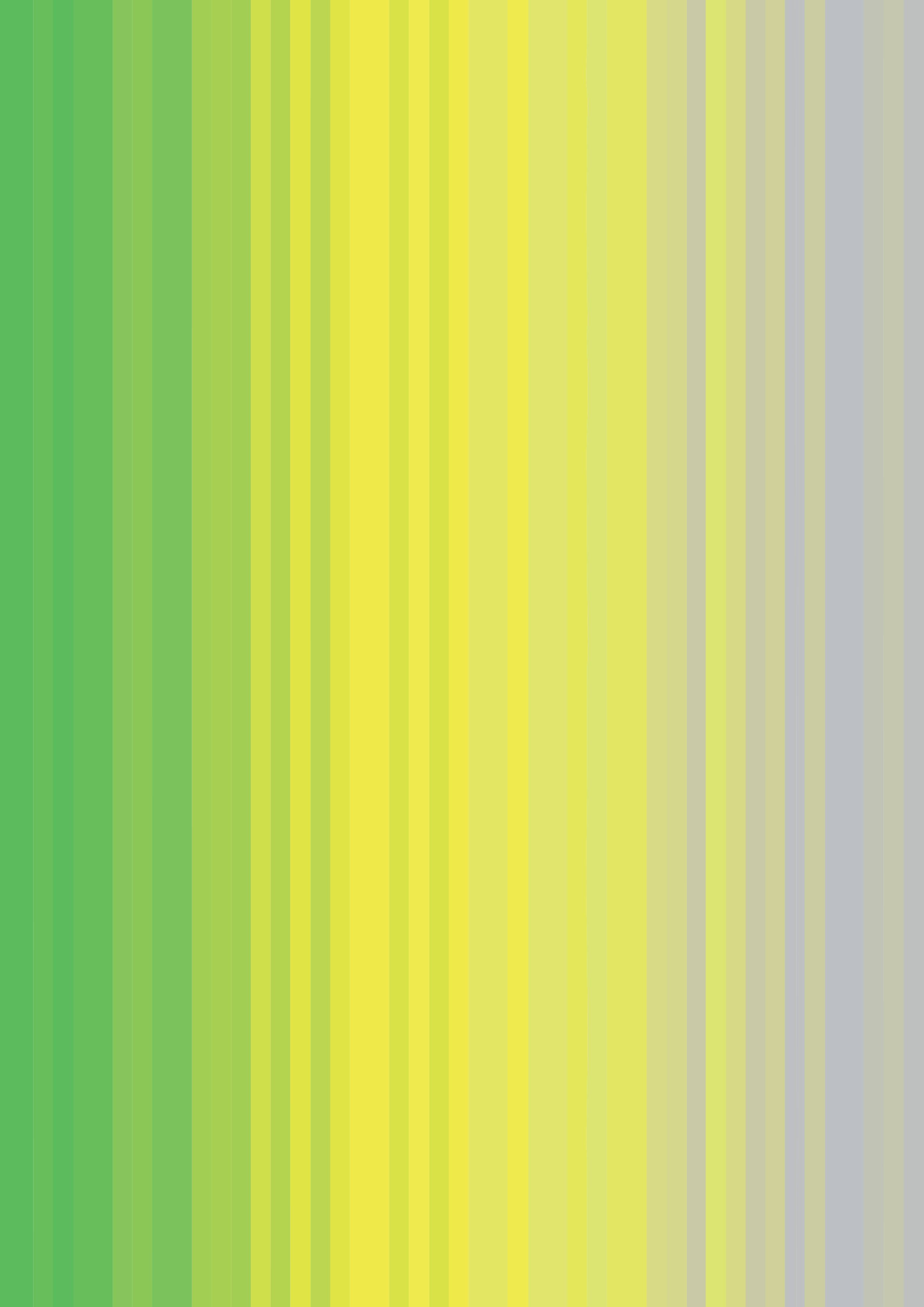
Royal Botanic Gardens
Kew

State of the World's Plants and Fungi

2023



State of the World's Plants and Fungi 2023

Tackling the Nature Emergency: Evidence, gaps and priorities

Contents

Introduction

What grows where? Knowledge about where to find particular species in nature must have been key to the survival of humans throughout our evolution. Over time, and as people colonised new land masses and habitats, interactions with the local biota led to a wealth of combined traditional and scientific wisdom about the distributions of species and their many uses.

Fast-forward to the present day, and much of our current scientific knowledge of global plant and fungal diversity comes from specimens hosted by the world's herbaria and fungaria, of which there are more than 3,000. But despite this wealth of knowledge and collections, one might be surprised to learn that, to date, we have not been able to answer one of the most fundamental questions in plant and fungal diversity with confidence – namely, how many species are there globally and in different parts of the world?

The consequences of our insufficient knowledge on biodiversity and distribution are manifold. Scientists may have drawn biased – or possibly even incorrect – conclusions on the patterns and underlying drivers of diversity. Beyond the impacts of knowledge gaps and inaccuracies on efforts to answer fundamental scientific questions, there are serious implications for conservation given that several targets in the *Kunming–Montreal Global Biodiversity Framework*, such as those related to protecting and restoring biodiverse habitats, rely on having robust biodiversity data.

