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HOW MANY PLANT SPECIES ARE THERE, WHERE ARE THEY, AND AT WHAT RATE ARE THEY GOING EXTINCT?

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ABSTRACT

How many flowering plant species are there? Where are they? How many are going extinct, and how fast are they doing so? Interesting in themselves, these are questions at the heart of modern conservation biology. Determining the answers will dictate where and how successfully conservation efforts will be allocated. Plants form a large taxonomic sample of biodiversity. They are important in themselves and directly determine the diversity of many other taxonomic groups. Inspired by conversations with Peter Raven, we set out to provide quantitative answers to these questions. We argue that there are 450,000 species, two thirds of which live in the tropics, a third of all species are at risk of extinction, and they are going extinct 1000 to 10,000 times the background rate. In obtaining these results, we point to the critical role of dedicated taxonomic effort and biodiversity monitoring. We will only get a good answer to the age-old question of “how many species are there?” when we understand the population biology and social behavior of taxonomists. That most missing species will be found in biodiversity hotspots reaffirms their place as the foci of extinction for decades to come. Important, but not yet addressed, are future studies of how long plant species take to become extinct in habitat fragments. These will deliver not only better estimates of extinction rates, but also the critical timeframe of how quickly one needs to act to prevent extinctions.

Key words: Biodiversity, discovery curves, extinction rates, flowering plants, missing species.

We ask four questions that arose in the context of 25 years of discussions with Peter Raven. How many plant species are there? Where are they? How many are going extinct, and how fast are they doing so? Raven has considered these questions throughout his career. Their extension to all species is obvious and, as such, they have an illustrious pedigree. For example, Westwood (1833) speculated “on the probable number of species of insects in the Creation.” These questions are also both hard to answer and exceptionally rich in the subsequent explorations we must undertake to get the final answers. We argue that there are 450,000 species, two thirds of which live in the tropics, a third of all species are at risk of extinction, and they are going extinct 1000 to 10,000 times the background rate. In obtaining these results, we point to the critical role of dedicated taxonomic effort and biodiversity monitoring.

We shall consider each of the questions in turn but not in the order that we thought about them. Pimm and Raven (2000), in a commentary that accompanied Myers et al. (2000), addressed the last question first by building simple scenarios of extinction based on the loss of tropical forests. It quickly became apparent that the answer would depend on how many species lived in tropical forests and, indeed, in which particular forests. In turn, that meant knowing not

only how many species were known, but also how many were still unknown to science. We start with those questions.

HOW MANY PLANT SPECIES ARE THERE?

There are two questions in estimating the total numbers of plant species: how many do we know, and how many do we not know, i.e., how many are still unknown to science? For shorthand, we will call the latter “missing species.” The first question might seem easy. The problem of synonymy (i.e., taxonomists giving different names to the same species inadvertently) complicates it. There have been several recent estimates of the currently known number of unique species of seed plants (Prance et al., 2000; Govaerts, 2001; Bramwell, 2002; Thorne, 2002; Scotland & Wortley, 2003; Paton et al., 2008), with the highest estimate (422,127; Govaerts, 2001) two times the lowest one (223,300; Scotland & Wortley, 2003).

The Plant List (<www.theplantlist.org>) is an ongoing collaboration between the Missouri Botanical Garden and the Royal Botanic Gardens, Kew. In May 2013, it estimated that there were 352,000 species of flowering plants (angiosperms; the same number as Paton et al., 2008), with 298,900 accepted names and 263,925 names yet to be assessed, though surely many of them will be synonyms. Because the

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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 ca. 100,000 species for a total estimate of ca. 400,000 species. These are monumental assessments, necessary because the individual names, identities, and relationships are the basis of so much subsequent science.

Yet, there are also questions that require estimating how incomplete this catalogue is. How much more effort will be required to complete it? Are we years, decades, or centuries away from a widely accepted answer? For consortia such as the Catalogue of Life (<http://www.catalogueoflife.org>), these are fundamental questions. At a local scale, projects such as the All Taxa Biodiversity Inventory ask how many species live in an area. For the Great Smoky Mountains National Park in the eastern United States, the answer is 7636 of all species combined (as of 5 October 2014 there are 7799 species, 931 of them new to science), with 923 of these (13%) new to science (<http://www.dlia.org/node/204>). That so many species of animals and plants are new in an otherwise well-explored area surrounded by major research universities is a testament to our ignorance about life's diversity.

