

What we know and don't know about Earth's missing biodiversity

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Estimates of non-microbial diversity on Earth range from 2 million to over 50 million species, with great uncertainties in numbers of insects, fungi, nematodes, and deep-sea organisms. We summarize estimates for major taxa, the methods used to obtain them, and prospects for further discoveries. Major challenges include frequent synonymy, the difficulty of discriminating certain species by morphology alone, and the fact that many undiscovered species are small, difficult to find, or have small geographic ranges. Cryptic species could be numerous in some taxa. Novel techniques, such as DNA barcoding, new databases, and crowd-sourcing, could greatly accelerate the rate of species discovery. Such advances are timely. Most missing species probably live in biodiversity hotspots, where habitat destruction is rife, and so current estimates of extinction rates from known species are too low.

How many species are there?

This deceptively simple question has a rich pedigree. In 1833, Westwood [1] speculated 'On the probable number of species of insects in the Creation'. Over recent decades, many have grappled with the question, reaching widely varying conclusions [2–6]. Clearly, far more species exist than taxonomists have named; most are missing from the taxonomic catalog. Alas, taxonomists have complicated matters by inadvertently giving multiple names to many known species. Chapman's recent, thorough compilation of estimates [7], plus new studies embracing novel methods of estimation, motivate our synthesis of recent progress.

Here, we highlight previous work and ask: How many missing species are left to discover? Where do these species live? What ecological traits might they possess? And, how can unresolved challenges in documenting diversity be best approached? We do not, however, conjecture about the total number of species on Earth. For some taxa, the numbers and their uncertainties are well known. For others, including insects and fungi, the estimates vary so widely as to overwhelm any simple attempt to estimate a grand total for all species.

Human activities currently drive species to extinction at 100–1000 times their natural rate [8]. It is likely that biologists will not discover many missing species before

they vanish and so will underestimate the magnitude of the contemporary biodiversity crisis [3,8,9]. The need to discover and describe species has never been more urgent [8,10]. Optimizing where to focus conservation interventions requires, in part, counting species accurately and knowing where they live [3]. Unfortunately, current conservation efforts work from an incomplete biodiversity catalog [11].

Today, describing the unknown animal species might cost US\$263 billion [12] and require centuries to complete. Given such obvious impracticalities, there is little choice but to rely on current estimates of total species numbers and their probable geographic distribution, using the best available information [2,3,13–15].

How many species are known?

Known species counts

Table 1 simplifies Chapman's [7] compilation of species numbers. We add additional data to illustrate key debates. As have others, we restrict our analyses to metazoans (fungi, plants, and animals) because for viruses, bacteria, and other microorganisms, the definition of 'species' is unclear. The column 'Currently Catalogued' counts known species within various taxonomic groupings, and represents the work of many thousands of taxonomists across hundreds of years. Despite this massive undertaking, simply adding up the numbers of 'known' species, even for well-studied groups such as birds, is itself not straightforward. (See 'Described Species Range', which shows the range of variability for different groups). Synonymy is the problem.

The problem of synonymy

A range of estimates arises because taxonomists have described some species many times. This is not surprising. The descriptions of species come from different taxonomists on different continents in different generations. Fixing this problem requires considerable effort. For flowering plants, for example, the highest estimate of known species is twice that of the lowest; synonymy is suspected to be upwards of 60–78% for many plant groups [16]. Because estimates of missing species use the number of known species as their basis, these uncertainties are fundamental.

Taxonomists recognize the seriousness of synonyms. Major botanic gardens now collaborate to produce the

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Table 1. Chapman's (2009) estimates of species numbers [7], with other noteworthy estimates discussed in the main text

Kingdom	Phylum/Division	Within Phylum	Major division	Data from Chapman [7] and sources therein		Estimated	Other Refs
				Currently catalogued	Described species range		
Fungi				98 998	45 173–300 000	1.5 M	
						611 000	[6]
						9.9 M	[38]
						3.5–5.1 M	[39]
						1.62 M	[35]
Plants				310 129		~390 800	
				215 644		298 000	[6]
	Vascular plants	Magnoliophyta		(~268 600)	223 300–315 903	(~352 000)	
			Monocots and selected non-monocots			352 000 + 15%	[9,13]
		Gymnosperms		(~1021)	846–1021	(~1050)	
		Ferns and allies		(~12 000)	10 000–15 000	(~15 000)	
	Bryophyta			16 236	13 370–23 000	~22 750	
	Algae			12 272	12 205–12 272	NA	
Animals	All terrestrial			1 233 500		8 740 000	[6]
	All marine			193 756		2 210 000	[6]
	Porifera			~6000	5500–10 000	~18 000	
	Cnidaria			9795	9000–11 000	N/A	
	Mollusca			~85 000	50 000–120 000	~200 000	
	Annelida			16 763	120,00–16,763	~30 000	
	Arthropoda	Tropical arthropods				3.6–11.4 M	[33]
		Arachnida		102 248	60 000–102 248	~600 000	
		Myriapoda		16 072	8160–17 923	~90 000	
		Insecta		~1 M	720 000–>1 M	5 M	
			Coleoptera	360 000–400 000		1.1 M	
			Diptera	152 956		240 000	
			Hemiptera	80 000–88 000			
			Hymenoptera	115 000		>300 000	
			Lepidoptera	174 250		300 000–500 000	
		Crustacea		47 000	25 000–68 171	150 000	
				20 000	20 000–25 000	(~80 000)	
	Platyhelminthes			<25 000	12 000–80 000	~500 000	
	Nematoda					>1 M	[22]
				7003	6100–7003	~14 000	
	Echinodermata			12 673	N/A	~20 000	
	Other invertebrates			64 788		~80 500	
	Chordata		Mammals	5487	4300–5487	~5500	
			Birds	9990	9000–9990	>10 000	
				10 052			^a
			Reptiles	8734	6300–8734	~10 000	
			Amphibians	6515	4950–6515	~15 000	
			Fishes	31 269	25 000–31 269	~40 000	

