microhabitat replicates are sampled and specimens processed, those species represented by uniques in the synoptic collection will be duplicated and then can be sent through the taxasphere.

Serious taxonomists who must do a revisionary study immediately can read the database to find lots with series and arrange to extract those from cold storage themselves. Common species that are found in many or most lots will have that many more prepared specimens ready for study in the duplicate collection.

SUMMARY

The rate at which *all* the foregoing can be done is 58 specimens and 13 species per hour. Therefore, using the rate of accumulation for additional species found in Panama forest foliage, 1.7 per m^3 of microhabitat, we should be able to sample 70,000 m^3 of microhabitat and process 50,000 species of beetles in 2½ years. In other words, we know the actors and where they are standing on the stage, and each has a number hanging around its neck. The taxasphere is another creature, and getting formal names on the inventoried species is highly dependent on the group of beetles, its history of studies, and its current taxonomist(s).

The advantages of the TWIG protocol are that (1) it is far more rapid than any of its predecessors; (2) data byproducts allow diverse follow-up studies beyond the inventory process; (3) targeted taxa known to be important to users can be piped readily (and continuously) through the taxasphere; (4) space and storage facilities are minimized because samples mostly are stored cold in two-dram shell vials or petri dishes until needed by a dedicated specialist; and (5) dedicated specialists will "donate" their time to the collections as they select and prepare specimens from cold storage, hence building collections becomes a shared taxaspheric process.

Beyond the inventory itself, such questions as "do beetles form discreet assemblages in tropical forests, or in any biotope anywhere?" can be tested. If so, how that information might be used for answering scientific questions and for developing conservation strategies is of considerable interest. The objective of this kind of study would be to fill a large gap in our understanding of hyperdiversity. For example, (1) what percentage do beetles contribute to a sample? (2) What is the fidelity of beetle faunules to microhabitats? (3) What is the rate of species turnover across extensive geographic space in the tropics? (4) What is the rate of local species replacement among and between tropical microhabitats? (5) What proportion of the total beetle fauna inhabits arboreal versus forest floor habitats? (6) What is the rate of change in composition of faunules with respect to altitude?

This information does not now exist on any meaningful scale for any hyperdiverse group of organisms. Without this information, it is impossible to scale any kind of locally derived estimate of biodiversity to even a regional perspective. With this information, I believe we can get much closer to estimating the magnitude of life on the planet. And with these kinds of data from three or four ATBIs, much finer estimates can be made elsewhere of actual amounts of biodiversity that are based on fewer samples and made with quicker inventories.

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