To tackle this challenge, this fifth edition of *State of the World's Plants and Fungi,* from the Royal Botanic Gardens, Kew (RBG Kew), focuses on the latest knowledge on the diversity and geographical distribution of plants and fungi. It relies on two major advances. The first is the release of the World Checklist of Vascular Plants complete with geographical distributions for all known species – a landmark achievement, led by RBG Kew's Rafaël Govaerts, which took more than 35 years of meticulous and highly collaborative work. And the second is the extraction of a wealth of new information on fungal diversity from analyses of environmental DNA in soil samples across the world, combined with morphological and molecular evidence from fungarium specimens.

In the following chapters, we present compelling stories demonstrating what we have learned from these and related sources of data, and how this understanding can help us foster future research and conservation. This report is based on groundbreaking research papers from many international teams of scientists. They are co-released in a collection of open-access articles titled 'Global Plant Diversity and Distribution' from the journals *New Phytologist* and *Plants, People, Planet*, and a review of global fungal diversity in the *Annual Review of Environment and Resources*.

We are grateful to the Sfumato Foundation for financial support, the journals' editorial boards, the expert reviewers, and all authors and other contributors to this important, timely and fruitful collaboration.

Just as our early ancestors needed to know what grows where for their own survival, so plants and fungi need us to know where they grow – to enable us to safeguard their continued existence for generations to come.

Professor Alexandre Antonelli
Director of Science
Royal Botanic Gardens, Kew

THIS FIFTH EDITION OF RBG KEW'S STATE OF THE WORLD'S PLANTS AND FUNGI FOCUSES ON THE LATEST KNOWLEDGE ON THE DIVERSITY AND GEOGRAPHICAL DISTRIBUTION OF PLANTS AND FUNGI.

STATE OF THE WORLD'S PLANTS AND FUNGI 2023 DRAWS ON THE EXPERTISE OF

200 SCIENTISTS FROM 102 INSTITUTIONS IN 30 COUNTRIES WORLDWIDE

WHAT'S IN A NAME?

In this chapter, we learn: how one scientist's desire to protect the rainforest led him to spend decades compiling a list of all known plant species; how the addition of location data to this list is proving to be a powerful tool for biodiversity research; and that creating the list helped to realise one of naturalist Charles Darwin's dreams.

350,386

SPECIES ON THE WORLD CHECKLIST OF VASCULAR PLANTS, AND COUNTING...

Being able to map the world's wild species – from towering rainforest trees to tiny orchids – is underpinning wide-ranging new research.

'CAN YOU GIVE ME A LIST OF ALL THE PLANTS IN THE WORLD, PLEASE?'

Wanting to identify plants that might be threatened by rainforest destruction in the late 1980s, Belgian student Rafaël Govaerts asked the botanic gardens in Brussels this question but was told no such inventory existed. Undeterred, he set about cataloguing all the plants known to science himself. Three decades later, in 2021, Govaerts finished compiling his first complete list, which involved identifying all the evidence that formed the basis for a plant taxon (such as a species, genus, family and so on) and confirming the 'accepted' name and any synonyms. Since then, existing information on the global distribution of each plant on the list has been added, bringing all this information together for the first time. This is enabling scientists to explore, like never before, patterns of plant richness, spread and extinction across the tree of life and the globe (see Figure 1).

'The list has already been used in very many published plant conservation assessments – for example, Botanic Gardens Conservation International has referenced the checklist for tens of thousands of tree species as the fundamental first step for determining extinction risk, so what I originally envisaged for the list has happened, and a lot more,' says Govaerts, who today heads up the Plant and Fungal Names team at the Royal Botanic Gardens, Kew (RBG Kew), where he has worked to deliver his mission since the 1990s. 'The Convention on Biological Diversity recognises that taxonomy is fundamental to conserving biodiversity because you need to know what plants exist before making assessments of how threatened they are. So, the idea that I had in the 1980s is now part of global policy, too.'