There are practical concerns, too, about knowing the number of missing species. Because they are most likely rare, their number and geographical distribution are essential to answering the second and third questions we ask.

There have been many previous attempts using, e.g., scaling laws in food webs, abundance, body size, and rarity to estimate the number of missing species (May, 1988, 1990, 1992). Recent attempts employ what surely seems like the most promising approach. As the pool of missing species declines, the numbers of discoveries will also likely decline in direct proportion (Solow & Smith, 2005; Wilson & Costello, 2005). The obvious analogy is with predator-prey interactions: taxonomists are the "predators," and as the supply of "prey" (i.e., missing species) declines, so too should the capture rate.

TAXONOMISTS ARE PREDATORS, MISSING SPECIES ARE PREY

Completely counter to this expectation, the numbers of both monocot and non-monocot species described per five-year interval have increased almost exponentially since 1950 (Joppa et al., 2011b). To take an example, since 1950, there have been 95 accepted species names for Onagraceae. From 1900 to 1949, taxonomists named only 43 species.

Moreover, a broad exponential increase in names applies to other taxa including mammals, spiders, amphibians, and example genera of marine gastropods (Joppa et al., 2011c). Under such circumstances, estimates of missing species from extrapolations of uncorrected discovery rates will be nonsense. (Only birds are exceptional and for which the taxonomic catalogue now appears almost complete.)

The underlying problem is that the total number of plant taxonomists active in any period has increased exponentially, too, doubling about every 30 years. (We define "taxonomists," simply as those who describe new species.) Broadly similar rates characterize the animal taxa. Again, excepting birds, the rates of increase are even higher over the last half century. Given this observation, it is not particularly surprising that the raw numbers of species described over time have increased as well. The number of taxonomists is a powerful predictor of the number of species described.

The solution to this problem also seems obvious: divide the number of species described by the total number of taxonomists and expect that this ratio will decline as the pool of missing species declines. This also fails.

The World Checklist of Selected Plant Families (WCSP; <http://www.kew.org/wcsp>) provides a sample of approximately 119,000 species of systematically revised species, including all of the monocots and selected non-monocot families. We show that for both monocots and selected non-monocot families, there was an increase in the number of species described per taxonomist, typically for the first century or so after Linnaeus (Joppa et al., 2011b). Taxonomists have likely increased the efficiency of their efforts since the mid 1700s when Linnaeus introduced the system of binomial nomenclature and founded modern taxonomic practice. There could be many reasons for taxonomists becoming more efficient over time, of course. Clearly, the world is easier to explore now than it was in the past; natural history collections are more accessible; techniques are better; there is more collaboration, and so on. In the predation analogy, the predators have become smarter over time.

Combining these considerations suggests a model where one predicts the numbers of species described per taxonomist over a given interval in terms of the continually diminishing pool of missing species, combined with some simple increase in the efficiency of the taxonomic enterprise. By doing so, we concluded that between 10% and 20% of the current species total are missing, suggesting that there are

probably about 450,000 species of flowering plants (Joppa et al., 2011b).

We also estimated the numbers of missing species family by family to assess which families might hold the greatest number (Joppa et al., 2011b). Then, we compared our estimates to those based on a selection of taxonomic experts who knew the families. There was broad agreement between the models and the experts.

Now, the details of what constitutes a taxonomist and who contributes what to a species description are elsewhere (Joppa et al., 2011c), but the Onagraceae are broadly typical of other families. In the century after Linnaeus (1753), 74 taxonomists described 141 Onagraceae species and mostly did so on their own. Since 2000, 34 taxonomists have contributed to descriptions and revisions of 47 species of Onagraceae. Single authors described only four of these species; the rest were collaborations. Collaborators are not mere assistants, however, but those who, at least eventually, describe species in their own right. Of those 34 recent taxonomists, 25 of them were senior authors on one or more descriptions. Joppa et al. (2011c) also show that taxonomists are becoming more specialized over time. The modern tendency is for taxonomists to work on only one or a few families and often in one broad geographic region. In the predation analogy, predatory taxonomists are now more social and more specialized than they were before.

For some plant families (e.g., Onagraceae), the number of species described per taxonomist does not obviously drop over time. This defies any effort to predict the number of missing species from simple description rates. Inspection of the descriptions shows that taxonomists (in this case, often Raven and his colleagues) are not “eating” species randomly but working their way through plant families, group by group. That is, taxonomists revise a family genus by genus, doing so at a rate that reflects the resources and time at their disposal. Genuinely new species as well as revisions of old ones appear in clusters by group, sometimes a few at a time, sometimes involving many. When the supply of unrevised genera dries up, we can expect the rates of description to drop dramatically.

