18 250 Years of Swedish Taxonomy

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HISTORICAL PERSPECTIVE

In hindsight, it is fascinating how little Linné (Linnaeus) knew about the diversity of the planet. Even as an internationally established naturalist in his forties, he wrote (Linné, 1749):

> If we estimate the plants to approximately 10,000, the worms to 2,000, the insects to 10,000, the amphibians to 300, the fishes to 2,000 and the tetrapods to 200, then there are 26,500 species of living beings in the world. Our own country has almost 3,600 of these; of domestic plants there are approximately 1,300 and 2,300 species of animals inhabit the country as far as we know.

If these numbers had been anywhere close to the true diversity of the planet, Linné would have named an astonishingly large portion of the existing species himself. In reality, Linné had barely scratched the surface in most organism groups, even in his home country of Sweden. It is true that he described the bulk of Swedish vascular plants and vertebrates but he clearly lacked an understanding of, or interest in, the diversity of other plants and animals. This is well illustrated by the insects, which I will be returning to throughout this chapter for examples illustrating the last 250 years of Swedish taxonomy. Insects account for about 80% of Swedish animal species and number in the tens of thousands but, in his *Fauna Suecica*, Linné (1761) listed only some 1,500 species that are still recognized today—a tiny fraction of the total.

Despite his taxonomic biases, or perhaps partly because of them, Linné inspired a large number of biologists in Sweden and around the world to study poorly known organism groups. This resulted in swift progress in the knowledge of the fauna and flora over the next century and half. For instance, Tullgren and Wahlgren (1922) estimated that some 15,000 species of insects were known from Sweden a century ago, an order of magnitude larger than the number Linné had listed in *Fauna Suecica*. Later in the 20th century however, the pace of discovery decreased significantly. This is particularly notable given the simultaneous increase in the number of professional biologists and it had a drastic effect on the exploration of European faunas and floras. For instance, in the peak period in the first half of the 19th century, entomologists described hundreds of new Swedish insect species every year but the rate had dropped an order of magnitude by the late 20th century (Figure 18.1).

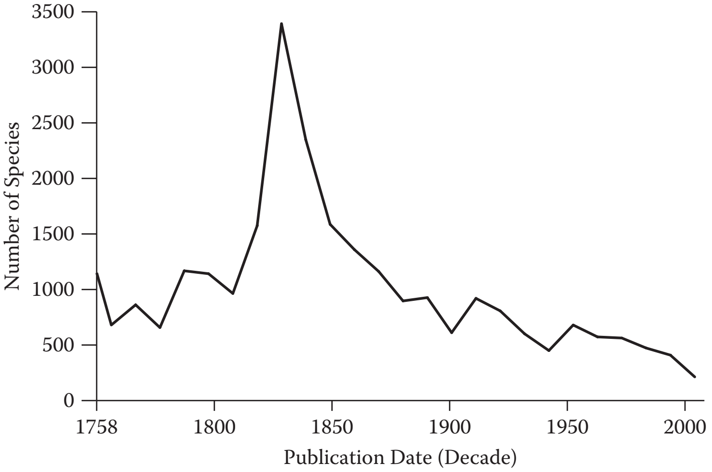

FIGURE 18.1 Date of description of the approximately 26,000 insect species known to occur in Sweden in 2009. Publication dates are grouped in decades after 1758 to even out yearly fluctuations. After the peak in the first half of the 18th century, the discovery rate dropped almost an order of magnitude toward the end of the 20th century. The STI will undoubtedly result in a significant boost in the coming decade, as more than 600 newly discovered species now await formal description.

Of course, there is often a significant time lag between the description of a new species and the first time it is collected in a particular region of interest. For instance, by the time Tullgren and Wahlgren published their overview of the Swedish insect fauna, more than 21,000 of our insect species had already been described but only 15,000 of those were known at the time to be Swedish. In other words, Tullgren and Wahlgren were unaware of a quarter of the Swedish species that had already been named. Much of the activity of Swedish entomologists in the 20th century consisted of adding these species to the Swedish list. By the turn of the century, Gärdenfors et al. (2003) estimated that 24,700 species of insects were known from the country. Fully two thirds of the species added since 1922 had already then been described based on material from other countries.