^a<http://www.birdlife.org/datazone/info/taxonomy>.

unique and continuously updated *World Checklist of Selected Plant Families* [17], which has largely resolved the problem of synonymy for approximately 110 000 species (all monocots, plus selected non-monocot families). Other rigorous attempts to confront synonymy include the 2011 symposium to eliminate separate names for asexual and sexual stages of certain fungi [18]. An estimated 66% of fungal names are synonymous [19].

How many species are unknown?

The completeness of global inventories varies greatly (see 'Estimated' in Table 1). Completeness ranges from approximately 97% for mammals, 80–90% for flowering

plants, 79% for fish, 67% for amphibians, roughly 30% for arthropods and <4% for nematodes [11,13,20–22] (Table 1). Across these groups, levels of completeness decline with the currently known numbers of species. Taxonomic effort is distributed approximately evenly among vertebrates, plants, and invertebrates, yet plants have approximately ten times, and invertebrates 100 times, more known species than do vertebrates [23,24].

Global inventories (Table 1 'Estimated') come from various methods, including the expert opinions of taxonomists specialized on the various taxa. Differing methods result in widely varying estimates; for instance, estimates for fungi vary nearly 20-fold. Methods fall into three basic

categories: extrapolations from fractions, extrapolations from taxonomic-scaling patterns and mechanistic model estimates.

Extrapolations from fractions of unknown species

Early, often-controversial estimates of missing species used fractions of missing species in samples. Hodkinson and Casson [25] used such fractions to predict the number of insect species globally. Finding that 62.5% of hemipteran species in a location were unknown, the authors projected the existence of 1.84–2.57 million insect species globally. Using an alternative extrapolation, Adamowicz and Purvis [26] calculated a correction factor for three different sources of diversity underestimation (differential taxonomic effort among biogeographical regions; multi-continental distributions of species; and morphology and genetics) and concluded that the number of known branchiopod crustaceans should more than double.

In such sample-based estimates, the key assumption that described species form a random, unbiased subset of all species will rarely hold. For example, for well-known terrestrial and marine taxa, a few species have large geographical ranges, and many have small ones, with the former being more common locally than are the latter [27]. Inevitably, common and widespread and, thus, taxonomically known, species will predominate in small samples, leading to a spurious confidence in taxonomic completeness that declines as samples become more complete. As we show later, even well-known vertebrate taxa are now yielding surprising numbers of new species, overlooked because of their small ranges or because of cryptic species complexes (Box 1).

The hyper-estimates of species numbers

The greatest uncertainties involve ‘hyper-estimates’, by which we mean individual totals of 5 million species or more. For example, Grassle and Maciolek [28] used the relationship between the numbers of seafloor invertebrates in samples of increasing area to extrapolate the total number of species in the deep sea. They estimated that the deep seafloor worldwide could have up to 10 million species, a total several orders of magnitude larger than that found in their geographically restricted samples.

Large numbers capture the public imagination and invite scientific controversy. In the case of marine invertebrates, such extrapolations from local to global seafloor diversity were unwarranted because of the obvious doubts about scaling up from small to a much larger geographical scales [29]. Several authors have highlighted the limitations of scaling up from estimates collected at a single spatial scale [3,15,30,31].

For tropical insects, the best-known hyper-estimate was Erwin’s [4] astounding conjecture of 30 million species. His approach started with the number of beetle species associated uniquely with a single species of tropical rainforest tree in Panama. This generated criticism, primarily from those concerned about the assumptions underlying such a ‘small to large’ extrapolation, but spawned considerable interest and research. Fundamental was the degree of host specificity of herbivorous insects on their food plants, which Erwin assumed to be high. Novotny *et al.* [32],

Ødegaard [15] and others found considerably lower host specificity, perhaps by a factor of four or five. The resulting global estimate of insect species richness has accordingly dropped sharply.

Recently, Hamilton *et al.* [21] highlighted the sensitivity of Erwin’s model to its input parameters. As with earlier studies, their estimate requires values for the average effective specialization of herbivorous beetle species across all tree species, a correction factor for beetle species that are not herbivorous, the proportion of canopy arthropod species that are beetles, the proportion of all arthropod species found in the canopy, and the number of tropical tree species. Their approach uniformly and randomly sampled plausible ranges for each of these numbers. Approximately 90% of these parameter combinations resulted in estimates of between 3.6 and 11.4 million species [33]. Although their parameter distributions are untested assumptions, Hamilton *et al.*’s approach suggests that Erwin’s estimate is exceedingly improbable.

Fungi are poorly known [34] and their diversity is hotly debated. Hawksworth [35] started with the 6:1 ratio of fungi to flowering plant species found in Britain, where both groups are well known, and extrapolated this ratio to the global total for flowering plants, yielding an estimate of 1.62 million species of fungi globally. May [36] was sharply critical because it again involved a small- to large-scale extrapolation. His key concern was that the species-rich tropics would not have the ratio of fungi to plants found in Britain. If so, then in tropical collections over 95% of the species encountered would be new, given that only approximately 70 000 fungi had been catalogued globally. The actual percentages of new species from tropical samples were much smaller. An alternative approach by Mora *et al.* [6] estimates 611 000 fungal species globally and seemingly supports May’s more conservative estimate of approximately 500 000 fungal species.

