The biodiversity of species and their rates of extinction, distribution, and protection

BIODIVERSITY STATUS

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S. L. Pimm,* C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, J. O. Sexton

BACKGROUND: A principal function of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is to "perform regular and timely assessments of knowledge on biodiversity." In December 2013, its second plenary session approved a program to begin a global assessment in 2015. The Convention on Biological Diversity (CBD) and five other biodiversity-related conventions have adopted IPBES as their science-policy interface, so these assessments will be important in evaluating progress towards the CBD's Aichi Targets of the Strategic Plan for Biodiversity 2011–2020. As a contribution toward such assessment, we review the biodiversity of eukaryote species and their extinction rates, distributions, and protection. We document what we know, how it likely differs from what we do not, and how these differences affect biodiversity statistics. Interestingly, several targets explicitly mention "known species"—a strong, if implicit, statement of incomplete knowledge. We start by asking how many species are known and how many remain undescribed. We then consider by how much human actions inflate extinction rates. Much depends on where species are, because different biomes contain different numbers of species of different susceptibilities. Biomes also suffer different levels of damage and have unequal levels of protection. How extinction rates will change depends on how and

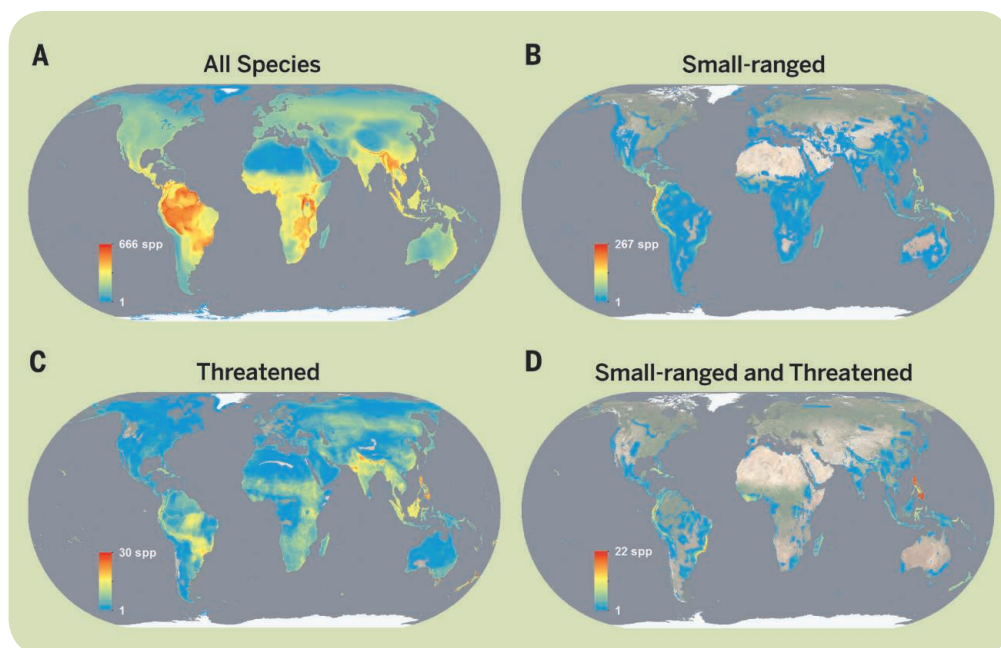where threats expand and whether greater protection counters them.

ADVANCES: Recent studies have clarified where the most vulnerable species live, where and how humanity changes the planet, and how this drives extinctions. These data are increasingly accessible, bringing greater transparency to science and governance. Taxonomic catalogs of plants, terrestrial vertebrates, freshwater fish, and some marine taxa are sufficient to assess their status and the limitations of our knowledge. Most species are undescribed, however. The species we know best have large geographical ranges and are often common within them. Most

known species have small ranges, however, and such species are typically newer discoveries. The numbers of known species with very small ranges are increasing quickly, even in well-known taxa. They are geographically concentrated and are disproportionately likely to be threatened or already extinct. We expect unknown species to share these characteristics. Current rates of extinction are about 1000 times the background rate of extinction. These are higher than previously estimated and likely still underestimated. Future rates will depend on many factors and are poised to increase. Finally, although there has been rapid progress in developing protected areas, such efforts are not ecologically representative, nor do they optimally protect biodiversity.

OUTLOOK: Progress on assessing biodiversity will emerge from continued expansion of the many recently created online databases, combining them with new global data sources on changing land and ocean use and with increasingly crowdsourced data on species' distributions. Examples of practical conservation that follow from using combined data in Colombia and Brazil can be found at www.savingspecies.org and www.youtube.com/watch?v=R3zjeJW2NVk.

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Different visualizations of species biodiversity. (**A**) The distributions of 9927 bird species. (**B**) The 4964 species with smaller than the median geographical range size. (**C**) The 1308 species assessed as threatened with a high risk of extinction by BirdLife International for the Red List of Threatened Species of the International Union for Conservation of Nature. (**D**) The 1080 threatened species with less than the median range size. (D) provides a strong geographical focus on where local conservation actions can have the greatest global impact. Additional biodiversity maps are available at www.biodiversitymapping.org.

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S. L. Pimm,[1]* C. N. Jenkins,[2] R. Abell,[3]† T. M. Brooks,[4] J. L. Gittleman,[5] L. N. Joppa,[6] P. H. Raven,[7] C. M. Roberts,[8] J. O. Sexton[9]

Recent studies clarify where the most vulnerable species live, where and how humanity changes the planet, and how this drives extinctions. We assess key statistics about species, their distribution, and their status. Most are undescribed. Those we know best have large geographical ranges and are often common within them. Most known species have small ranges. The numbers of small-ranged species are increasing quickly, even in well-known taxa. They are geographically concentrated and are disproportionately likely to be threatened or already extinct. Current rates of extinction are about 1000 times the likely background rate of extinction. Future rates depend on many factors and are poised to increase. Although there has been rapid progress in developing protected areas, such efforts are not ecologically representative, nor do they optimally protect biodiversity.

One of the four functions of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is to "perform regular and timely assessments of knowledge on biodiversity" (*1*). In December 2013, its second plenary session approved starting global and regional assessments in 2015 (*1*). The Convention on Biological Diversity (CBD) and five other biodiversity-related conventions have adopted IPBES as their science-policy interface, so these assessments will be important in evaluating progress toward the CBD's Aichi Targets of the Strategic Plan for Biodiversity 2011–2020 (*2*). They will necessarily follow the definitions of biodiversity by the CBD introduced by Norse *et al.* (*3*) as spanning genetic, species, and ecosystem levels of ecological organization. As a contribution, we review the biodiversity of eukaryote species and their extinction rates, distributions, and protection.

Interestingly, several targets explicitly mention "known species"—a strong, if implicit statement of incomplete knowledge. So how many eukaryote species are there (*4*)? For land plants, there are 298,900 accepted species' names, 477,601 synonyms, and 263,925 names unresolved (*5*). Because the accepted names among those resolved is 38%, it seems reasonable to predict that the same proportion of unresolved names will eventually be accepted. This yields another ~100,000 species for a total estimate of 400,000 species (*5*). Models predict 15% more to be discovered (*6*), so the total number of species of land plants should be >450,000 species, many more than are conventionally assumed to exist.