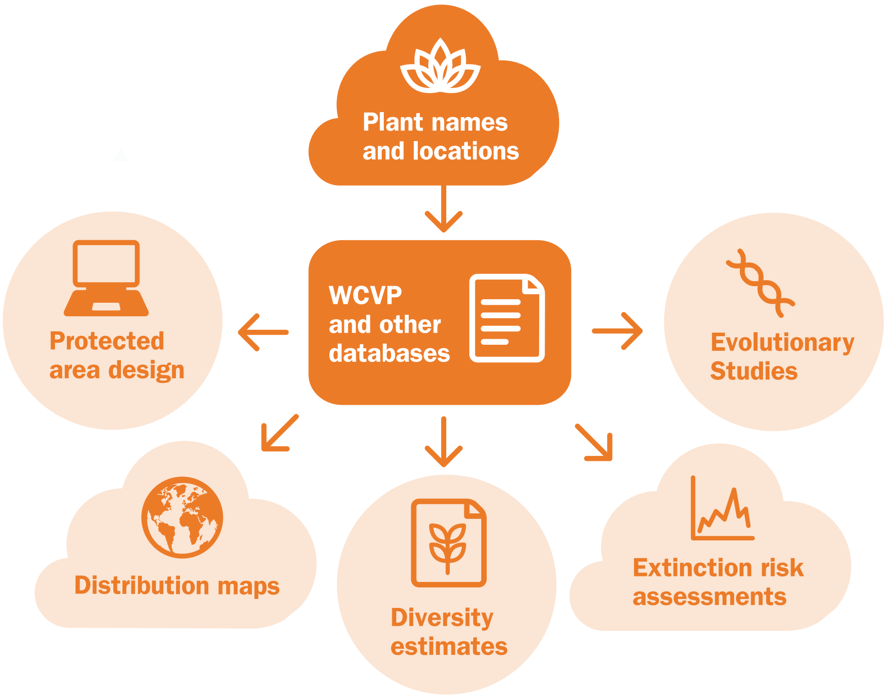
The list is known officially as the World Checklist of Vascular Plants (WCVP). Vascular plants, which are are those with specific tissues for conducting water and nutrients around their structures, make up the vast majority of plant species on Earth. They include the flowering plants, other seed plants such as conifers and cycads, and also ferns, horsetails, clubmosses and quillworts, but exclude groups such as mosses and algae.

NAMING NAMES

Species are described and named using the long-established scientific naming protocol of a genus name with a specific epithet – such as *Betula pendula*, the silver birch. Classifying and naming organisms in this way is an attempt to parcel up the seemingly endless diversity of life so we might better understand, protect, manage and sustainably use it. But the list of names is constantly evolving as new species are encountered and described, and as species and the relationships between them are redefined in the light of new scientific evidence. These revisions can lead to new names superseding old ones – and the emergence of multiple synonyms associated with a single accepted name. As this chapter was being written, there were 1,422,515 names on the WCVP. These included 1,033,367 names at species level, of which 350,386 were 'accepted'.

FIGURE 1: It all starts with names and places

The first step towards understanding, protecting and sustainably using biodiversity is to identify, describe and name species. The World Checklist of Vascular Plants (WCVP) combines names with geographical data to underpin a wide range of biodiversity research.



THE LIST OF PLANT NAMES IS CONSTANTLY EVOLVING AS NEW SPECIES ARE ENCOUNTERED AND DESCRIBED, AND THE RELATIONSHIPS BETWEEN SPECIES ARE REDEFINED IN LIGHT OF NEW SCIENTIFIC EVIDENCE.

Gustavia longifolia is used in South America as a medicine, food and fuel. Having name and distribution data for useful plants can ensure they are included in conservation strategies.

Although the WCVP now contains taxonomic and geographical data for all known vascular plant species, Govaerts' work is far from complete. This is because around 2,500 plant species are named as new to science every year (see Chapter 3). And whereas, in the past, a selection of printed library journals was a one-stop shop for finding out about these new names, today the information is spread among a huge variety of printed and online journals, portals and databases.

'It is becoming harder to keep track of all the new species,' admits Govaerts. 'Fundamentally the checklist is of scientific data that is peer-reviewed and published in scientific publications, so in that sense it hasn't changed that much. But there are a lot more data out there that are not published in scientific works, and on one hand you want to keep up to date but you also need to make sure the data are of suitably high quality.'

The International Plant Names Index (IPNI), also maintained by Govaerts' team, is the foundation for the WCVP. The Index is an up-to-date register of the plant names published globally, compiled by RBG Kew, the Harvard University Herbaria and the Australian National Herbarium. It includes each plant name's correct spelling, who published it, information on the 'type' specimen (the reference specimen connected to the name), and the place and date of publication. Once names from IPNI are added to the WCVP, Govaerts consults botanical literature, herbarium specimens and experts to determine which names represent currently accepted species. Each name is tagged in the WCVP as accepted, a synonym or 'unplaced' (unable to be assigned).

Once all names within a particular plant family are present on the checklist, or if that group of plants has been recently updated, the relevant data are sent to one or more experts in that family for feedback. This helps to ensure that the checklist is as robust as can be. In 2019, Govaerts received more than 2,000 feedback emails, and made 500,000 edits to the WCVP data.

PUTTING PLANTS ON THE MAP

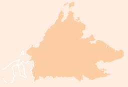
The recently completed work to add geographical data began in a structured way in 1994. This involved amalgamating information already published in regional checklists and publications detailing plants from a particular region. The sources ranged from booklets on plants within individual protected areas to continental-scale assessments compiled over decades. Govaerts and his team began with Europe before working, over the years, across all the major regions of the world. As for all data in the WCVP, standard protocol was followed: in this case, the use of the 'botanical country' level of the World Geographical Scheme for Recording Plant Distributions (see Box 1). Life-form and climate-zone data were also added for most accepted species at this stage. As this edition of *State of the World's Plants and Fungi* shows, adding geographical data to WCVP is a game-changer for botanical research (see Box 2, overleaf), helping to reveal a new perspective on the geographical origin of the orchid family (see Chapter 5), highlighting regional 'darkspots' where we lack knowledge on biodiversity (see Chapter 7), and revealing countries' varying attitudes towards protecting their unique plant species (see Chapter 10).