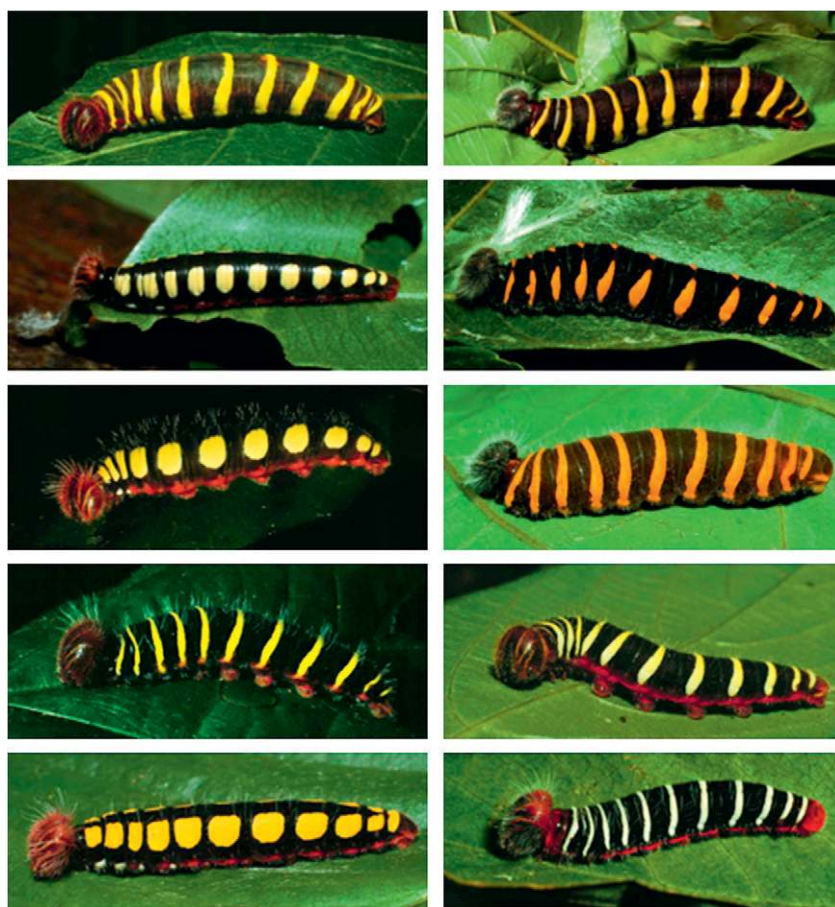
Such low estimates of fungi have spawned strident criticism. First, small, quickly obtained samples will not be random ones, but dominated by well-known, widespread species. Second, Hawksworth [35] emphasized not only fungal and plant associations, but also the strong associations of fungi with insects. Each beetle species might have its own unique fungus. Third, Bass and Richards [37] point out that, over the past decade, new methods in molecular biology and environmental probing have substantially increased the rate of descriptions of species.

Cannon [38] estimates approximately 9.9 million species of fungi, whereas O’Brien *et al.* [39] estimate 3.5–5.1 million species. Very high genetic diversity in soil samples (491 distinct genomes in pine-forest soil samples and 616 in soils from mixed-hardwood forests) underlay these hyper-estimates. They emerge from extrapolating from local to global scales, so previous concerns about scaling also apply here. At present, there are no comparable genomic surveys in tropical moist forests showing exceptional fungal richness, as would be expected if the above hyper-estimates are correct. Moreover, no one has yet shown how communities of fungal genomes change over large geographical areas. In an important potential advance to this debate, Blackwell [40] lists locations and hosts known to contain rich, and

Box 1. Cryptic species

Advances in DNA barcoding created a wave of species discovery [76,77]. Many new discoveries are 'cryptic' species (Figure 1), that is, not single species, but complexes of closely related species with highly similar morphologies [78]. The description of cryptic species has grown exponentially over the past two decades [78,79], with 60% of newly described species now derived from cryptic complexes [52]. For many poorly studied groups, it is possible that the number of cryptic species is actually an order of magnitude higher than the number currently described (D. Bickford, personal communication).

Amazingly, taxonomists have found cryptic species to be quite evenly distributed among major metazoan taxa and different biogeographical regions [79]. Even the best-studied regions of the world, including those predicted to contain few unknown species [20], could have far higher numbers of missing species than previously estimated. Incorporating cryptic species into spatial models that predict unknown biodiversity should considerably improve the accuracy of future estimates. Environmental DNA, a novel survey method using DNA in water or other environmental samples, might prove useful for finding rare or missing species and thereby improving future biodiversity inventories [80,81].



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Figure 1. Ten species of cryptic caterpillars in the *Astraptes fulgerator* complex from the Guanacaste Conservation Area in Costa Rica. Adapted, with permission, from [76].

poorly known, fungal communities. These are places where one might test key hypotheses.

Scaling the tree of life

Another way to estimate the numbers of species links them to the numbers of higher taxonomic levels, such as families and orders. Arguments arise over the correct level of higher taxonomic unit to use, as well as the previous criticisms of using ratios to extrapolate from one place to another [41].