For animals, recent overviews attest to the question's difficulty. About 1.9 million species are described (*7*); the great majority are not. Costello *et al.* (*8*) estimate 5 ± 3 million species, Mora *et al.* (*9*) 8.7 ± 1.3 million, and Chapman (*7*) 11 million. Raven and Yeates (*10*) estimate 5 to 6 million species of insects alone, whereas Scheffers *et al.* (*11*) think uncertainties in insect and fungi numbers make a plausible range impossible. Estimates for marine species include 2.2 ± 0.18 million (*9*), and Appeltans *et al.* estimate 0.7 to 1.0 million species, with 226,000 described and another 70,000 in collections awaiting description (*12*).

Concerns about biodiversity arise because present extinction rates are exceptionally high. Consequently, we first compare current extinction rates to those before human actions elevated them. Vulnerable species are geographically concentrated, so we next consider the biogeography of species extinction. Given taxonomic incompleteness, we consider how undescribed species differ from described species in their geographical range sizes, distributions, and risks of extinction. To understand whether species extinction rates will increase or decrease, we review how and where threats are expanding and whether greater protection may counter them. We conclude by reviewing prospects for progress in understanding the key lacunae in current knowledge.

Background Rates of Species Extinction

Given the uncertainties in species numbers and that only a few percent of species are assessed for their extinction risk (*13*), we express extinction rates as fractions of species going extinct over time—extinctions per million species-years (E/MSY) (*14*)—rather than as absolute numbers. For recent extinctions, we follow cohorts from the dates of their scientific description (*15*). This excludes species, such as the dodo, that went extinct before description. For example, taxonomists described 1230 species of birds after 1900, and 13 of them are now extinct or possibly extinct. This cohort accumulated 98,334 species-years—meaning that an average species has been known for 80 years. The extinction rate is $(13/98,334) \times 10^6 = 132$ E/MSY.

The more difficult question asks how we can compare such estimates to those in the absence of human actions—i.e., the background rate of extinction. Three lines of evidence suggest that an earlier statement (*14*) of a "benchmark" rate of 1 (E/MSY) is too high.

First, the fossil record provides direct evidence of background rates, but it is coarse in time, space, and taxonomic level, dealing as it does mostly with genera (*16*). Many species are in monotypic genera, whereas those in polytypic genera often share the same vulnerabilities to extinction (*17*), so extinction rates of species and genera should be broadly similar. Alroy found Cenozoic mammals to have 0.165 extinctions of genera per million genera-years (*18*). Harnik *et al.* (*19*) calculated the fractions of species going extinct over different intervals. Converting these to their corresponding rates yields values for the past few million years of 0.06 genera extinctions per million genera-years for cetaceans, 0.04 for marine carnivores, and, for a variety of marine invertebrates, between the values of 0.001 (brachiopods) and 0.01 (echinoids).

Second, molecular-based phylogenies cover many taxa and environments, providing an appealing alternative to the fossil record's shortcomings. A simple model of the observed increase in the number of species S_t in a phylogenetic clade over time, t, is $S_t = S_0 \exp[(\lambda - \mu) \times t]$, where λ and μ are the speciation and extinction rates. In practice, λ and μ may vary in complex ways. Estimating the average diversification rate, $\lambda - \mu$, requires only modest data. Whether one can separate extinction from speciation rates by using species numbers over time is controversial (*20*, *21*) and an area of active research that requires carefully chosen data to avoid potential biases. With the simple model, the logarithm of the number of lineages [lineages through time (LTT)] should increase linearly over time, with slope $\lambda - \mu$, but with an important qualification. In the limit of the present day, the most recent taxa have not yet had time to become extinct. The LTT curve

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should be concave, and its slope should approach λ [20, 21]. This allows separate estimation of speciation and extinction rates.

Unfortunately, in the many studies McPeek [22] compiled, 80% of the LLT curves were convex, whence μ = 0. If currently recognized subspecies were to be considered as species, then a greater fraction of the LTT curves might be concave, making μ > 0. This suggests that taxonomic opinion plays a confounding role and one not easily resolved, whatever the underlying statistical models. The critical question is how large an extinction rate can go undetected by these methods. Generally, if it were large, then concave curves would predominate, but that falls short of providing quantification.

Third, data on net diversification, λ – μ, are widely available. Plants [23] have median diversification rates of 0.06 new species per species per million years, birds 0.15 [24], various chordates 0.2 [22], arthropods 0.17, [22], and mammals 0.07 [22]. The rates for individual clades are only exceptionally >1. Valente et al. [25] specifically looked for exceptionally high rates, finding them >1 for the genus Dianthus (carnations, Caryophyllaceae), Andean Lupinus (lupins, Fabaceae), Zosterops (white-eyes, Zosteropidae), and cichlids in East African lakes.

There is no evidence for widespread, recent, but prehuman declines in diversity across most taxa, so extinction rates must be generally less than diversification rates. This matches the conclusion from phylogenetic studies that do not detect high extinction rates relative to speciation rates, and both lines of evidence are compatible with the fossil data. This suggests that 0.1 E/MSY is an order-of-magnitude estimate of the background rate of extinction.

Current Rates of Species Extinction

The International Union for Conservation of Nature (IUCN), in its Red List of Threatened Species, assesses species' extinction risk as Least Concern, Near-Threatened, three progressively escalating categories of Threatened species (Vulnerable, Endangered, and Critically Endangered), and Extinct [13]. By March 2014, IUCN had assessed 71,576 mostly terrestrial and freshwater species: 860 were extinct or extinct in the wild; 21,286 were threatened, with 4286 deemed critically endangered [13]. The percentages of threatened terrestrial species ran from 13% (birds) to 41% (amphibians and gymnosperms) [13]. For freshwater taxa [26], threat levels span 23% (mammals and fishes) to 39% (reptiles).

Efforts are expanding the limited data from oceans for which only 2% of species are assessed compared with 3.6% of all known species [27]. Peters et al. [28] assessed the snail genus Conus, Carpenter et al. [29] corals, and Dulvy et al. [30] 1041 shark and ray species. Overall, some 6041 marine species have sufficient data to assess risk: 16% are threatened and 9% near-threatened, most by overexploitation, habitat loss, and climate change [13].

The direct method of estimating extinction rates tracks changing status over time. Most changes in IUCN Red List categories result from improved knowledge, so the calculation of the Red List Index measures the aggregate extinction risk of all species in a given group, removing such nongenuine changes [31]. Hoffmann et al. [32] showed that, on average, 52 of 22,000 species of mammals, birds, and amphibians moved one Red List category closer to extinction each year. If the probability of change between any two adjacent Red List categories were identical, this would yield an extinction rate of 450 E/MSY. The probability is lower for the transition from critically endangered to extinct [33], however, perhaps because the former receive disproportionate conservation attention.

Extinction rates from cohort analyses average about 100 E/MSY (Table 1). Local rates from regions can be much higher: 305 E/MSY for fish in North American rivers and lakes [34], 954 E/MSY for the region's freshwater gastropods [35], and likely >1000 E/MSY for cichlid fishes in Africa's Lake Victoria [36]

Studies of modern extinction rates typically do not address the rate of generic extinctions, but direct comparisons to fossils are possible. For mammals, the rate is ~100 extinctions of genera per million genera years [13] and ~60 extinctions for birds [13, 37].