BOX 1: Keeping plant data consistent

The World Geographical Scheme for Recording Plant Distributions was developed to ensure consistency between botanical – particularly taxonomic – databases. Developed by Biodiversity Information Standards (TDWG), it provides definitions and codes for recording plant distributions at four levels. WCVP records data at Level 3.

Malesia (Level 2)

Borneo (Level 3)



Sabah (Level 4)

Level 1	Level 2	Level 3	Level 4
Continents: Europe; Africa; Asia-Temperate; Asia-Tropical; Australasia; Pacific; Northern America; Southern America; Antarctic	**Regions:** Each continental area is divided into between two and ten subcontinental regions. For example, Antarctic is divided into Subantarctic Islands and Antarctic Continent.	**Botanical countries:** Regions are divided into botanical countries, which in most cases equate to political countries, although some large countries are split and outlying areas are sometimes excluded.	**Basic recording units:** Generally only used for states or provinces of large countries, and major islands and archipelagos, reflecting political boundaries.

An example of the four levels and their codes for the Malaysian state of Sabah.

Level 1:
Asia-Tropical (4)

Level 2:
Malesia (42)

Level 3:
Borneo (BOR)

Level 4:
Sabah (BOR-SB)

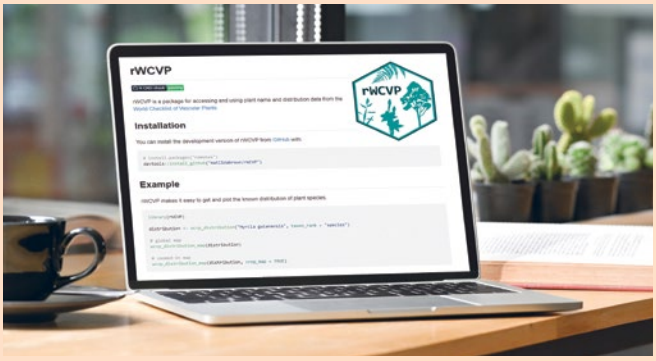
Calamus zollingeri, an important commercial rattan species.

Names are key to managing wild-harvested rattans sustainably

The World Checklist of Vascular Plants (WCVP) has provided the core names to enable RBG Kew scientists to sequence all 500 species of rattan, in a project aimed at helping conserve vital wild biodiversity. Stems from rattans, which are spiny, climbing palms from the tropical forests of Asia, the Pacific and Africa, are harvested extensively from the wild to make furniture and other products for the multibillion-dollar cane industry. With commercially valuable species vulnerable to overharvesting and extinction, knowing how many species of rattan exist, where they occur and how big their populations are is essential to ensuring they can be conserved successfully and managed sustainably.

The researchers combined data from the WCVP and RBG Kew's herbarium collections for their study. The WCVP provided the latest information on the taxonomy and names of all rattan species, which underpinned the work to sequence the DNA of multiple specimens of each species. Having all 500 species sequenced will facilitate DNA-based authentication of rattans, and contribute to building a framework for future work to conduct effective conservation assessments, regulate trade, and sustainably use this important group of palms.

BOX 2: Putting the World Checklist to work



Anyone can access the World Checklist of Vascular Plants and peruse the data it contains via an online portal called Plants of the World Online. This site enables the user to search by country or plant name, and to access other RBG Kew resources. However, for more complex analyses, researchers at RBG Kew have developed a bespoke software package called rWCVP to simplify the process of interrogating the data. It is designed to help users answer questions that regularly crop up in biodiversity research, such as: How many species are there in region X? How do I merge two datasets? How many species are in a particular family?

Often, the first step in botanical research is to reconcile the names of species. For example, a botanist might have historic herbarium specimens that are labelled with old names from before the plant's correct position on the tree of life was known. Because WCVP includes a 'paper trail' detailing the history of a particular plant's classification, the researcher can search for their specimen names using rWCVP and identify what the current accepted name is before carrying out further studies. This function can also help to match names that are wrongly spelled. There are various search methods available to users, including using phonetic pronunciation.

If a species name is found to be a synonym, rWCVP can identify whether it is 'homotypic' (where a species has simply changed name) or 'heterotypic' (for example, where two or more scientists independently published different names for the same species using different reference [type] specimens). Correctly distinguishing between the two is important for accurately answering research questions and informing on-the-ground conservation.