We have yet to model this circumstance. It is clear that as we delve deeper into particular plant families, the complex social behavior and working habits of taxonomists become more important in driving the rates of species’ descriptions. Nonetheless, for large sets of species (e.g., all monocots), the basic model of taxonomists as predators gives a good statistical

description of how many missing species receive names each year.

WHERE ARE THE MISSING SPECIES?

Obviously, we can apply these “taxonomists as predators” models to predicting *where* missing species live. The WCSP gives species locations based on classifying the world into 369 regions. Only 33 of these ranges have sufficient endemics to run our models, but by judiciously combining regions, we grouped about 72% of the species in 50 broad areas (Joppa et al., 2011a). For example, many countries in Central America are quite small and individually have few endemics. Yet, a combined 9% of all known species occur there. The remaining 28% of species occur in two or more of the regions as we defined them.

So, where is plant diversity highest once we adjust for where we think the missing species occur? Our analyses leave untouched the idea that plant species are mostly tropical; almost exactly two thirds (65.7%) of all species, known and missing, live in the tropics (Joppa et al., 2011a). That is exactly the fraction that Raven (1981) asserted were tropical.

We predicted that the great majority of the missing species would be in the region from Mexico to Panama (6% of all the predicted missing species), Colombia (6%), Ecuador to Peru (29%), Paraguay, Argentina, and Chile (5%), southern Africa (16%), and Australia (8%). These areas combined have 70% of all the species we predict are missing. All of these areas are biodiversity hotspots (Myers et al., 2000), which leads directly to our next question.

HOW MANY PLANT SPECIES ARE GOING EXTINCT?

Estimating the fraction of plant species threatened with extinction requires that we understand how many species are missing from the taxonomic catalogue (Joppa et al., 2011b). Brummitt et al. (2008) suggested that 20% of known plant species are threatened. Take this estimate, and then add to that our result that there are 10%–20% more missing species. Then assume that essentially all of these missing species have small geographical ranges and are locally rare. That is likely why they are missing, after all! We predict that they are in the biodiversity hotspots that, by definition, have high levels of habitat loss. Thus, the missing species are also surely threatened with extinction. This argument predicts that 27%–33% of all plant species are likely threatened. These estimates are based on immediate threats and do not consider further development of

destructive factors, including climate disruption (Pimm, 2009), during the remainder of this century.

So, how good are the assumptions that the missing species have small ranges and that taxonomists will indeed find them in the biodiversity hotspots? Understanding where missing species are likely to live is vital in setting international priorities for conservation and ensuring that we find and protect the missing species before we drive them to extinction.

Answering this question requires several of the basic “laws” of biodiversity. By “law” we mean generalizations or patterns, if you will, that apply widely and across many taxa. The first law is that *the average geographical range size of a group of species is very much larger than the median range*. For vertebrate taxa, there are now global maps of species’ ranges. The average of the geographical ranges of 1684 species of mammals in the New World is 1.8 million km², but 50% of those species have ranges smaller than 250,000 km², a seven to one ratio. For the region’s three main bird groups (non-passerines, suboscine passerines, and oscine passerines), the ratios are between five and eight to one. For amphibians, they are 40 to one. Simply, there are many species with small ranges and few with large ranges.

We do not have comparable data for flowering plants, unfortunately. In the sample of systematically revised species compiled from the WCSP database (Joppa et al., 2011a), one half of the species occur in regions that individually are no larger than 1.4 million km². Of course, these species do not occur over the entire extent of the region in which they occur. Moreover, many other regions contain small-ranged species. Therefore, 1.4 million km² sets a high upper limit for the median range size of a flowering plant. There are surely many plant species with small ranges.

The next law of biodiversity is that *species with small ranges are geographically extraordinarily concentrated*. In total, 88 of the 369 regions covering only 5% of the ice-free land surface combined hold 30% of the known plant species, while 111 regions covering a combined total of 10% hold 40% of the species.

Currently, small geographical range is overwhelmingly the best statistical predictor of whether a species will be in danger of extinction. Indeed, sufficiently small geographical range combined with an occurrence in areas of extensive habitat loss classifies a species as being “threatened” under the IUCN Red List criteria (<http://www.iucnredlist.org/static/categories_criteria_3_1>). Understanding ex-

tinguishing rates requires knowing whether the areas where species with small ranges are concentrated coincide with places where there is extensive habitat loss.