How does incomplete taxonomic knowledge affect these estimates? Given that many species are still undescribed and many species with small ranges are recent discoveries, these numbers are surely underestimates. Many species will have gone or be going extinct before description [8, 15]. Extinction rates of species described after 1900 are considerably higher than those described before, reflecting their greater rarity (Table 1). Moreover, a greater fraction of recently described species are critically endangered (Table 1). Rates of extinction and proportions of threatened species thus increase with improved knowledge. This warns us that estimates of recent extinction rates based on poorly known taxa (such as insects) may be substantial underestimates because many rare species are undescribed.

In sum, present extinction rates of ~100 E/MSY and the strong suspicion that these rates miss extinctions even for well-known taxa, and certainly for poorer known ones, means present extinction rates are likely a thousand times higher than the background rate of 0.1 E/MSY.

The Biogeography of Global Species Extinction

Human actions have eliminated top predators and other large-bodied species across most continents [38], and oceans are massively depleted of predatory fish [39]. For example, African savannah ecosystems once covered ~13.5 million km². Only ~1 million km² now have lions, and much less area has viable populations of them [40]. Recognizing the importance of such regional extirpations, we concentrate on the irreversible global species extinctions and now consider where they will occur.

General patterns—"laws" [41]—describe species' geographical distributions. First, small geographical ranges dominate. Gaston [42] suggests a lognormal distribution, although many taxa have more small-ranged species than even that skewed distribution (Fig. 1). In Fig. 1, 25% of most taxa have ranges <10^5 km² and, for amphibians, <10^3 km².

These sizes substantially overestimate actual ranges. Figure 1 assumes that, for plants, the presence in one of the 369 regions of the World Checklist of Selected Plant Families (WCSPF) [43] means the species occurs throughout the entire region. Similar, Fig. 1 assumes that the Conus species occur throughout the ocean within their geographical limits. These outer boundaries of the estimated ranges are too large. Of course, species are further limited to specific habitats within the outer boundaries of their ranges [44, 45].

A second law is that small-ranged species are generally locally scarcer than widespread ones [41]. Combined, these two laws have consequences. First, unsurprisingly, taxonomists generally describe widespread and locally abundant species before small-ranged and locally scarce ones [46]. Even for well-known vertebrates, taxonomists described over half the species in Brazil with ranges <20,000 km² after 1975 [47].

Second, since the majority of species are undescribed, one expects that samples from previously unexplored regions would contain a preponderance of them. Indeed, the fraction of undescribed species should provide estimates of how many species there are in total [11, 12]. In practice, small

Table 1. Extinction rates calculated by cohort analysis and fractions of species that are critically endangered (CR). Data from [13, 37, 50, 51]. Bird species thought to be "possibly extinct" are counted as extinctions.

When described	Species	Extinctions	Species-years	Extinction rate	CR	% CR
Birds						
Before 1900	8922	89	1,812,897	49	123	1.4
1900 to present	1230	13	98,334	132	60	4.9
Amphibians						
Before 1900	1437	14	212,348	66	37	2.6
1900 to present	4972	22	206,187	107	483	9.7
Mammals						
Before 1900	2983	36	500,252	72	70	2.3
1900 to present	2523	43	176,858	243	126	5.0

samples across dispersed locations include widespread, common species and few rare ones. For example, in samples across ~6 million km^2 of Amazonian lowlands, a mere 227 species accounted for half the individual trees, suggesting that the Amazon might be floristically quite homogeneous. However, the samples contained 4962 known tree species, and many that could not be identified (48). The Amazon might contain as many as 16,000 species (48). Only accumulating species lists while quantifying sampling effort can provide compelling estimates of how diversity varies geographically and thus how many total species there are.

Uncertainties about where species are may be more limiting than not knowing how many species there are. The IUCN maps 43,000 species (13). Almost half are amphibians, birds, and mammals. The most common—but least informative map for conservation—is of species richness. Widely distributed species dominate these maps, whereas the majority of species with small ranges are almost invisible (fig. S1). An essential accompaniment maps out small-ranged species, such as the richness of species with less than the median range size (49) or, for coarsely defined regions, those endemic to each region. Figures 2 to 5 provide examples for mammals and amphibians (13, 50, 51), flowering plants (43), freshwater fish (52), and marine snails of the genus Conus (28). Supplementary materials provide details (53). There are similar maps for 845 reef-building coral species (29), coastal fish, various marine predators, and invertebrates (54, 55).

Where there are the most species, one might expect the most species of all range sizes—large and small alike. Surprisingly, species with small ranges are geographically concentrated. The highest numbers of bird species live in the lowland Amazon, whereas small-ranged species concentrate in the Andes (fig. S1). Although mapped at a much coarser scale, freshwater fish also often attain their highest diversities in large rivers flowing through forests. A striking exception is the high numbers in East African rift lakes (Fig. 4). The Philippines have the greatest number of Conus species; the concentrations of small-ranged species are elsewhere (Fig. 5). Other marine taxa are similar (55).

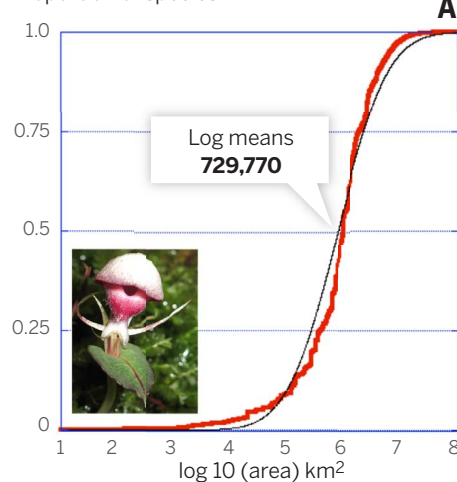Many past extinctions have been on islands, but current patterns of threat are geographically much broader (49, 56). Rare species—either widespread but scarce (such as top predators and other large-bodied animals) or with small geographical ranges and so often locally scarce (41)—dominate the lists. Species with small ranges are disproportionately more likely to be threatened than those with larger ones (49, 57). Interestingly, for a given range size, a smaller fraction of island species are threatened than for those on continents, likely because island species are locally more abundant (49).

Concentrations of threatened species more closely match concentrations of small-ranged species than they do total species numbers and so are more informative about where currently threatened species live and where species may become threatened in the future (49, 50) (Fig. 2 and fig. S1).

Myers et al. (58) made the vital and separate point that habitat destruction is greatest where the highest concentrations of small-ranged species live. As it were, small-ranged species are born vulnerable and then have the greater threats thrust upon them. Myers et al.'s hotspot definition combines a minimum number of small-ranged plant species and sufficiently high habitat loss.
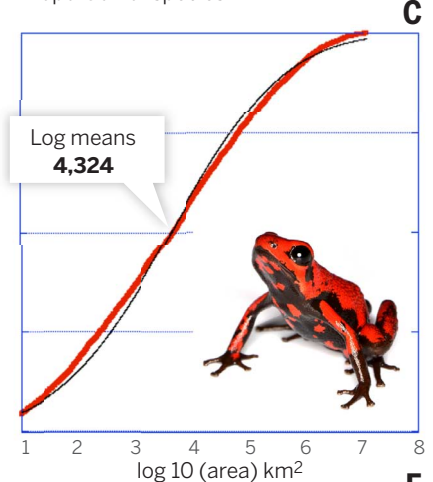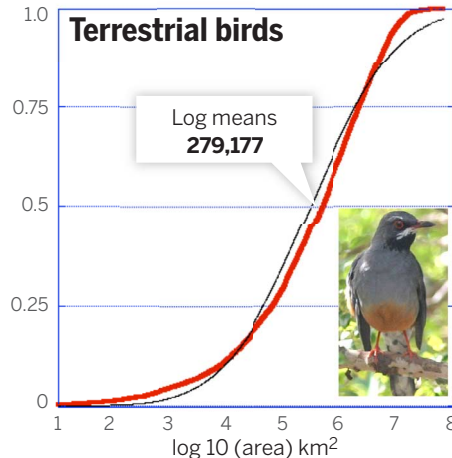