One might suspect that the decline in species discovery rates merely reflected the inventory nearing its completion, especially in Sweden with its depauperate and well-researched fauna. However, other factors were also at play. In the 20th century, many biologists started questioning the importance of inventorying species and instead turned their attention to the general principles of biology, drawing funds and students away from taxonomy. The resources that remained were not spent very efficiently with respect to the goal of completing the inventory. Conservatism combined with the prevalent emphasis on curiosity-driven research resulted in an inordinate concentration of attention on comparatively well-known organisms. This created the impression that floras and faunas were better known than they actually were, especially in Europe. Thus, toward the end of the 20th century, it was still unclear how close biologists actually were to completing the inventory of macroscopic life in Sweden or any other region containing a nontrivial number of species.

TIDES TURN

In the 1990s, tides turned. Several prominent biologists had been arguing for some time that we were facing a biodiversity crisis ultimately threatening the survival of mankind, and politicians finally responded. By linking biodiversity with economic interests, the Convention on Biological Diversity (http://www.cbd.int) succeeded in 1992 in putting taxonomy on the political agenda. Several of the parties to the convention, among them Sweden, worked in the following years to promote inventorying efforts and taxonomic capacity-building in the tropics through the Global Taxonomy Initiative (GTI), which was officially launched in 1998.

The Swedish backing of the GTI inspired a critical look at the actual knowledge of the Swedish fauna and flora and the state of taxonomy in Sweden. At the same time, the work on the Swedish Red List, led by the Swedish Species Information Center (Artdatabanken), emphasized the large number of species-rich groups that could not be judged according to the official International Union for Conservation of Nature (IUCN) criteria because of the lack of taxonomic knowledge and easily accessible identification guides. Thanks to these factors and a favorable political situation, we were able to convince the Swedish government in 2001 of the need for an initiative focused on the Swedish flora and fauna.

who is "we"?

THE SWEDISH TAXONOMY INITIATIVE

Announced by the Swedish government in the spring of 2001, the goal of the Swedish Taxonomy Initiative (STI) is to complete the inventory of the multicellular species occurring in the country within twenty years. All species are to be documented scientifically, and the species that can be identified by amateur naturalists are to be presented in a well-illustrated biodiversity encyclopedia commissioned by the Swedish Parliament. The project is coordinated by the Swedish Species Information Center but involves a large number of participating academic institutions, natural history museums, and biologists in Sweden and abroad.

The focus on multicellular species was a strategic decision based on the goal of reaching out to amateur naturalists and the general public. Whereas Swedish amateur naturalists play an important role in monitoring the macroscopic flora and fauna, they are unlikely to be able to contribute productively when it comes to microscopic species, which are often identified using molecular genetic tools. Macroscopic species are also more susceptible to environmental changes and extinction because of their smaller population sizes, making it more critical to monitor their abundance. This is not to deny that macroscopic diversity is dwarfed by the incredible diversity of bacteria and unicellular eukaryotes, which is worthy of a charting initiative of its own. However, such an initiative would have to be designed completely differently.

The STI was officially launched in 2002 and, after a start-up phase of three years, the project has been fully funded since 2005. Of the current funding, about 30 million SEK (2.6 M €) per year is used for project administration and production of the encyclopedia, while about 15 million SEK (1.3 M €) is granted in support of taxonomic research and inventory projects on poorly known organism groups. In addition, about 20 million SEK (1.7 M €) is used to help Swedish natural history collections to participate in the project. Over a twenty-year period, this sums up to 1.3 billion SEK or just over 1 billion €. It may sound like a massive investment but it is still almost an order of magnitude smaller than the projected cost of the Large Hadron Collider (Achenbach, 2008), the world's largest and highest-energy particle accelerator, and the investment is spread over a longer time period.

addition okay?

The early years of the STI have been dominated by two major inventorying efforts. A marine inventory was started in 2006 and finished its last field season in 2008. On land, poorly known insect groups were targeted in the Swedish Malaise Trap Project, which operated a number of Malaise traps across the country from 2003 to 2006. Sorting and identifying this material will occupy biologists for years to come. In addition to the large-scale inventories, a number of taxonomic research projects on poorly known organism groups have also been funded and about ten training grants for PhD students have been awarded.

The first volume of the *Encyclopedia of the Swedish Flora and Fauna* (*Nationalnyckeln*), covering butterflies, was officially presented to the Swedish Parliament and Her Royal Highness Crown Princess Victoria, patron of the STI, in April of 2005 (Figure 18.2). Six additional volumes have been published since then, covering groups ranging from mosses to millipedes. The main text is in Swedish and summarizes the characteristics of each species, as well as its distribution, biology, and conservation status. The key facts are also given in English and the identification keys are bilingual.