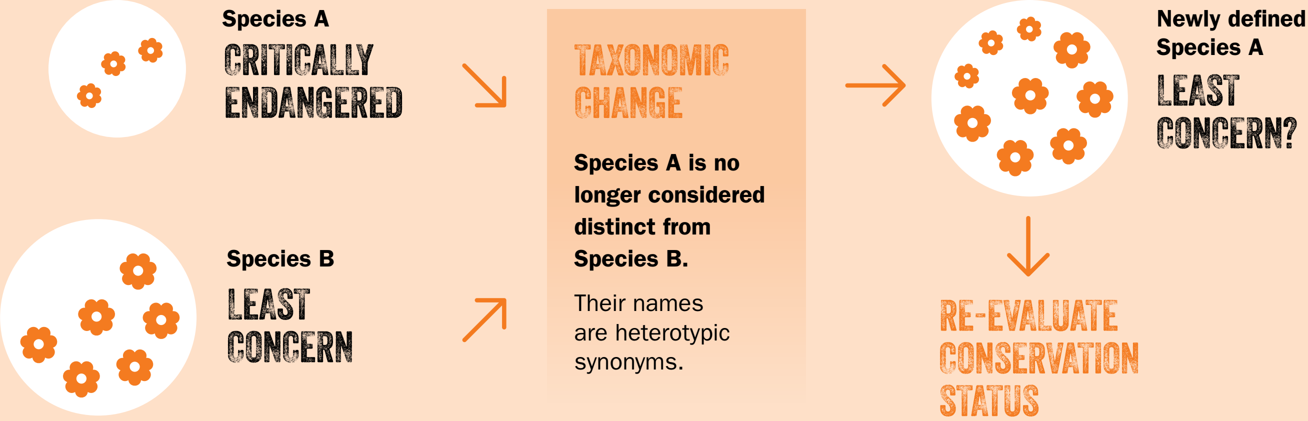
For example, if two species that were once considered distinct have been merged, one of the names is retained as an accepted name, and the other is treated as a heterotypic synonym (see below). This may affect the conservation status of the species; if an assessment was carried out on one of the original species before the merge took place, then this work will need updating. The conservation status of the newly defined species may well be different, particularly as it will have a larger population and thus potentially a lower extinction risk. So, it can be important to find out if a species has heterotypic synonyms to ensure conservation assessments are accurate, and so that limited conservation resources can be focused on the species that most need them.

The rWCVP package can also be a starting point for helping researchers to identify 'Important Plant Areas' (IPAs) and 'Key Biodiversity Areas' (KBAs). IPAs are sites that support globally threatened plant species and habitats or have exceptional plant richness – or both, while KBAs are sites that are globally important for the long-term survival of biodiversity of any kind. Identifying sites that meet the criteria for IPAs and KBAs is vital for prioritising conservation actions, and relies on having an accurate species list.

For tropical countries with thousands of species, a user might employ the package to plot all the known plants and then focus in on those that have very small ranges or occur only in a few areas and are potentially threatened. This list can then be used as the basis for gathering more information on those species, which can help identify potential areas for designating as IPAs or KBAs. The package is helpful, too, for putting national or regional data in a global context, which is required for some of IPA and KBA criteria.

Why do names matter?

Knowing whether a species has heterotypic synonyms can be important for conservation. In the example below, an extinction risk assessment for Species A, placing it in the Critically Endangered category, was carried out before it was recognised to be part of Species B. From the moment of the taxonomic change, the original assessment of Species A was no longer applicable. Without such knowledge, limited conservation resources may be spent on low priority populations of a widespread species.



Species A is no longer considered distinct from Species B.

Their names are heterotypic synonyms.

For Govaerts, necessity was the mother of the WCVP's invention. A similar need for data on plants to support research at other institutions has led to the parallel development of three other similar checklists. First, World Plants (WP) was started in the early 1990s by Dr Michael Hassler to create a digitised and publicly available global checklist of vascular plants. It is widely used for its taxonomic treatment of ferns and has been accessible online since 2019. It forms part of the Catalogue of Life, an authoritative list of the world's species, of which the WCVP is also a founding dataset.

Meanwhile, Curator of the Botanical Gardens of Leipzig, Germany, Dr Martin Freiberg, and collaborators created the Leipzig Catalogue of Vascular Plants (LCVP), which forms part of Freiberg's LifeGate project to build a biodiversity portal with an interactive map of the tree of life. The data on vascular plants have been downloadable since 2020. And World Flora Online (WFO) was founded in 2012 (building on earlier venture The Plant List – a working list of all known plant species), in response to the 2011–2020 *Global Strategy for Plant Conservation's* target to produce an online flora of all known plants. The WFO portal was launched in 2019, with the first version of its plant list released in May 2021. The Plant List and WFO are broader in scope than the other checklists as they also include the Missouri Botanical Garden's bryophyte list (encompassing mosses, liverworts and hornworts), compiled by Dr John Brinda.

UNITING THE BIG FOUR

In 2023, Dr David Schellenberger Costa, Research Fellow at the University of Leipzig and the German Centre for Integrative Biodiversity Research (iDiv), gathered together Govaerts and other plant-list curators to assess the similarities and differences between the lists, with a view to possibly harmonising them in the future. Their analysis revealed that while the lists provided identical information on about 60% of plant names, there were some incongruencies. Furthermore, due to the different motivations of the compilers and varying approaches used, there were other important differences between the lists that made comparisons difficult. For example, they differed in the database formats used, the frequency with which they were updated and the range of publications consulted during compilation.