Flowering plants
Proportion of species
A
Log means
729,770
log 10 (area) km^2

Conus
Proportion of species
B
Log means
215,513
log 10 (area) km^2

Amphibians
Proportion of species
C
Log means
4,324
log 10 (area) km^2

Terrestrial birds
D
Log means
279,177
log 10 (area) km^2

Terrestrial mammals
E
Log means
115,602
log 10 (area) km^2

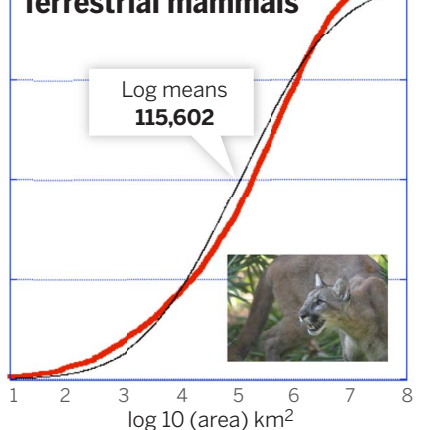**Fig. 1. The sizes of geographical ranges.** (**A** to **E**) In red, the cumulative proportions of species against log range size in km^2 for selected groups of species. In black, the lognormal distributions with the same corresponding log means and variances. Numbers are the log means. See details in (53). The photographs are from S.L.P., except the plant—an undescribed species of *Corybas* orchid (Stephanie Pimm Lyon) and a newly discovered frog, *Andinobates cassidyhornae* (Luiz Maziergos). All reproduced with permission.

Quantitative data from the WCSPF (43) have clarified these areas (59).

Future Rates of Species Extinction

The overarching driver of species extinction is human population growth and increasing per capita consumption. How long these trends continue—where and at what rate—will dominate the scenarios of species extinction and challenge efforts to protect biodiversity.

Before the last decade, most applications developed extinction scenarios from simple assumptions of land use change as a primary driver of biodiversity loss, employing the species-area relationship (14). For example, Pimm and Raven (60) projected 18% extinction by 2100 due to deforestation to date in tropical forest hotspots and 40% extinction if these regions retained natural habitat only in currently protected areas.

Until recently, these scenarios were the only empirically validated models. The validations focused on vertebrates, globally (61) or regionally: eastern United States (62), South American Atlantic Forest (63), and insular Southeast Asia (64). There was excellent correspondence between the numbers of species predicted to go extinct and those that did (62) or, for more recent deforestation, with those threatened (61, 63, 64). There are discussions about the underlying theory of such estimates (65). Nonetheless, when one counts all the extinctions likely to follow deforestation (66), these estimates are conservative.

Theory predicts that many more extinctions are possible with severe habitat fragmentation (67), as observations confirm (68).

Pereira et al.'s review of projected future extinctions (69) classified and compared various models. Strikingly, the six sets of projections predicted a hundred-fold range of extinction rates. This emerged from the different drivers considered (land use change, climate change, or both), model approaches, taxonomic coverage, and geographic scale. Given this range, there is an urgent need for validation of projections against documented extinctions to date. Few studies attempt this. Here, we consider the prospects for such validation with newly available data that can reduce the uncertainties.

Climate disruption will cause species extinctions, but the range of estimates is large. Thomas et al. (70) estimated that 15 to 37% of various taxa would be committed to extinction by 2050 for a mid-range warming scenario. Specific studies for birds estimated that >400 species of land birds out of 8750 studied (4.6%) would experience a range reduction greater than 50% by year 2050 (71). For Western Hemisphere land birds, intermediate extinction estimates based on projected climate-induced changes in current distributions ranged from 1.3% (1.1°C warming) to 30% (6.4°C warming) of the 3349 species studied (72). A global assessment of expected warming-induced range contractions estimated that 184 to 327 montane bird species (out of 1009) would lose

>50% of their range and result in range sizes of <20,000 km^2 (73).

Cheung et al. (74) used a global climate model to predict range shifts, extinction, and invasion intensities based on ocean warming up to 2050 for 1066 species of exploited marine fish and invertebrates. They predicted that poleward range movements would lead to species' extinctions from tropical and subpolar latitudes of 4 and 7% respectively, with mostly range readjustments in between. They attribute the lower extinction probabilities than on land (70) to greater freedom of movement in the sea. Enclosed seas, like the Mediterranean, could trap clusters of endemic species against insurmountable barriers (75). Nor did they consider any other potential extinction drivers, such as ocean acidification (76), overfishing (30), or the inability of sessile species—such as brooding corals—to move.

On land, the effects of climate disruption remain unclear for several reasons. A key uncertainty is whether climate disruption and habitat destruction harm overlapping sets of species or broadly different ones—and they may act synergistically. Climate disruption seems to be an added threat (77). Some studies explicitly combine species-area projections of species loss to incorporate climate change as a driver, via models of changing global vegetation (78), and suggest that 12% of species will become extinct. Other studies estimate that 7 to 24% of plant species (79) will become extinct. The impacts
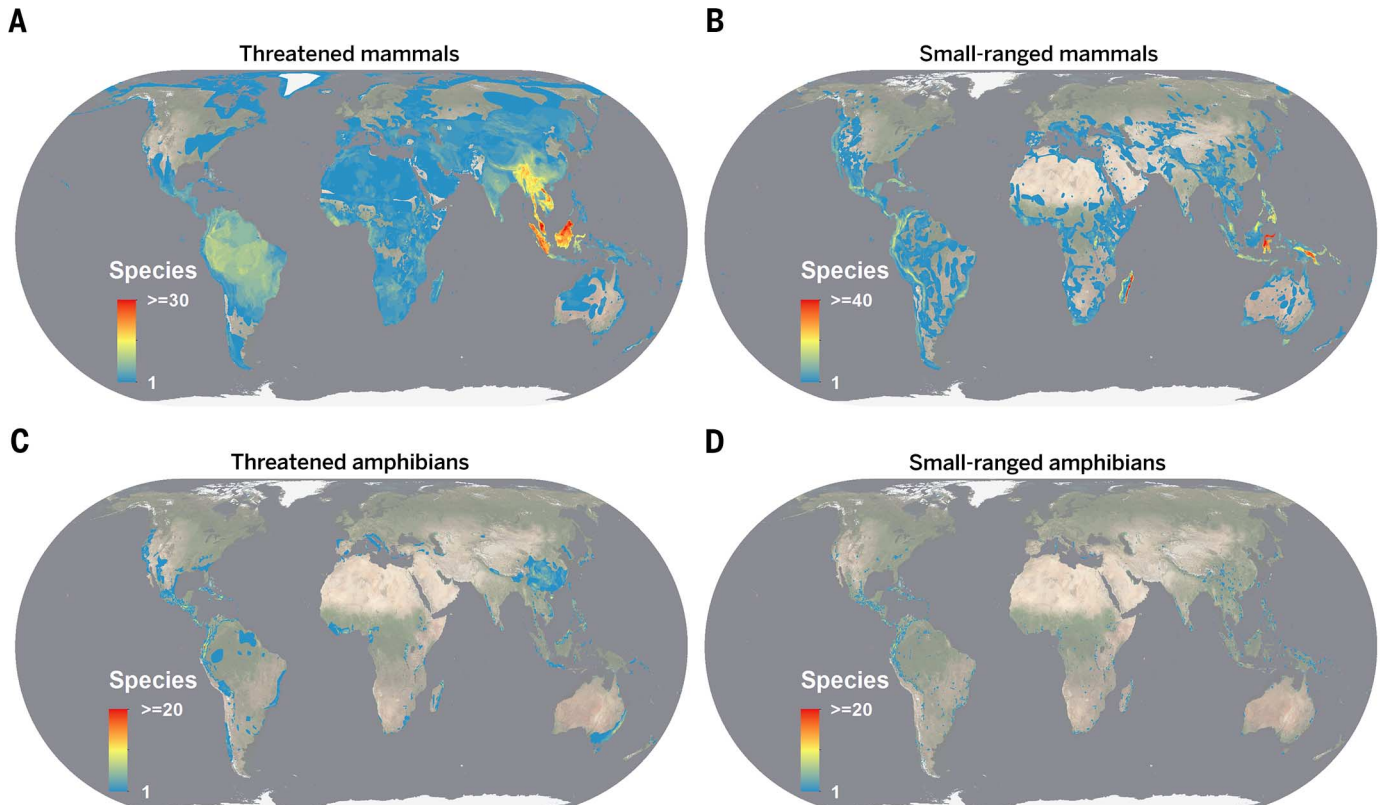