Ricotta *et al.* [42] described scaling patterns across different taxonomic levels of seed plants, asserting that they could use such relationships 'to predict species richness in a given area with considerable accuracy'. Mora *et al.* [6]

slightly modified this approach to estimate the total number of species 'on earth and in the ocean'. They used the rates of description to fit asymptotic regression models to taxon-accumulation curves over time for different taxonomic levels. Using the asymptotic estimates for animals, the ratios of classes per phyla, orders per class, families per order, and genera per family were strikingly similar. On this basis, they posited that the ratio of species per genus would be the same globally and so predicted 8 750 000 terrestrial and 2 210 000 marine species. There is no particular theoretical reason to make this final supposition, but to the extent that they could compare the best available estimates of numbers of species within phyla, there was broad agreement with their predictions.

Bass and Richards [37] and Blackwell [40] criticized Mora *et al.*'s [6] estimates for fungi, because the numbers of higher fungal taxa, including even phyla, are still increasing. The number of genera is not asymptoting, making it hard to use Mora *et al.*'s approach. Moreover, synonymy is also a potential problem in fungal genera and families.

Mechanistic models of taxonomists as predators, missing species as prey

None of the work described thus far incorporates a mechanistic understanding of species discovery. Early efforts estimated the asymptotic number of species over time assuming that the curve's first derivative, the rate of description, will decline [6,11,43–45]. By analogy, one views this as a model with 'predators' (taxonomists) exploiting a continually declining 'prey' population (the numbers of missing species). For birds globally, and for some taxa regionally, the rates of description are indeed slowing and asymptotic approaches provide reasonable estimates. Mora *et al.* [6] also used this approach to estimate the numbers of higher taxa.

For most taxa, not only are the rates of species description increasing, but they are also doing so exponentially, so

ruling out estimates of asymptotes. The numbers of taxonomists are also increasing exponentially [46]. To account for this, a more truly mechanistic model accounts for taxonomic effort and taxonomic efficiency required to document previously unknown species [13,20,47,48]. Joppa *et al.* [9,13] initially proposed this strategy, noting it shares an intellectual lineage with traditional 'catch per unit effort' approaches used in fishery models. It defines 'taxonomic effort' as the number of taxonomists involved in describing species and 'taxonomic efficiency' as an increase in the number of species described per taxonomist, adjusted for the continually diminishing pool of as-yet-unknown species. Importantly, the model uses maximum likelihood techniques, allowing confidence intervals about any estimate.

How well does this model perform? Validating it by expert opinion revealed broad agreement with its predictions [13], but the method encounters two problems. First, in some cases, the numbers of species described per taxonomist remain approximately constant even as the pool of missing species inevitably declines. Individual taxonomists probably describe only so many species in a year, regardless of how many missing species there are, and