'People often ask: "Which list should I follow?", "Why are there four?" and "Which one is best?",' explains Govaerts. 'And as the different curators of them, we thought we should collaborate to find the answers and move towards eventually forming one list.'

The curators agreed that exploring and comparing the lists was a beneficial exercise for several reasons. First, it highlighted errors, such as incorrect coding, special characters in names, missing authors and so on. Also, by matching names across databases, it paved the way for new information that was currently missing from some lists to be incorporated. For example, geographical information might be added to WFO, while links to IPNI could strengthen LCVP and WP to allow name changes to be synchronised. They also found that the process helped to make each curator more personally aware of the strengths and weaknesses of their own product and approach. They felt that the exercise would help them to improve the lists and identify specific ways in which they could harmonise existing, or import missing, content going forward.

'Maintaining global checklists is a never-ending task, as new species are discovered and taxonomies updated,' says Dr Schellenberger Costa. 'Thus, in the long run, only a collaborative approach can be sustainable. Nevertheless, having several of those checklists right now, some essentially created by single dedicated individuals, enabled us to identify ways for improvement and spot errors, increasing the quality of any future version of the checklists.'

The study revealed, too, that each of the lists had its own philosophy and purpose. In this regard, the curators felt that their work to detail each list's provenance, the specific data included and the work processes used to compile it would enable scientists to make more informed choices as to which list would best suit their work. For example, the philosophy behind WFO was that it was inclusive – run by a consortium of more than 50 botanical institutions to support conservation and the sustainable use of plants. In comparison, the strategy behind the WCVP was to have the most scientifically up-to-date published and expert-reviewed data to underpin wide-ranging research. The question remains as to how the four lists should be integrated, but the curators have taken an important first step in trying to bring the lists together towards a global consensus.

Interestingly, Govaerts was not the first person to seek a list of all the plants in the world; 19th-century naturalist Charles Darwin had requested the same from RBG Kew and upon learning that one did not exist, he left a bequest to produce such a list. The result was *Index Kewensis*, a list of seed plants maintained by RBG Kew from 1885, which later provided the foundation for IPNI in 1999. And while the four modern checklists may have their differences, they all used IPNI as their core data. When he made his bequest, Darwin had specifically requested that the list should include the distribution of plants by country. Nearly a century and a half on, his wish, like Govaerts', has finally become a reality.

This chapter is based on the following peer-reviewed publications, preprint and repository:

Antonelli, A., et al. (2023). Why plant diversity and distribution matter. Editorial, 'Global Plant Diversity and Distribution'. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19282

Brown, M.J.M., et al. (2023). rWCVP: a companion R package for the World Checklist of Vascular Plants. *New Phytologist.* DOI: https://doi.org/10.1111/nph.18919

Govaerts, R., et al. (2021). The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data* 8: 215. DOI: https://doi.org/10.1038/s41597-021-00997-6

Kuhnhäuser, B.G., et al. (2023). RattanID – a molecular identification toolkit for rattan palms. *Zenodo*. DOI: https://doi.org/10.5281/zenodo.7895955

Schellenberger Costa, D., et al. (2023). The big four of plant taxonomy – a comparison of global checklists of vascular plant names. *New Phytologist*. DOI: https://doi.org/10.1111/nph.18961

FINDING OUT THE FUNDAMENTALS OF FUNGI

In this chapter, we learn: that prior estimates of fungal diversity ranged from 250,000 to 19 million; why between 92% and 95% of fungi have yet to be scientifically described; why naming protocols used for plants are unsuited to fungi; and that the stage is set for the rapid acceleration of knowledge on the fungal kingdom.

A NEW ESTIMATE OF

2,500,000

SPECIES CONFIRMS FUNGI AS THE SECOND LARGEST KINGDOM OF EUKARYOTES AFTER ANIMALS

This whitelaced shank mushroom (*Megacollybia platyphylla*) has a visible fruiting body, but many fungi remain hidden.

EXPANDING OUR KNOWLEDGE OF FUNGI IS THE NEXT FRONTIER OF BIODIVERSITY SCIENCE. MAINLY AS A RESULT OF THEIR COVERT LIFESTYLES, THESE ENIGMATIC ORGANISMS HAVE LONG BEEN OVERLOOKED BY RESEARCHERS.

They live as thread-like structures or in single-celled form within soil or other organic materials, in water or on rock, with only a small percentage of species on occasion flaunting spore-making mushrooms, brackets or other structures that can be easily studied. As a result, only 155,000 species have been formally named, while estimates of the total diversity have ranged from 250,000 in the 1800s to as many as 19 million species in recent decades. Now, scientists have come up with a far more robust estimate for the number of fungal species on Earth. This will greatly help to define the scale of the task to track down, name and safeguard fungal biodiversity in the coming years.