Fig. 2. Fine-scale patterns of terrestrial vertebrate diversity. (**A**) The numbers of threatened mammal species and (**B**) those with ranges smaller than the median range size. (**C**) and (**D**) show the corresponding maps for amphibians. See details in (53).

of climate disruption are complex. A meta-analysis compared 188 predicted with 130 observed climate change responses and suggested that 10 to 14% of species would become extinct (80). Moreover, the interactions of environmental drivers with intrinsic biological traits (e.g., geographic range, body size, and reproductive rate) indicate that species' responses to increased human population density will become increasingly uncertain (81).

Another uncertainty is that none of Pereira et al.'s (69) models assessed population viability and habitat suitability. Rather, they take indirect approaches, such as some fraction of their present range, as in (70). Approaches incorporating viability provide strong empirical foundations for estimating extinction risk (82). Some regional studies have employed them, however, including a study of South African Proteaceae (83).

Above all, there are few empirical tests. The above methods assume species moving poleward, to higher elevations, or to deeper depths to remain in their climate envelopes. Using fortuitous repeats of surveys done decades ago, diverse studies find substantial lags in upslope movements for plants (84), insects (85), and birds (86). These question the fate of species now living outside past climate envelopes. Furthermore, the few studies that consider predictions of changing geographical ranges from the past to the present and then calibrate them against present ranges do not always find compelling matches (87).

For freshwater species, direct and indirect habitat modification, including pollution (88) and the already extensive and continuing fragmentation and flow regulation of rivers (89), are clearly major drivers of extinction, especially for species with limited dispersal abilities. Existing alterations to freshwater systems may already have compromised species' viability to the extent that no level of future protection might prevent extinction (90).

Introduced species, including diseases, are a major cause of extinctions and the main cause of recent bird extinctions (37). Some 10% of plant species are endemic to islands small enough for introduced herbivores to be a major threat (59). We know of no estimates of extinction rates from introduced species. Such extinctions can unfold quickly and unpredictably, as the destruction of Guam's endemic avifauna by an introduced snake (91) and the destruction and possible extinction, primarily by the Nile perch, of as many as 200 Lake Victoria haplochromine cichlids demonstrate (36).

In sum, there are few empirically tested predictions of future extinctions. Typical scenarios consider what can be predicted—extinctions from deforestation or climate disruption—but not potentially important processes—disease, introduced species, or hydrological changes—that one cannot easily model.

How Will Protection Slow Extinction Rates?

Among the many uncertainties in projecting future extinction rates, a particularly important one is the effect that conservation actions might have in reducing them (92). For instance, the rate at which mammals, birds, and amphibians have slid toward extinction over the past four decades would have been 20% higher were it not for conservation efforts (32).

The destruction of natural habitats is the major threat to species (13). Thus, protected areas, while diverse and differing substantially in their purposes and levels of protection (93), are essential to reducing extinctions. Aichi Target 11 seeks the protection of >17% "ecologically representative" terrestrial and freshwater ecosystems and >10% of coastal and marine ecosystems (2), whereas CBD's Global Strategy for Plant Conservation (GSPC) Target 4 seeks >15% of "each ecological region or vegetation type" (94).
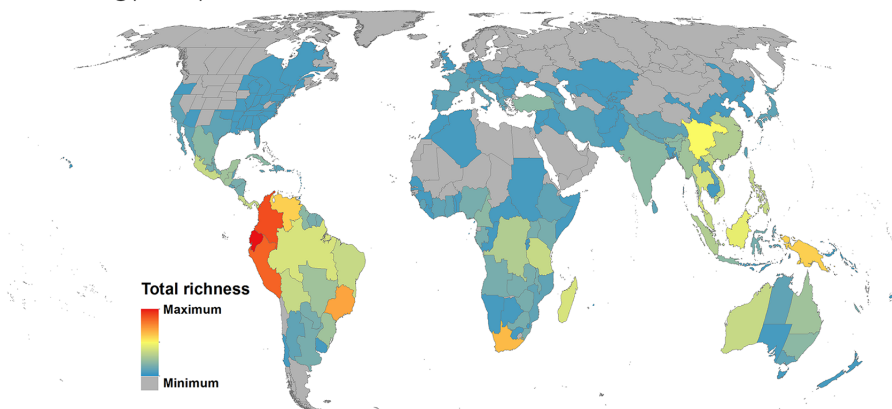
In 2009, 12.9% of the total land area was under some legal protection, up from <4% in 1985 (95). Protected areas are biased toward areas where there is little human pressure (96). Coverage varies between 4% and 25% protection of 14 major terrestrial biomes (96). Of the world's 821 terrestrial ecoregions, half had <10% of their area protected (96).

How well these areas capture species within their boundaries now and in the future is an essential input to predict future extinction rates (50, 60). Rodrigues et al. (97) analyzed threatened mammal, bird, amphibian, and turtle ranges combined with the World Database on Protected Areas (93). Overall, 27% of threatened amphibians, 20% of threatened birds, 14% of threatened mammals, and 10% of threatened turtles live outside protected areas. Subsequent analyses have set targets for representation scaled in inverse proportion to range size (98)—for example, 100% representation for species with ranges <1000 km^2, 10% representation for ranges >250,000 km^2, and a linear interpolation for species in between. Only ~46% of birds, ~39% of mammals, and ~19% of amphibians reach or exceed their targets (98).