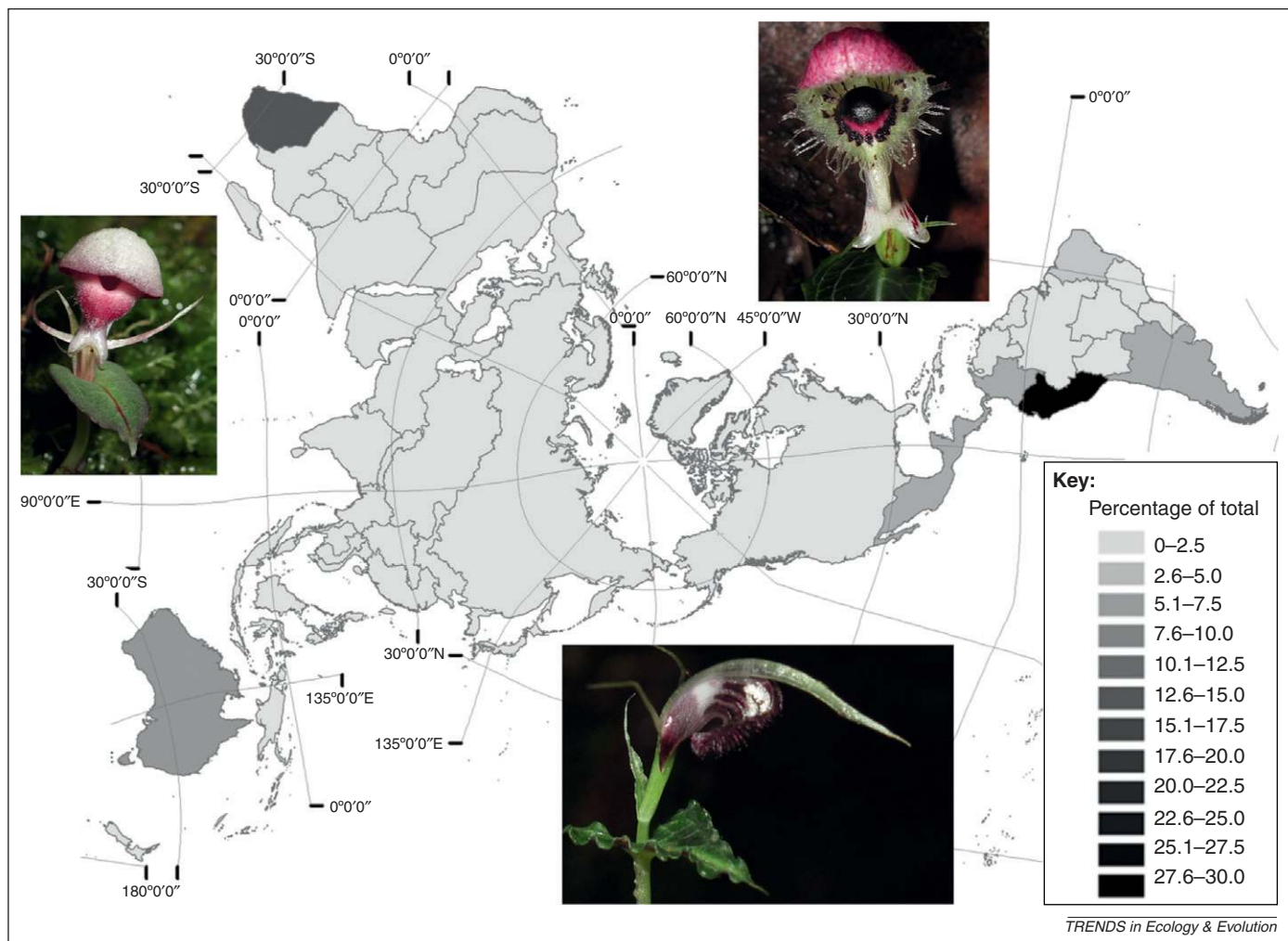


Figure 1. The percentages of missing plant species predicted to occur in various regions suggest that existing biodiversity hotspots, such as southern Africa, Central America, and especially the northern Andes, hold the greatest numbers. However, unexpectedly low predicted numbers in places such as New Guinea might reflect their inaccessibility to scientists, causing missing-species numbers to be underestimated. Stephanie Pimm Lyon photographed these three orchids in the genus *Corybas*; similar to most of the members of this genus that she collected in New Guinea in 2012, she considers these probably new to science. Adapted, with permission, from [9].

perhaps work through the backlog methodically, genus by genus. Second, although taxonomic efficiency increases in a broadly linear way for most taxa, for others, more complex patterns suggest alternative functions [9,13].

Where are the missing species?

Knowing where species live is vital for setting international priorities for conservation. Incomplete information might leave one unable to prioritize effectively where to allocate conservation efforts. For example, the 'biodiversity hotspots' [49] combine a measure of habitat destruction (<30% habitat remaining) with the numbers of known endemic flowering plant species (>1500). These areas have become international priorities for conservation, with large resources allocated for their preservation [50]. The incomplete catalog of flowering plants begs our asking: Will knowing where the missing species are located alter conservation priorities? Are missing species concentrated in imperiled habitats where they are at risk of extinction? If so, can they be found before they go extinct?

Several studies identify areas of high missing biodiversity for prioritizing future conservation efforts [9,20,47,48,51–54]. Recently, Joppa *et al.* [9] suggest that missing plant species will concentrate in the biodiversity hotspots (Figure 1), places such as Central America, the northern Andes and South Africa, where, by definition, the threat of habitat loss is greatest. These predictions have limitations, obviously, because factors such as remoteness or political instability reduce the rate of species description in some regions. Expanding on Joppa *et al.* [9], Laurance and Edwards [55] highlighted their probable underestimation of the importance of the Asia-Pacific region, such as the Philippines and New Guinea,

as centers of missing plant species (Figure 1). The Asia-Pacific region might also have many unknown amphibian and mammal species [20]. Despite such limitations, biodiversity hotspots will surely sustain large numbers of missing species. As we discuss below, missing species tend to have small geographical ranges.

These findings bring both good and bad news. The good news is that most missing species occur in places that are already global conservation priorities. The bad news is that most of these species are in areas already under dire threat of habitat loss. By instilling an appropriate sense of urgency, focusing species-discovery efforts on hotspots would result in 'taxonomy that matters' [56]. Discovering unknown species in hotspots would help to underscore their exceptional biological diversity and uniqueness. Invaluable insights would also be gained into the traits these species display and the services they could potentially provide (Box 2).

Are missing species different?

To extend our analogy of 'taxonomists as predators', taxonomists are surely searching for the most obvious 'prey', inadvertently selecting species with traits that are most conducive for discovery. As the pool of missing species diminishes, one would expect those remaining to have traits that make them harder to find (Figure 2). For example, the unique biota of deep-sea hydrothermal vents was discovered only during the late 1970s, whereas a nocturnal stream-dwelling lizard from high in the Peruvian Andes was described only this year [57]. This begs the question: are missing species functionally different from those already described?

Certainly, the first European expeditions across the African savannahs had little trouble in finding and

Box 2. Biodiversity services

That species provide novel pharmaceuticals and products, are a source of disease-resistant germplasm for crops, and yield myriad insights into the functioning of nature, are familiar ideas [82]. Cone shells (Figure 1) provide a particularly compelling example of how rare or unknown species imperiled by current environmental threats could yield important benefits for humanity [83]. For instance, venom from the magician cone snail (*Conus magus*) can be used to develop a pain

reliever 1000 times more powerful than morphine [84], whereas compounds from other *Conus* species are being used to treat many neurological diseases [85]. The rate of description of *Conus* species is still high [46], suggesting that many more species are missing. Many live on tropical reefs where environmental damage is extensive and increasing, suggesting that species will go extinct before their value can be appreciated.



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Figure 1. Examples of cone shells. Chivian *et al.* [83] estimate that 50 000 toxins occur in known species of *Conus*, arguing that it might be the most pharmacologically important genus in nature. Photograph reproduced, with permission, from Keoki Stender.