FIGURE 18.2 An important product of the Swedish Taxonomy Initiative is the *Encyclopedia of the Swedish Flora and Fauna* (*Nationalnyckeln*). The richly illustrated volumes include identification keys to all species and summarize essential information about diagnostic characters, life history, distribution, and conservation status of each species.

The volumes are richly illustrated by some of the best scientific illustrators and photographers in the country. More than 100 volumes are planned in total, making this the largest publishing project attempted in Sweden so far.

MORE DIVERSITY THAN EXPECTED

At the start of the STI, it was estimated that some 50,000 species of multicellular organisms were known from the country, almost half of which were insects (Gärdenfors et al., 2003). Even those of us involved in launching the STI did not expect the discovery of a vast number of additional species. I remember giving a talk in 2001, in which I ventured a guess that the project might add a couple of thousand new species records, and result in the discovery of a couple of hundred species new to science. We emphasized that the most important aspect of the project was that it enabled school kids, laymen, and amateur naturalists to discover and identify a larger fraction of the rich biological diversity of their home country, even in their own back yards. In this way, we could both improve the quality of environmental monitoring and increase public appreciation of biological diversity. In particular, many of us hoped to see the STI result in Swedish biodiversity monitoring, to a large extent relying on amateur naturalists, target a broader and more representative sample of species.

Relatively soon, however, it became clear that the Swedish flora and fauna were less well known than most of us had thought, as STI-funded activities resulted in the discovery of a surprisingly large number of new species. During a workshop in 2007 focused on meiofauna, for instance, twelve international experts were able to add some 100 species to the Swedish list, eigheen of which were new to science, in just two weeks. This represented a 2% increase in the number of marine species known from Sweden. Since 2002, a significant number of new species have also been added to the Swedish list of many other organism groups, but the results are most striking for the insects.

FIGURE 18.3 The Swedish Malaise Trap Project ran 61 Malaise traps from 2003 to 2006 at 44 sites representing a wide variety of habitats across the country, a sample of which is seen here. In the winter of 2004–2005, eleven more traps were deployed at eight additional sites. Traps were emptied year round and, at least in the southern third of the country, they produced significant numbers of insects even in the middle of the winter.

THE SWEDISH INSECT FAUNA

Already from the start of the STI, it was clear that the remaining challenges in completing the insect inventory mainly involved groups in the orders Hymenoptera and Diptera. Many of these groups are known to be easily collected using Malaise traps. The design of these traps was originally described by René Malaise, an avid collector and former curator at the Swedish Museum of Natural History in Stockholm. Legend has it that the idea came to Malaise when he observed insects gathering underneath the roof of his tent and eventually escaping through a hole. Many entomologists have refined the design since, but the trap is still essentially a tent-like construction of thin fabric, in which the two long sides have been removed and replaced with a central wall (Figure 18.3). Many insects that are trapped try to escape by moving upward and toward the light. The Malaise trap exploits this fact by having a roof shaped like an inverted funnel and ending in a large plastic jar half-filled with ethanol. Malaise traps are not only efficient in catching small flying insects, mostly Hymenoptera and Diptera, but many other insects also end up in the traps, including wingless species that crawl up the trap and into the collecting jar.

The scientific committee of the STI was persuaded early on that a large-scale Malaise trap inventory was warranted and the Swedish Malaise Trap Project was launched in 2003. A total of sixty-one Malaise traps were deployed for three years at forty-four different localities across the country, representing a wide variety of habitats (Karlsson et al., 2006). Eleven additional Malaise traps at eight additional sites were run for about half that time period. The traps were emptied year round

Ref. list says 2005.
Which is correct?

and, in the southern third of the country, they produced significant numbers of insects even in the middle of the winter.

When the traps were removed in 2006, it was estimated that the total catch contained some 40 million specimens. At the time of the last comprehensive tally a year ago, about 20% of this material had been sorted to major groups and 5% had been identified to species. The identified material contained some 600 species new to Sweden, more than 400 of which were new to science. In total, the Malaise trap program and other taxonomic research projects have expanded the Swedish list of insects with almost 1,900 species since 2003. About 600 of these are new to science, most of them still awaiting formal description.