The unique contribution to conservation from Myers et al. (2000) was to note not only that small-ranged species are geographically concentrated, but also that perversely most are located in areas with disproportionately high levels of habitat destruction. Cincotta et al. (2000) added high human population growth to the list of threats to these biodiversity hotspots.

Given that we have shown the taxonomic catalogue is short by 10%–20%, then how would an understanding of where the missing species live alter our views of hotspots? For obvious reasons, new species discoveries are overwhelmingly of species that have small geographical ranges. Will knowing where the missing species reside change the way we set conservation priorities? Will relative priorities change as taxonomists complete the catalogue? Will new priorities become apparent? Are the missing species in places where they are likely to be threatened? Will we discover them before they become extinct?

We have already anticipated the answers to these questions: the hotspots hold the majority of the species we predict to be missing. The missing species are in harm’s way and possess small ranges. Myers et al. (2000) concluded that the hotspots are where species are going extinct. Our estimates of where the missing species occur do not contradict this conclusion (Joppa et al., 2011a). What the estimates do show is that extinctions are even more likely to be concentrated in hotspots than we previously thought.

Are there some places where recent habitat loss might cause the region to now qualify under criteria from Myers et al. (2000) as a hotspot? New Guinea, e.g., has far greater than 1500 endemic plant species but was not originally included as a hotspot due to relatively intact natural vegetation. Ongoing loss of natural habitat through logging, mining, and road construction (Shearman et al., 2009) could make the region a likely candidate for inclusion as a hotspot in the near future. Increased access could also lead to an increase in the descriptions of new species, of course. New Guinea’s inaccessibility may explain its low rates of description and the predictions of there being few missing species.

EXTINCTION SCENARIOS

Pimm and Raven (2000) used results from Myers et al. (2000) to develop scenarios of how many species would become extinct. We used the familiar

species-area relationship ($S = cA^z$) that relates the number of species (S) to area (A), using two parameters, c and z , for which z is vital. The parameter c is a constant of proportionality. For samples of different sizes within continuous habitat, z is very small (Rosenzweig, 1995). This describes, e.g., the observation that the number of tree species in the Great Smoky National Park is not that much smaller than the total number across eastern deciduous forest from Florida to Maine and westward to the prairies.

Now, what happens after habitat destruction? Two things: first, some species will go extinct immediately, because they lived only in the destroyed area. Metaphorically, they go extinct “overnight.” The second wave of extinction invokes a separate species to area relationship, that for oceanic islands where the areas involved are isolated. Here, z is much larger, typically about one fourth (Rosenzweig, 1995), meaning in simple terms, an island one half the size of a larger one will have 85% as many species.

The difference between the two relationships comes from Preston’s (1962) classic work. He understood that for isolated populations there is a minimum viable population size. Suppose we reduce the total number of individuals by one half, shrinking as it were the larger island to the smaller one. Then 15% of the species would have population sizes too small to be viable. After habitat loss, some species will go extinct “overnight,” but many more will linger until chance events eventually doom them. Such experiences fit well with much practical experience of endangered species. In addition, it fits with what we know of the risks from stochastic events and inbreeding in small populations (Brooks et al., 2011).

There are now many calibrations of forest losses and subsequent extinctions, at least for birds and mammals, the taxa that we know best. Pimm and Askins (1995) asked how many bird species we expect to go extinct following the loss of forests in eastern North America. About 150 species lived in those forests, but only 30 of these were endemic to those forests. Pimm and Askins applied the island species-area relationship (because by 1870 eastern North America was a series of forest islands) to the 30 endemic species, because the other species survived in Canada and elsewhere in North America. This model predicts four and one-half extinctions. As forests were cleared in the 18th and 19th centuries, there were four documented forest bird extinctions, and one species became endangered.

Many other studies find similar, compelling agreements between forest losses and either the number of actual extinctions or the number of

endangered species (Brooks et al., 1997, 1999a; Cowlshaw, 1999; Brook et al., 2003). Armed with this agreement, Pimm and Raven (2000) took the estimates of endemic species in the hotspots Myers et al. (2000) defined, with the estimates of remaining habitat and, thus, predicted the total extinctions that would occur. For example, Myers et al. estimated that only 7.5% of the Atlantic coast rainforest of Brazil remains and that this area contained 2.7% of their estimate of 300,000 plants as endemics to this area. The continued rate of species descriptions should eventually yield 3.6% of 450,000 species of plants (Joppa et al., 2011a) for this area. Applying the species-area calculation, about one half of the endemic plant species in this region should be endangered (ca. 4000 according to Myers et al., but 7200 with the missing species included).