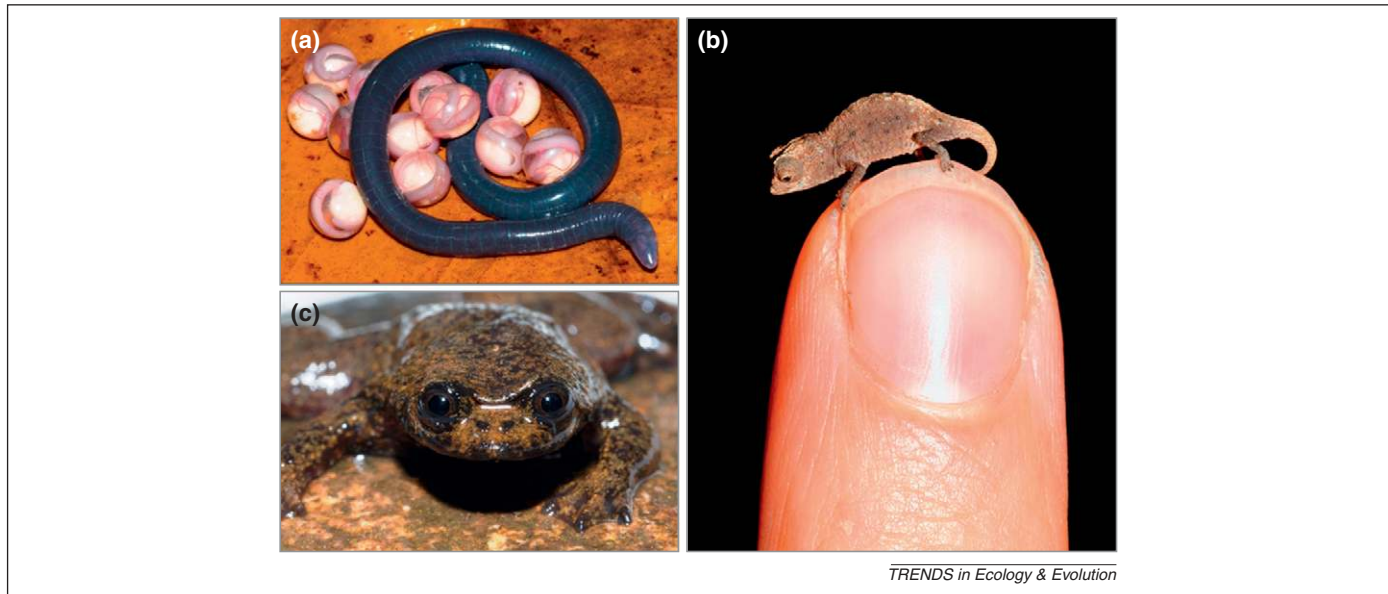


Figure 2. Many undiscovered species are difficult to find because they are cryptic, small in size or have small geographic ranges. Shown are (a) a recently discovered burrowing caecilian species from India, (b) a newly discovered chameleon (*Brookesia micra*) from Madagascar that is the smallest lizard in the world, and (c) a locally endemic waterfall frog (*Barbourula kalimantanensis*) from Borneo. Photographs reproduced, with permission, from Biju Das (a), Frank Glaw (b), and David Bickford (c).

describing large-bodied wildebeests, giraffes, and elephants. The remaining unknown mammal species are smaller. Similarly, taxonomists have described larger-bodied species sooner in a variety of animals, including British beetles [58], South American songbirds [59], and Neotropical mammals [60]. However, this trend evidently varies among taxa. Body size in most animal groups is highly right-skewed [61,62] and, thus, the tendency for newly described species to be small bodied might simply reflect a random sample of the overall size distribution, rather than small-bodied animals being harder to find or describe [63]. Body size and year of description strongly correlate in insects, but this phenomenon varies considerably among different insect taxa [2,64].

However, scientists still find larger-bodied species in remote or poorly studied parts of the world (Figure 3). Many islands in the Philippines, for instance, remain unexplored. Recent discoveries there include a 2-m long monitor lizard (*Varanus olivaceus*) [65] and a large-bodied fruit-bat (*Styloctenium mindorensis*) [66]. Local communities hunt both. Along with small body size, geographical remoteness affects the rate at which taxonomists discover species.

Unknown species might also be less colorful or obvious than their described brethren. We hypothesize, for instance, that taxonomists will describe brightly colored bird species earlier than drab, earth-toned bird species. Species with cryptic behaviors also tend to be discovered later (Figure 2). For instance, as-yet-undescribed shore fish are likely to be those that hide in deeper waters [51], whereas researchers recently discovered a fossorial caecilian, representing an entirely new family (Chikilidae), only after 1100 h of digging holes in the ground [67]. Animals with elusive life histories can be discovered even in the best-studied parts of the world. A recently described fossorial salamander in the southeastern USA not only represents a new genus (*Urspelerpes*), but

is also among the smallest salamander species ever found [68].

Finally, taxonomists describe small-ranged species later than more widely distributed ones [63,64,69]. Such trends are evident in holozooplankton [69], fleas [70], leaf beetles [71], Palaearctic dung beetles [72], South American oscine songbirds [59], and Neotropical mammals [60].

Missing species will typically be more vulnerable than are described species. Most often, two key factors combine to determine the threat level for a species under the IUCN Red List criteria: its geographical range size and the amount of its habitat loss. We have already emphasized that missing species are generally concentrated in the places where habitat loss is greatest. In showing that missing species also tend to have small ranges, we can be certain that many will eventually be listed as ‘threatened’; that is, if they do not become extinct first.