THE NEW SPECIES

The new species are far from a random sample of insects. If we analyze previous estimates of the Swedish insect fauna, it is obvious that they have been significantly biased in terms of feeding niches (Figure 18.4). The insects known to Linnaeus were predominantly phytophagous; he obviously collected insects mainly in or around plants. The larger the fraction of the fauna known to us, the larger the proportion of parasitic species (the light areas in the pie charts). The part of the pie consisting of saprophagous species and their parasitoids, the community associated with the decomposition of organic compounds, has also grown significantly with increased knowledge of the fauna.

The new species added since 2003 essentially continue this trend: they tend to be saprophagous species or parasitoids. A significant portion of the new species identified thus far are scuttle flies (Diptera: Phoridae). They are extremely abundant and ubiquitous—one in every 30 specimens collected in the Swedish Malaise Trap Project is a scuttle fly. About 300 species of phorids were recorded from Sweden in 2003; we now have seen material of some 800 and expect that the total may be around 1,100. The biology is known only for a few species, some of which are parasitoids, but one might suspect that the latter represent the exception and that most scuttle flies are saprophagous or fungivorous.

Another group with many new species are the Mycetophilidae (fungus gnats). They are definitely saprophagous or fungivorous, like many new species in the family Cecidomyiidae (gall midges and relatives). The Figitidae represent yet another example of a group that has been previously overlooked. They are small parasitic wasps attacking various insect larvae, often Diptera larvae developing in decomposing organic matter. The genus Trybliographa (Figure 18.5) alone is now known to contain more than 50 species in Sweden, about half of which are undescribed.

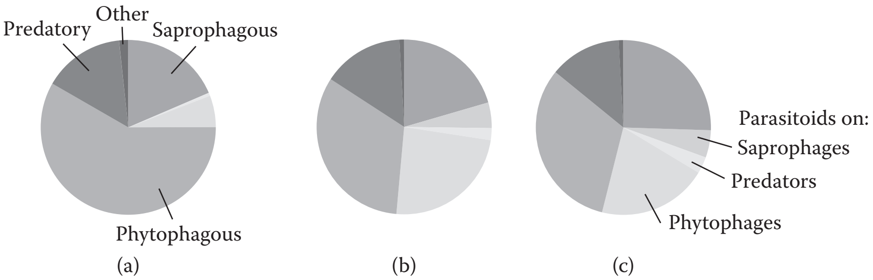

FIGURE 18.4 Larval or nymphal feeding niches of the known Swedish insect fauna at different points in time: (a) Linné (1761); (b) Tullgren and Wahlgren (1922); (c) Gärdenfors et al. (2003). As the knowledge of the fauna has increased, it has become obvious that previous estimates were significantly biased toward phytophagous species and against parasitoids and saprophagous species. Note, for instance, that Linné mainly knew phytophagous species (dark section) and very few parasitoids (lightly colored sections). Results from the STI suggest that the trend toward larger fractions of parasitoids and saprophagous species will continue as the last portions of the fauna are charted.

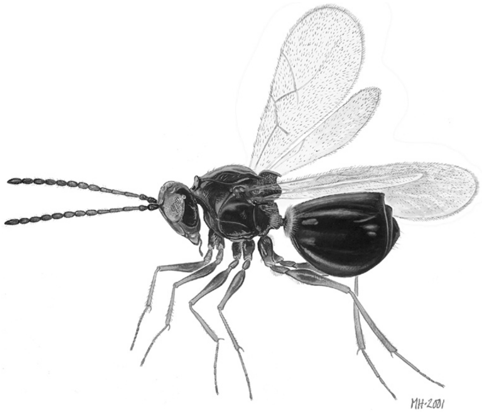

FIGURE 18.5 A representative of the genus Trybliographa (Hymenoptera: Figitidae: Eucoilinae). The species belonging to this genus are parasitoids of anthomyid larvae developing in fungi or decomposing parts of green plants. Thus, being small parasitoids of saprophagous species, they combine many of the characteristic properties of the new species discovered in the STI. About half of the fifty or so currently known Swedish species of Trybliographa are still undescribed. Illustration by Martin Holmer.