These global gap analyses are vulnerable to commission errors—species appearing to occur when they do not—resulting from the overlay of the coarse-resolution species maps with the high-resolution protected area boundaries (99). These can generate a false sense of security:
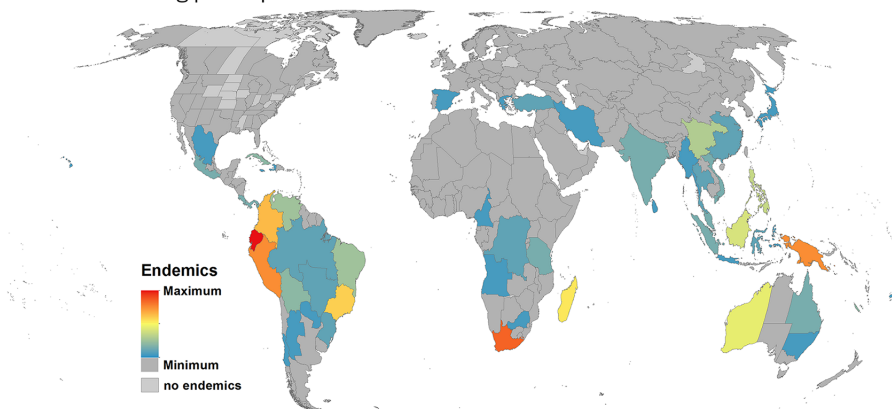
A

All flowering plant species

B

Endemic flowering plant species

Source: World Checklist of Selected Plant Families

Fig. 3. Relative numbers of flowering plant species in the different regions used by the World Checklist of Selected Plant Families (43). (**A**) All species and (**B**) endemic species. See details in (53).

Species thought safely represented may be going extinct. Alternative approaches that accept higher omission errors, although less efficient, are less problematic. Thus, for birds, protected areas cover only 49% of sites documented to hold the entire population of at least one highly threatened species (*56*) and only 51% of globally important sites for birds (*100*).

Do protected areas work? Certainly, some fail completely: Even large national parks in West Africa have lost lions and many of their prey (*40*). For freshwater species populations, occurrence within reserves is no guarantee of protection, given external threats like flow modification and lack of explicit reserve management to meet freshwater objectives (*101*). Protected forests generally retain their forest cover (*102*), have far fewer anthropogenic fires than unprotected areas (*103*), and do not attract higher than expected human population growth to their perimeters (*104*). Most studies do not assess plant and animal populations directly, and remaining habitats are often too small, or too heavily exploited, to retain all of their species (*105*). Those that do track species reveal that protected areas deliver substantial outcomes for preventing extinctions. Globally, species with >50% of the sites of particular importance for them protected are sliding toward extinction only half as rapidly as those with <50% of their important sites protected (*100*).

Ocean protection lags behind that on land. A 2013 assessment (*106*) reported ~10,000 marine protected areas (MPAs) covering 2.3% of the oceans. Aichi Target 11 admits "other effective area-based conservation measures," so this assessment included large fishery management zones closed to certain fishing gears, including some in New England, Florida, and New Zealand. These were not established for biodiversity conservation and, in the New Zealand case, were proposed by the deep-sea fishing industry, avoiding places important for fishing (*106*). A more conservative assessment (*107*) estimates 1.8% global coverage.

As on land, marine protected area coverage is uneven. Reserves are often absent where threats to biodiversity are highest, such as fishing grounds and oil and gas leases. Beyond the 200 nautical mile limits of national jurisdiction, 0.17% of open waters are protected, compared with 8% of continental shelves (*106*). Coastal coral reefs are the best protected, with 18.7% within protected areas by 2006 (*108*). Only 2% were in MPAs considered to be of adequate size, management, level of protection, and connectivity, however. Moves to establish large and remote sites as MPAs, such as the U.K.'s British Indian Ocean Territory, have contributed strongly to recent growth in protection, suggesting that the Aichi target of 10% coverage may be attainable (*109*). Marine protected areas that are no-take, well-enforced, old, large, and isolated by deep water or sand are disproportionately successful in retaining their species (*110*).

Aichi Target 11 seeks protection of 17% of terrestrial lands (*2*), whereas the GSPC seeks

to protect 60% of plant species (*94*). Are both targets possible simultaneously? The concentration of small-ranged species is such that were land protected efficiently to capture biodiversity, the 17% so selected would encompass part of the ranges of 81% of plant species and all the ranges of 67% (*59*). How might the prediction that 15% more plant species are currently undescribed change these selections? Joppa *et al.* (*111*) used rates of species' description corrected for taxonomic effort and predicted that undescribed species will be in the known concentrations of species with small ranges, leaving current priorities unchanged.

These plant priorities match those for terrestrial vertebrates. Some 89% of bird species, 80% of amphibians, and 74% of mammals live within these plant priority areas (*59*). Percentages for species with ranges smaller than the median are 88%, 82%, and 73%, respectively (*59*). With updated data, these results capture Myers *et al.*'s (*58*) observation that conserving a large fraction of species is possible in limited areas if authorities choose protected areas cognizant of what species they contain (*112*). Areas of high freshwater fish diversity match some areas of high terrestrial diversity, but such congruence cannot

be assumed: Exceptions include the high-diversity freshwater systems of the Ganges and Mekong deltas (*113*) (Fig. 4.) Moreover, protecting freshwater species will require managing landscapes and water use beyond reserves' fence lines and well into larger catchments (*101*).

What We Know, What We Do Not, and How to Fix the Gaps

We know enough to see that our ignorance about species' numbers, distributions, and status strongly affects key biodiversity statistics. Two examples illustrate the consequences. First, ~20% of known plants are thought threatened (*114*). Adding the predicted 15% of undescribed species—almost all will be rare and in places with extensive habitat loss (*36*)—suggests that 30% of plant species are threatened (*6*). Climate disruption threatens additional species.

Second, only 6.5% of the 632 *Conus* species are threatened. Another 14% are "Data Deficient"—there is insufficient information to assess their status, typically because they are rare and have small geographical ranges (*28*). Were better knowledge to deem them threatened, the map of where threatened species occur would change substantially (Fig. 5). Investment in extending
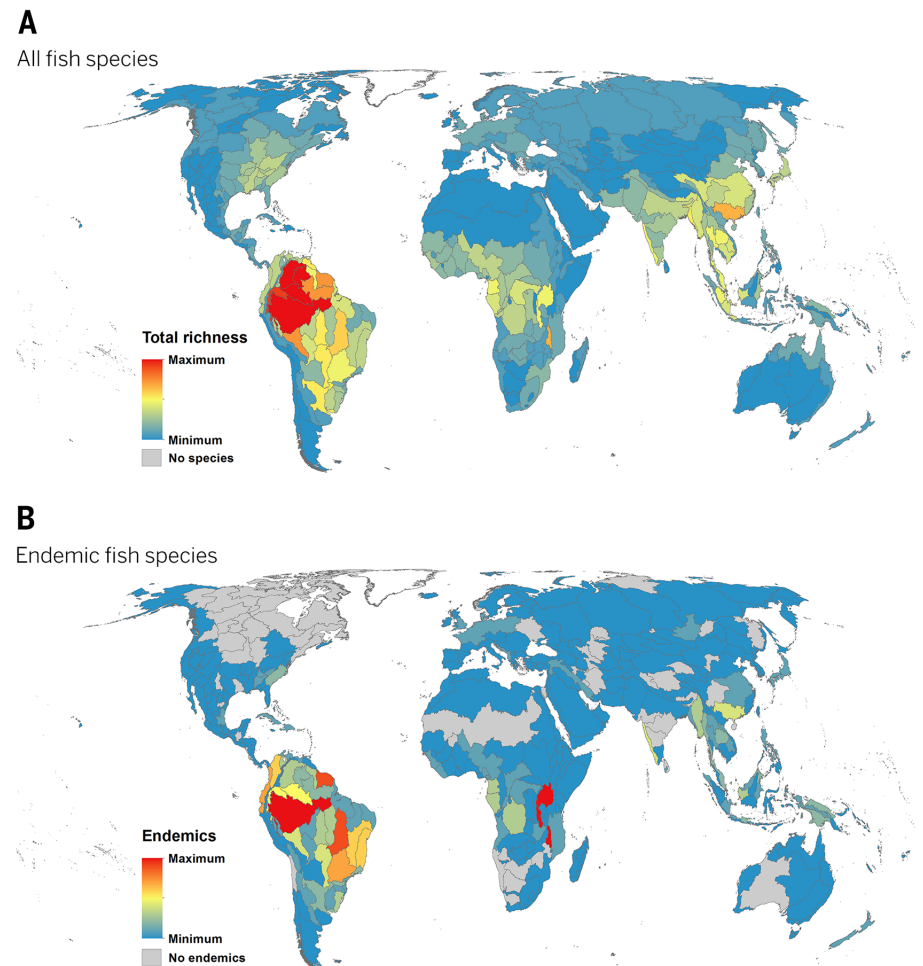
A