This and similar calculations have uncertainties, of course. This example suggests that the largest uncertainty is surely that the estimate of the missing species comes from present rates of species descriptions. Those rates now reflect collecting and systematic revisions of plants from a mere 7.5% of the region’s original forested area. There is a strong possibility that there may have been many extinctions across this area that are not estimated by our “taxonomists as predator” models of species discovery. Simply, there are the species we know, some of which are threatened and some of which are not. Second, there are the species we estimate are missing from the taxonomic catalogue. We argue above that surely all of these are threatened. There is a final class of species: those that went extinct before we could even estimate that they were missing from the taxonomic catalogue.

Most of the remaining Atlantic Coast forest habitat is in mountains. Almost all of the lowland forests are gone. How many species occurred in the lowland forests before they were destroyed is beyond our present ability to model. What we know of the region’s orchids is that one half of the records are from only one location and a quarter of the 600 species in the state of Espírito Santo (ca. 46,000 km²) are endemic to it (Pimm, 2005). Almost certainly, the median range size of orchids (at least) was so small that many species could have lived in areas completely destroyed before taxonomists explored them.

HOW LONG DOES EXTINCTION TAKE?

Apart from the small fraction of species that go extinct “overnight” after habitat loss, most species linger, declining inexorably toward extinction. The obvious question is how long does this take? For the

birds in eastern North America, we know it took decades after the low point of forest cover in 1870 before the species finally expired. Pimm and Raven (2000) assumed 50 years for the half-life. This affirms the biodiversity hotspots as the foci of extinction for decades to come. Studies of how long plant species take to be lost from habitat fragments that parallel those for birds (Brooks et al., 1999b; Ferraz et al., 2003) are vital, not only to get better estimates of extinction rates, but also to give an idea of how quickly one needs to act to prevent extinctions.

The background rate of plant and animal extinctions—those before human impacts—appear to be about one extinction per ten million species per year (de Vos et al., 2014). Amphibians, birds, and mammals have current extinction rates of approximately 100 extinctions per million species per year, (that is, 1000 times faster). If currently threatened species last a century, a most optimistic scenario, the extinction rates will be ten times higher. Plants have a higher fraction of threatened species than do these vertebrates so the plant extinction rates are likely to be comparable or higher.

Pimm and Raven (2000) considered the dynamics of unfolding habitat losses only briefly. They considered two scenarios: extinctions based on how much habitat remained in 1990 within the biodiversity hotspots and how much habitat was protected, assuming that only this area would remain intact. Since then, there have been new threats to species in the form of oil-palm cultivation, especially in Southeast Asia, but also encouraging signs in the increase of the global total of protected areas (Jenkins & Joppa, 2009) and the success of protected areas in reducing habitat loss (Joppa et al., 2008; Joppa & Pfaff, 2011). Exactly where protected areas are established is a key variable in driving extinction rates (Rodrigues et al., 2004), and many protected areas are not in the necessary places (Joppa & Pfaff, 2009).

Finally, Pimm and Raven (2000) did not consider global change. Given our predictions that the greatest numbers of threatened plant species are likely to be the northern Andes, the coastal forest of Brazil, Mexico, and Central America, and other mountainous areas, this raises an obvious question. Because the latitudinal gradient of temperatures in the tropics is weak, the way species will avoid the effects of climate disruption will be to move to higher elevations (Pimm, 2009). That almost inevitably means less suitable areas for species, some of which may simply run out of space as their ranges move higher into the mountains, if they can get there in the first place (Forero-Medina et al., 2011). These species are likely

to be separate from those species threatened by habitat loss, making climate disruption an added and potentially significant extra cause of extinctions.

DISCUSSION: WHAT WE NEED TO KNOW

Asking how many species there are suggests that we will only get a good answer when we understand the population biology and social behavior of taxonomists (Joppa et al., 2011c). We cannot understand where species live unless we know where the missing species occur. Likely, we also need to know where species have already become extinct before taxonomists started their explorations and classifications. How fast species become extinct requires knowledge of how long species last in the habitat fragments that are presently their only homes. It also requires an understanding of how many species live in tropical mountains too close for comfort to the mountain tops given minimum projected global temperature rises of 2°C.

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