To hone down the range of estimates, a team of fungus specialists comprehensively assessed current knowledge on the topic. By forensically examining recent predictions for fungal diversity produced via four main academic pathways – scaling laws; fungus:plant ratios; actual versus previously known number of species; and DNA-based studies – they calculated that there are likely to be 2–3 million species of fungi globally, with a best estimate of 2.5 million (see Figure 1). This means that more than 90% of fungal species remain unknown to science. The race is now on to find, describe and name those species – which may contain valuable medicinal compounds or possess other useful properties – at a time when biodiversity loss is at crisis point.

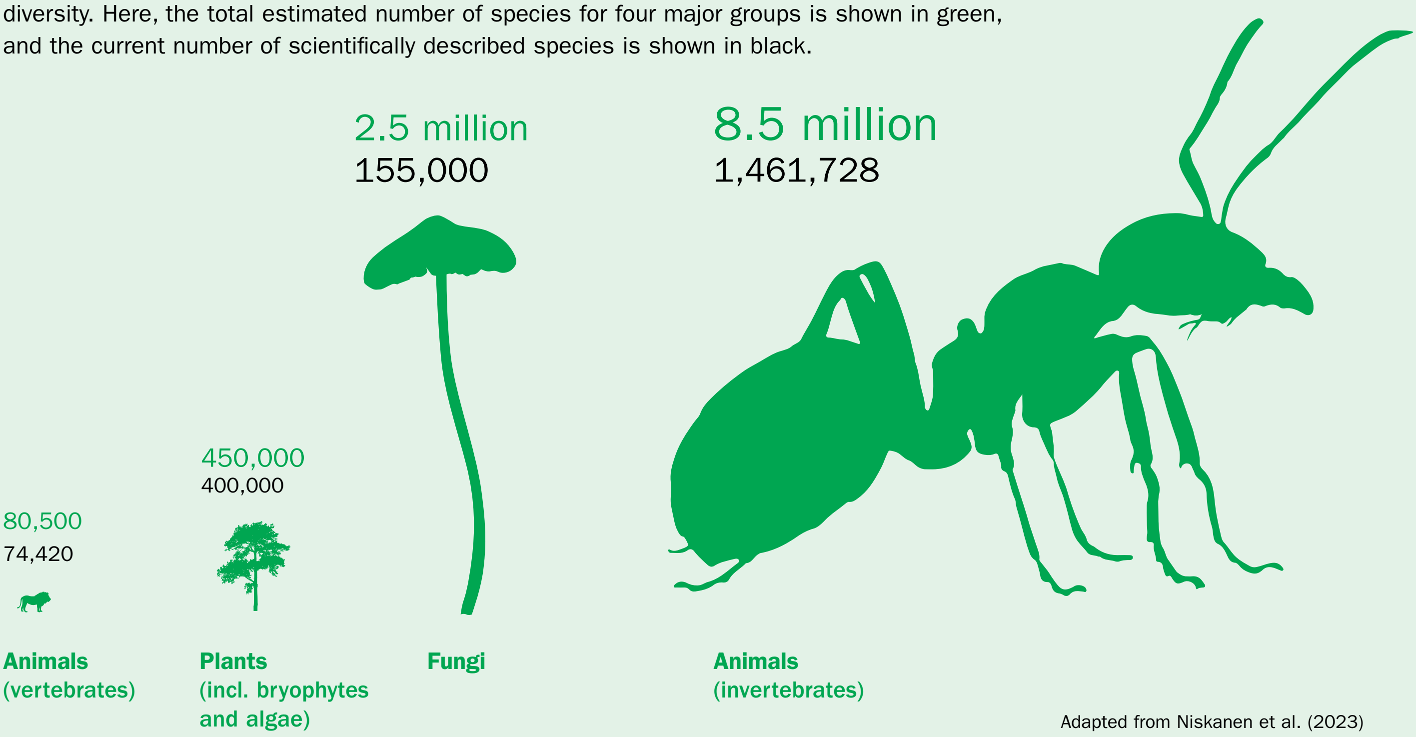
'Naming and describing species is the vital first step in documenting life on Earth,' says Dr Tuula Niskanen, former Research Leader at the Royal Botanic Gardens, Kew (RBG Kew) and now Senior Curator at the Finnish Museum of Natural History, Helsinki, who led the research. 'Without knowing what species there are and having names for them, we won't be able to share information on the key aspects of species' diversity, make any assessments of their conservation status to know whether they are at risk from extinction, or explore their potential to benefit people and society. It is essential to know what species of fungi we have here on Earth and what we need to do for them, so that we don't lose them forever.'

ELUSIVE ORGANISMS

Fungi first appeared around 1.3 billion years ago, when they diverged from a common ancestor of animals and other related organisms. Instead of being able to ingest food in the way animals do, fungi must absorb nutrition from their surroundings. Doing so efficiently requires a large surface-to-volume ratio and a wet environment. As a result, fungi are either multicellular, with thin filaments called hyphae that form a network or 'mycelium', or yeasts that are simple, spherical and single-celled. Their nutritional strategy means that most species of fungi are forced to live inside their food or in direct contact with it, in moist environments. The vast majority of mycelia therefore remain hidden. Fungi are divided into those that feed off dead matter (saprotrophs), which

FIGURE 1: How species diversity differs between animals, plants and fungi

An updated estimate confirms fungi as second only to invertebrate animals with regards to species diversity. Here, the total estimated number of species for four major groups is shown in green, and the current number of scientifically described species is shown in black.