All fish species

B

Endemic fish species

Fig. 4. Relative numbers of freshwater fish species in the different freshwater ecoregions (*52*). (**A**) All species and (**B**) endemic species. See details in (*53*).

the coverage of the IUCN Red List to its target of 160,000 species assessments is a priority (*115*).

What is the progress toward getting better knowledge, and what are the prospects for continued improvements? Aichi Target 19 calls for data to be "widely shared." Recent online efforts toward this goal include the Global Biodiversity Information Facility (GBIF) (*116*), with 420 million records and 1.45 million species' and subspecies' names, and the Ocean Biogeographic Information System (*117*), with 38 million records of 115,000 species. Species 2000 seeks to create a validated checklist of all species, and the Tree of Life (*118*) and TimeTree (*119*) provide phylogenetic relationships.

Communities of taxonomists now address the tedious but vital issue of synonymy and placing their lists and taxonomic decisions into the public domain. Large databases include the World Register of Marine Species (*120*), which has checked 95% of 221,000 marine species, and FishBase, with 32,700 species of fish (*121*). WCSPF (*43*) has currently assessed ~110,000 plant species (*5*).

New technologies help. Genetic barcoding (*122*) offers the potential to identify animal species quickly for US$1 per sample from a small, but unique, DNA sequence. Barcoding for plants is slightly more difficult. For the great majority of unknown species in animal taxa with few taxonomic specialists, this will surely become the predominant method of discovering new species. It raises the controversial idea that many species may become known by a number derived from barcoding and not—or not only—from conventional descriptions (*123*). The potential to find new species and untangle clusters of cryptic species (*124*) is also being realized. Less appreciated is that cost-effective barcoding by batches of species is now possible. Powerful new statistical methods (*125*) estimate how many species may be present in an area and how these overlap with other samples from increasing sampling efforts. Combined with batch barcoding, there is the promise of rigorous estimates of what fractions of undescribed species are present in poorly sampled areas—the most direct way of estimating how many species there are.

Even for species that are mapped, substantial uncertainties remain. The highest apparent numbers of vertebrate species in South America (fig. S1) are close to research centers, as are many GBIF records. The most important consequence of having a public species' range map is that it challenges observers to confirm or amend it.

Although GBIF (*116*) is the repository for information into which other sources feed, the diversity of those sources merits comment. They include professional organizations, such as Tropicos (*126*), with 4.2 million specimens. The fastest growth in understanding species' distributions comes from large numbers of amateurs. Birdwatchers are most numerous: eBird (*127*) became an international depository in 2010 and already has >100,000 observers and >100 million observations. It permits fine-scale mapping and month-by-month changes in distribution. Such wealth of data skews broad biodiversity assessments (*128*), motivating efforts for less popular taxa.

To be useful, observations require identifications, and identifying organisms requires training and skill. Recent advances in photo-sharing technology and social networking provide new opportunities. Apps like iNaturalist (*129*) allow division of labor between amateur observers uploading mystery field observations from smartphones and skilled identifiers who later catalog these observations from the photos provided. Cooperation between amateurs and experts now produces high volumes of quality data for diverse taxa. iNaturalist has already logged over half a million records and become the preferred app for incorporating crowd-sourced data into national biodiversity surveys in Mexico and elsewhere. The Reef Life Survey is generating similar advances for marine biodiversity (*130*).

Crowd-sourced data, especially when including data on sampling effort, provide substantial opportunities to monitor a broad range of species over time and across broad geographical areas—exactly the requirements needed to assess the various scenarios for future extinction.
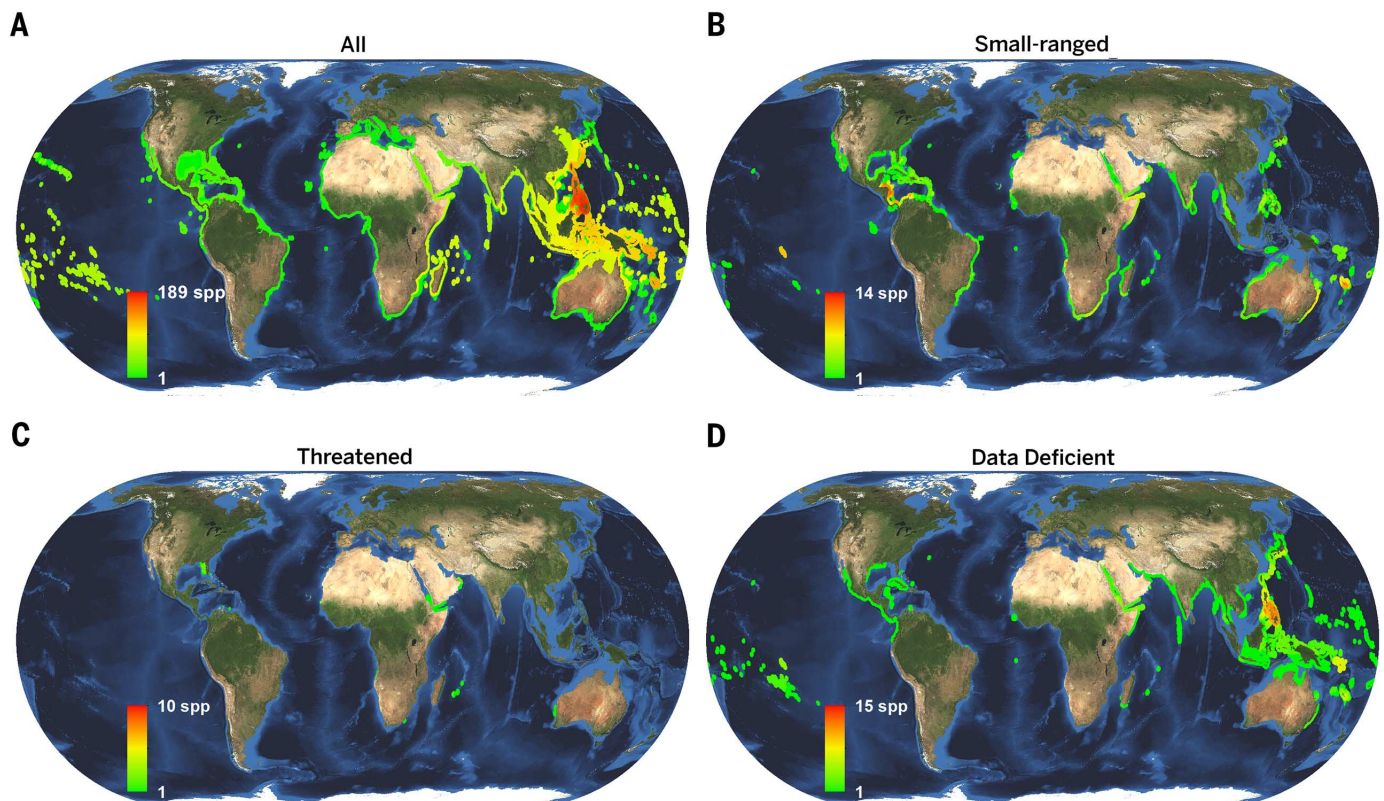