The high vulnerability of missing species is evident in Brazil, which has the largest number of amphibian species globally (Figure 4). Although local amphibian diversity is especially high in the western Brazilian Amazon, the greatest concentration of species with small geographic ranges is in the coastal hotspot of the Atlantic forest [27]. Taxonomists described most of these small-ranged species only within the past two decades, a pattern similar to that for mammals in Brazil [47]. Missing species, such as those only recently discovered, will probably also be in such vulnerable areas. Only approximately 7% of the original Brazilian Atlantic forest remains [27].

All this signals that researchers are underestimating the magnitude of the current extinction crisis, because many undiscovered species will both have small ranges and occur in threatened hotspots [20]. Including estimates of missing species increases the percentage of threatened plants to 27–33% of all plant species [13]. If many species are cryptic (Box 1), the figure could be even higher.



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Figure 3. Relatively large, conspicuous species are still being discovered in remote or poorly studied areas. Shown are (a) an undescribed jay species (*Cyanocorax* sp.) from the Amazon basin, (b) a recently discovered fruit bat (*Styloctenium mindoroensis*) and (c) monitor lizard (*Varanus bitatawa*) from the Philippines. Photographs reproduced, with permission, from Mario Cohn-Haft (a), H.J.D. Garcia/Haribon Foundation (b), and Joseph Brown (c).

Prospects

Relative to the task at hand, taxonomists are describing species slowly. Although the catalog of flowering plants should be complete in a few decades [13], recent estimates suggest another 480 years is needed to describe all the species on Earth [23], or possibly 1000 years just to describe all fungi [40]. Yet, the outlook is considerably brighter than one might suppose, for several reasons.

Herbaria and museums might harbor many of the missing species. For example, Bebbler *et al.* [73] found that existing herbarium material typically took decades to describe. They estimated that perhaps half of all missing plant species were already in herbaria.

Recent advances in DNA barcoding make it easier to discriminate similar species [74,75], thereby accelerating species descriptions and generally aiding better taxonomy. Barcoding is also inherently a quantitative technique, allowing statistical sampling methods to estimate what fraction of samples are missing species and how species turn over geographically. Potentially, barcoding can address many of the methodological concerns we have highlighted here. Nonetheless, the use of 'floating barcodes' (ones without associated morphological descriptions of organisms) generates considerable debate.

The genetic methods used to detect fungi discussed above are rapidly expanding knowledge of what could be an extremely diverse group, but one poorly sampled by traditional morphological approaches.

Many communities of taxonomists are now addressing the tedious but vital issue of synonymy and placing their lists and taxonomic decisions into the public domain. These include websites for flowering plants (<http://www.kew.org/wcsp/>), spiders (<http://research.amnh.org/oonopidae/catalog/>) amphibians (<http://research.amnh.org/herpetology/amphibia/index.php>), birds (<http://www.birdlife.org/datazone/info/taxonomy>), and mammals (<http://www.bucknell.edu/msw3/>). Global efforts to catalogue all species, such as All-Species (<http://www.allspecies.org>), GBIF (<http://www.gbif.org>), Species 2000 (www.sp2000.org), and Tree of Life (<http://www.tolweb.org/tree/phylogeny.html>), are also now readily available online.

Efforts to map where species occur are progressing. The most obvious advance is using smartphones and software-website applications such as iNaturalist (<http://www.inaturalist.org>) that link data directly into the IUCN Red Lists, the Global Biodiversity Information Facility, and other pre-existing databases. Crowd-sourcing of species mapping could greatly expand these databases, which are major