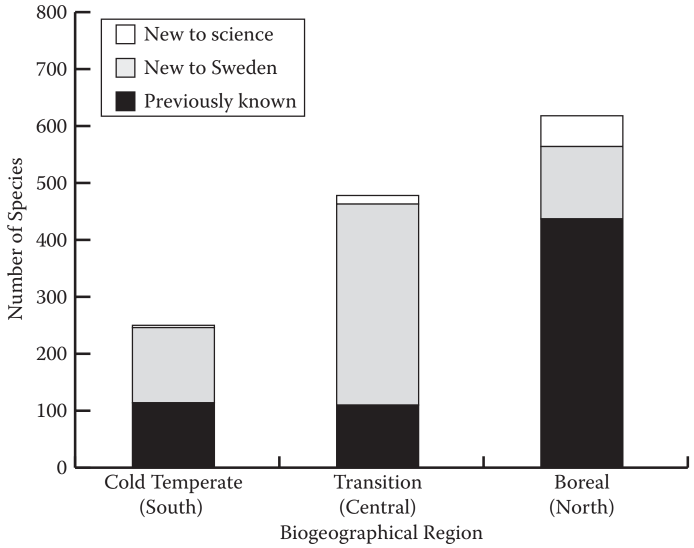

FIGURE 18.6 A large fraction of the new species discovered in the STI are from northern Sweden, which is not surprising given the focus on the southern third of the country in previous collecting. This figure illustrates this through a geographical breakdown of the species of fungus gnats and relatives (Diptera: Mycetophiloidea) currently known from Sweden (Kjaerandsen et al., 2007; Kjaerandsen, pers. comm.). New species to science and to Sweden are those that were undescribed or not previously recorded from the country in 2003, at the start of the STI. Thanks to material collected by Karl Müller, the mycetophilid fauna of northern Sweden was unusually well documented before the start of the STI.

Another notable but perhaps obvious feature of the new species is that they tend to be small and inconspicuous. Otherwise, they would hardly have escaped the attention of amateur naturalists and professional entomologists for so long. A fairly large proportion of the new species are also from northern Sweden (Figure 18.6). This is hardly surprising given that previous collecting efforts have focused on the heavily populated southern third of the country, which shares a large fraction of its fauna with intensely inventoried neighbors such as Denmark and Germany.

TABLE 18.1
The Most Prolific Authors of Swedish Insect Species

Rank	Author	No. Species
1	Linné (Linnaeus)	*1,470*
2	Thomson	*1,291*
3	Zetterstedt	*1,001*
4	Fabricius	*977*
5	Meigen	*929*
6	Gravenhorst	*734*
7	Walker	*596*
8	Fallén	*560*
9	Holmgren	*456*
10	Haliday	*324*
11	Dennis	*311*
12	Schiffermüller	*309*
13	Kieffer	*293*
14	Gyllenhal	*292*
15	Erichson	*276*
16	Hübner	*268*
17	Loew	*261*
18	Graham	*259*
19	Förster	*242*
20	Zeller	*233*

Note: Our current estimates suggest that the total number of Swedish insects left to be described is in the thousands, still making it feasible for ambitious young taxonomists to make it to the top twenty on this list.

So how many species of insects are there actually in Sweden? Using a combination of total diversity estimates based on the samples from the Swedish Malaise Trap Project and expert guesses, we are currently trying to answer this question. Our preliminary numbers point toward a total fauna of around 31,000 species. If this is correct, then there are still somewhere between 4,000 and 5,000 insect species left to discover. So far, about one third of the new species we have found have been undescribed, but it seems likely that this proportion will go up, if anything, as the inventory proceeds to the most obscure groups. Although it is hard to believe, this actually means there is still room for young ambitious taxonomists to make it to the top-twenty or even top-ten list of the most prolific authors of Swedish insect species (Table 18.1). Indeed, still in 2009, there may be more undescribed species of insects in Sweden than the total number known to Linné.

ORGANIZING BIODIVERSITY INVENTORIES

Perhaps the most important lesson to draw from the STI results is that our current knowledge of floras and faunas, even in such comparatively well-investigated regions as Europe, is still seriously biased. For instance, we still know very little about species performing critical ecosystem services, such as saprophagous and parasitic insects. There are likely to be other biases as well that are less obvious and therefore impossible to correct for. This compromises our ability to monitor environmental changes effectively, underpinning the need for completing the biodiversity inventory as quickly as possible.