Fig. 5. The distribution of species in the marine snail genus *Conus*. (**A**) The numbers of all species; (**B**) those with ranges smaller than the median range size; (**C**) those threatened; and (**D**) data-deficient species for which there is insufficient data to assess their status. Figure S2 provides a detail of the Cape Verde islands, where a large number of small-ranged species live. The terrestrial background is shown in approximately true color to show the distribution of forests (dark green) and drylands (buff) and oceanic bathymetry (darker colors mean deeper water). See details in (*53*).
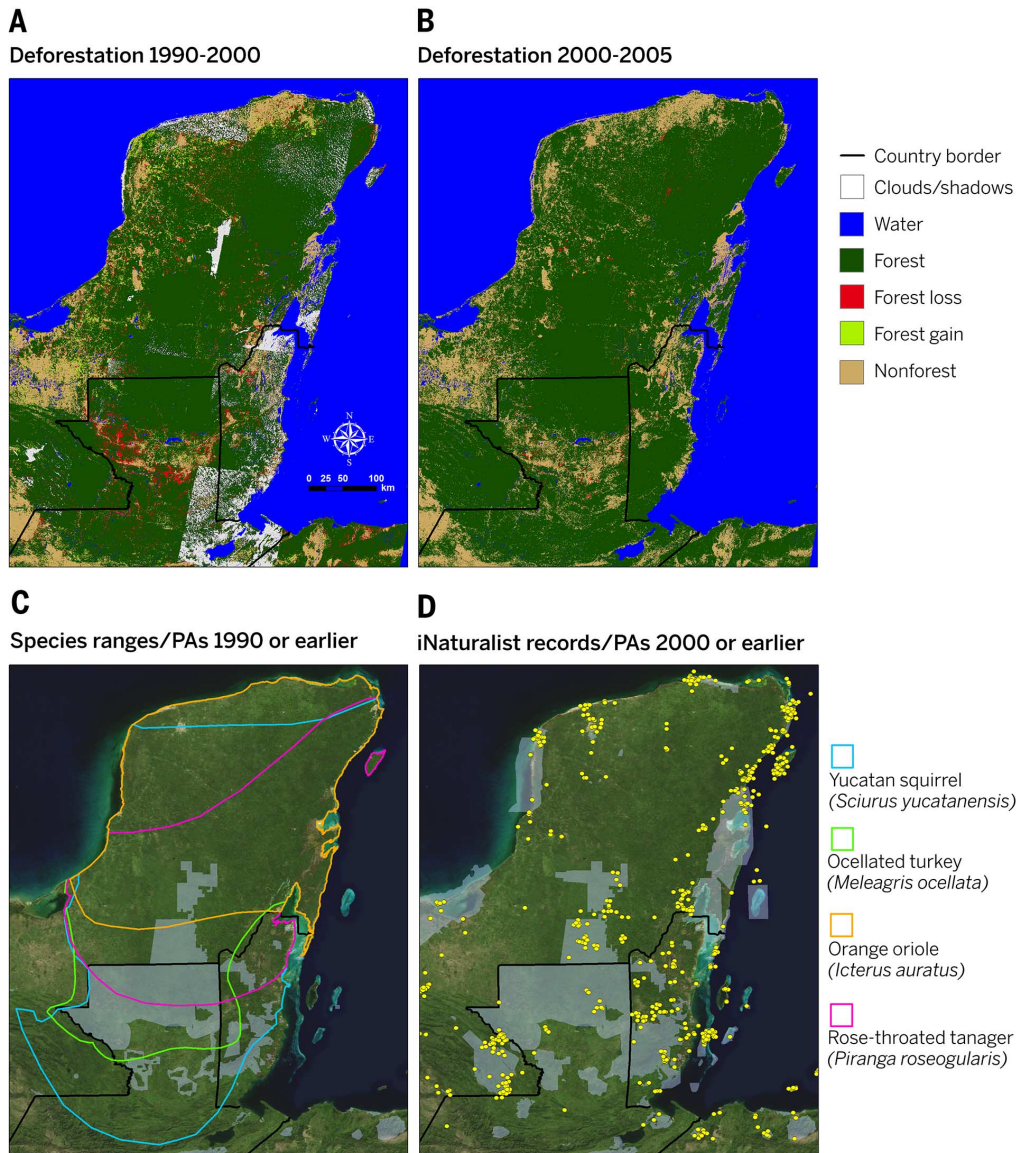
A
Deforestation 1990-2000

B
Deforestation 2000-2005

— Country border
☐ Clouds/shadows
■ Water
■ Forest
■ Forest loss
■ Forest gain
■ Nonforest

C
Species ranges/PAs 1990 or earlier

D
iNaturalist records/PAs 2000 or earlier

☐ Yucatan squirrel
(*Sciurus yucatanensis*)

☐ Ocellated turkey
(*Meleagris ocellata*)

☐ Orange oriole
(*Icterus auratus*)

☐ Rose-throated tanager
(*Piranga roseogularis*)

Fig. 6. Combining databases to assess the changing status of biodiversity. Maps (**A**) and (**B**) show land cover change in the Yucatan peninsula of Central America. Forest-cover data for 2000 to 2005 available at www.landcover.org/data/landsatFCC. Although protected areas increased over time, there was extensive deforestation in lowland Guatemala from 1990 to 2000 (shown in red), some of it in protected areas. Forest loss slowed from 2000 to 2005. (**C**) Deforestation has reduced and fragmented the ranges of four exemplar species endemic to the Yucatan. (**D**) All iNaturalist records from this area. See details in (*53*).

The numbers and kinds of online databases have increased dramatically in recent years and will continue to do so. Global estimates of land cover from remote sensing [e.g., (*131*)] diversified with the 2009 opening of the U.S. Geological Survey Landsat archive and subsequent efforts to collect and calibrate global repositories of Landsat images going back to the early 1970s (*132*, *133*).

Even more promising is combining data sources. Studies now permit detailed assessments of the current status of species by trimming available range maps using remotely sensed estimates of elevation and remaining habitats (*134*) and connecting directly to metapopulation models of fragmented ranges (*45*). Figure 6 provides an example

of the extent to which species' ranges have been lost and fragmented by deforestation—and when this happened. It also shows where forest remains outside of protected areas, how it has been lost from within them, and the potential of crowd-sourced data to monitor species' distributions.

Combining such sources anticipates an ability to assess biodiversity continuously and provide a template onto which crowd-sourced data could validate predictions of changing species' distributions. Global biodiversity monitoring can now move to combining databases of increasing scope and certainty at regular intervals. These coming advances will increasingly enable scientists and policy-makers to understand the

status, trends, and threats to Earth's biodiversity and to act accordingly to protect it.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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References (*135, 136*)

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