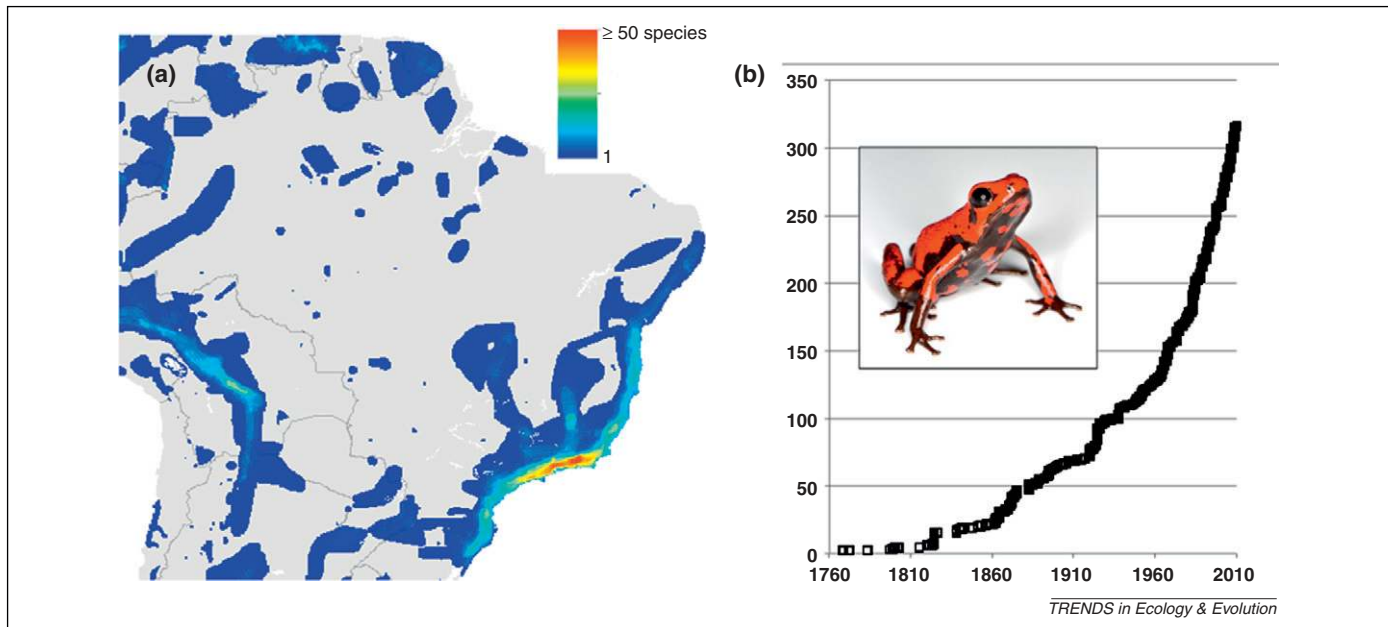


Figure 4. Although amphibian species reach their peak local diversity in the Brazilian Amazon, the greatest concentration of small-ranged species is in the Brazilian Atlantic forests (a). (b) The number of small-ranged species in Brazil is increasing exponentially, with most discovered only recently. Reproduced, with permission, from [27] (a) and [47] (b); photograph reproduced with permission from Luis A. Mazariegos.

contributions to knowledge of where species live. Such databases are already promoting the discovery of missing species, revealing those that do not fit known descriptions.

Finally, even if it might not be practical or even desirable to describe every species, cataloguing carefully selected taxa, locations, or regions might generate important insights [56]. Better quantification of the number and locations of known species afford a fighting chance to set effective conservation priorities, even if the taxonomic catalog is incomplete.

Acknowledgments

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Erratum to: “What we know and don’t know about Earth’s missing biodiversity”

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In our recent TREE review paper entitled “What we know and don’t know about Earth’s missing biodiversity” [1], a subtle but important error was inadvertently introduced by the typesetter.

A central feature of this paper was [Table 1](#), which listed known and estimated numbers of species for a variety of different taxa. Unfortunately, the Phylum/Divisions column of [Table 1](#), from Platyhelminthes through Chordata,

Table 1. Chapman’s (2009) estimates of species numbers [7], with other noteworthy estimates discussed in the text

Kingdom	Phylum/Division	Within Phylum	Major division	Data from Chapman [7] and sources therein		Estimated	Other sources
				Currently catalogued	Described Species Range		
Fungi				98,998	45,173 - 300,000	1.5M	
						611,000	[6]
						9.9 M	[38]
						3.5-5.1M	[39]
						1.62M	[35]
Plants				310,129		~390, 800	
				215,644		298,000	[6]
	Vascular Plants	Magnoliophyta		(~268,600)	223,300 - 315,903	(~352,000)	
			monocots and selected non-monocots			352,000 + 15%	[9,13]
		Gymnosperms		(~1,021)	846 - 1,021	(~1,050)	
		ferns and allies		(~12,000)	10,000 - 15,000	(~15,000)	
	Bryophyta			16,236	13,370 - 23,000	~22,750	
Animals	Algae			12,272	12,205 - 12,272	NA	
	All Terrestrial			1,233,500		6,530,000	[6]
	All Marine			193,756		2,210,000	[6]
	Porifera			~6,000	5,500 - 10,000	~18,000	
	Cnidaria			9,795	9,000 - 11,000	NA	
	Mollusca			~85,000	50,000 - 120,000	~200,000	
	Annelida			16,763	12,000 - 16,763	~30,000	
	Arthropoda						
		tropical arthropods				3.6 -11.4 M	[33]
		Arachnida		102,248	60,000 - 102,248	~600,000	
		Myriapoda		16,072	8,160 - 17,923	~90,000	
		Insecta		~1M	720,000 - >1M	5M	
			Coleoptera	360,000 - 400,000		1.1M	
			Diptera	152,956		240,000	
			Hemiptera	80,000 - 88,000			
			Hymenoptera	115,000		>300,000	

Table 1 (Continued)

Kingdom	Phylum/Division	Within Phylum	Major division	Data from Chapman [7] and sources therein		Estimated	Other sources
				Currently catalogued	Described Species Range		
			Lepidoptera	174,250		300,000 - 500,000	
		Crustacea		47,000	25,000 - 68,171	150,000	
	Platyhelminthes			20,000	20,000 - 25,000	(~80,000)	
	Nematoda			<25,000	12,000 - 80,000	~500,000	
						>1M	[22]
	Echinodermata			7,003	6,100 - 7,003	~14,000	
	Others - Invertebrates			12,673	NA	~20,000	
	Chordata			64,788		~80,500	
			Mammals	5,487	4,300-5,487	~5,500	
			Birds	9,990	9,000-9,990	>10,000	
			Birds	10,052			^a
			Reptiles	8,734	6,300-8,734	~10,000	
			Amphibians	6,515	4,950-6,515	~15,000	
			Fishes	31,269	25,000-31,269	~40,000	

^awww.birdlife.org/datazone/info/taxonomy.

was shifted downward by one row. This created a misalignment between those taxa and their associated values for known and estimated species.

We provide here a corrected version of Table 1. We apologize for failing to detect this error at the galley stage and kindly thank Lukas Schärer of University of Basel, Switzerland for alerting us to it.

Reference

- 1 Scheffers, B.R. *et al.* (2012) What we know and don't know about Earth's missing biodiversity. *Trends Ecol. Evol.* 27, 501–510

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