From a scientific perspective, completing the inventory of life on Earth is probably best accomplished by having specialists focus on the global fauna or flora of one organism group at a time. This is the approach taken by the National Science Foundation in its recent Planetary Biodiversity Inventories program. The STI represents the alternative method of focusing on a geographic area instead, and completing the inventory across all organism groups. This is known as an ATBI (All Taxa Biodiveristy Inventory). Although not ideal from a scientific standpoint, national ATBIs may be easier to organize and fund than taxon-based projects. In fact, the parties to the Convention of Biological Diversity are all committed to inventorying and monitoring their biological diversity. One possible interpretation, nemoral justified by the STI and similar efforts, is that this involves a commitment to fund national ATBIs.

Was there anything missing from this sentence? Please check.

Floras and faunas are almost always shared to a large extent across national borders, which raises difficult questions concerning the fair share of costs for national ATBIs. For instance, if the STI were successful, it would complete most of the ATBIs of a number of neighboring Northern European countries as well. This means that an isolated national ATBI places an unreasonable burden on a single country, involving a cost that will almost certainly be prohibitive in biodiversity-rich regions. At the same time, it also means that regional collaboration, if organized efficiently, could potentially reduce the cost of national ATBIs very significantly.

In fact, even though the Swedish flora and fauna are depauperate, it is doubtful whether the STI itself would succeed in completing the inventory without any participation of neighboring countries. Therefore, it was welcome news when the Norwegian government announced in 2008 that it would launch a taxonomic initiative of its own. The Finnish government has also actively supported inventorying efforts in recent years through the PUTTE project, thereby contributing to the Nordic collaboration needed for the STI to be successful.

any further definition?

IMPLICATIONS FOR THE FUTURE

In addition to savings through regional collaboration, the cost of national ATBIs could also be reduced significantly in the future thanks to the development of new informatics tools. As mentioned earlier, the production of the biodiversity encyclopedia accounts for almost half the cost of the STI. The reason is that the production is so labor-intensive: information needs to be manually extracted from the literature and summarized, distribution maps need to be assembled, illustrations need to be completed, etc.

In the future, taxonomists are likely to have access to convenient tools for producing ontology-tagged, machine-readable phylogenetic analyses and species descriptions (for recent manually produced examples, see Buffington and van Noort, 2007; Liljeblad et al. 2008; Pyle et al., 2008). They may also be mandated by the nomenclatural codes to make specimen records, scientific names, and illustrations available through open Web databases or Web portals, such as GBIF (http://www.gbif.org), ZooBank (http://www.zoobank.org) and Morphbank (http://www.morphbank.net), when describing new taxa.

Machine harvesting of this information would in principle allow automatic production of Web pages matching the content now presented by STI in the *Encyclopedia of the Swedish Flora and Fauna*, but dynamic so that the information would always be up to date. The technology to do this is now being developed by the Encyclopedia of Life project (http://www.eol.org), which may thus slash the cost of national ATBIs in half. Of course, there is still an enormous amount of legacy data to deal with before an automated system can compete successfully with traditionally produced books, but a growing number of digitization initiatives are now busy addressing this challenge.

Molecular genetics techniques may also contribute to making national ATBIs more feasible and powerful, if not cheaper. A number of STI-funded research projects now routinely use DNA barcoding and mining of existing sequence databases to help identify species more rapidly. With the material collected in the marine and terrestrial inventories funded by the STI, there is also a unique opportunity to barcode the bulk of Swedish multicellular species in one fell swoop in the coming years. This would enable a number of interesting future developments, among them the possibility of continuous monitoring of biological diversity with automated traps using DNA-based identification of collected specimens.

DNA barcoding cannot completely replace traditional taxonomy, however. One reason is that amateur naturalists derive so much of their inspiration from the reward of being able to identify species with no tools other than simple optical aids. The general public also tends to be less excited by DNA sequences than by the morphological adaptations and life histories of the organisms themselves. Ultimately, the support for biodiversity conservation depends on this kind of popular involvement, especially as long as the biological environment is still rich enough to make the immediate consequences of biodiversity loss less obvious.

The development over the next few decades will be critical to the well-being of generations to come, maybe even to the survival of mankind. Biodiversity inventorying is likely to be one of many crucial efforts helping us address these challenges. One would imagine that Linné would be happy to know that taxonomy is again considered a societal priority and proud that Sweden is playing an important role in completing the task that he originally set before himself.

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