Adapted from Niskanen et al. (2023)

dwell in soil, water, dead wood or leaf litter, and those that live off live organisms (biotrophs). Biotrophs can be harmless, beneficial, or harmful to their hosts, depending on the relationship between the organisms.

Most fungi disperse their spores by air, on animals or in water droplets. To do so, they must first form spore-bearing structures, which include familiar mushrooms, truffles and bracket fungi. These are often ephemeral or appear seasonally. However, fungi that form lichens have persistent spore-bearing structures. Forming symbiotic relationships with algae or bacteria (or both), these fungi are able to feed off carbohydrates photosynthesised by their partners, so do not need moist environments to thrive. Fungi range in size from tiny to huge. Recorded as extending across more than 10 km^2, a single genetic individual of the dark honey fungus, *Armillaria ostoyae*, is one of the largest organisms on Earth.

SEEKING CLARITY

Rapid advances in genomics (the study of an organism's entire complement of DNA) and metagenomics (scrutiny of the DNA from a community of organisms) over the last few decades had made it clear that we only knew a fraction of the global funga. Based on the most extensive previous estimates, scientists considered the number of fungal species was most likely to lie between 1.5 and 6.3 million. All these figures were based on the extrapolation of existing data and had varying levels of uncertainty associated with them, mainly due to insufficient sampling. Many of the predictions had been made on an ad hoc basis, without quantitative assessments, or had made misguided assumptions. Even the quantitative assessments had tended to focus on particular groups of fungi, potentially missing insights that might come from scanning the full range of biodiversity. By taking a critical look at these works, and the underlying data and methods used, the scientists hoped to significantly narrow down the range of estimates.

FOUR MODES OF INVESTIGATION

The taxonomic system by which organisms, including fungi, are classified has eight main levels – or taxa – which, from highest to lowest, are: domain, kingdom, phylum, class, order, family, genus and species. The first approach the researchers examined was the use of scaling laws, which involves predicting species diversity from patterns in the numbers of 'higher taxa' – considered, in this case, to be those between phylum and genus – and the count of currently known species in each. A major study that had used scaling laws had estimated that 611,000 species of fungi exist. However, the study's authors considered the number of known species to be 43,271, less than half the actual number at that time of around 100,000. The research team calculated that using the correct figure would increase the global richness estimate to 1.4 million but concluded that even this figure was likely an underestimate, as further higher fungal taxa had become known in the intervening decade.

The second method the researchers examined, fungus:plant ratios, had been used far more widely than scaling laws, and under a variety of scenarios, including to examine the proportions of plants and fungi in small local areas, countries and specific plant taxa. One issue with this method was that a clear framework was lacking. For example, some studies included only fungi directly associated with plants, while others considered all fungi recorded for a given area for which the number of plants was known. This meant that the calculated estimates for global fungus:plant ratios ranged between 6:1 and 10:1, with ratios for individual sites or hosts reaching as high as 89:1. Country-based ratios were generally more in agreement with each other, extending between 2.5:1 and 5.1:1 for Japan, the USA, Canada, Germany and France. The UK figure was 9:1 when considering only native plants but 2.6:1 when including non-native plants, which also host fungi listed in the national species list.

Because fungus:plant ratios vary across latitudinal zones, separate estimates are required for tropical, temperate and Arctic biomes. After examining the varied predicted figures and the different interpretations of the global fungus:plant ratio approach, the research team arrived at a mean estimate of 5:1 for temperate areas and of 3.5:1 for tropical ones. With roughly one-third of plant species occurring outside of the tropics and two-thirds inside, this resulted in a figure of 1.56 million fungi. However, the scientists concluded that this figure was likely an underestimate as it would not take into account hidden diversity within taxa. Diversity can sometimes be overlooked if what is thought to be a single species is, in fact, a 'species complex', a group of very closely related species that are hard to distinguish from each other and sometimes only discovered following DNA analyses. In addition, some fungal groups, such as endophytes, which live inside plant tissue, are difficult to detect and may be missing from inventories used in the fungus:plant ratio calculations.

The third approach involved the research team examining a major study that had analysed the amount of hidden diversity in presumed-known fungal species. The authors of the study had arrived at a ratio of 11.3:1 for the number of actual-versus-presumed species across a large taxonomic sample drawn from multiple research projects. They had used this ratio to extrapolate the currently known species, 150,000 at the time, to 1.7 million. However, the research team corrected this base reference to 130,000, to match the number of known species at the onset of most studies on species complexes that were included in the study. This yielded a prediction of 1.47 million species instead.

The final approach the research team examined was that of a DNA-based method called environmental metabarcoding, which has emerged in recent years as the most powerful tool for documenting fungal diversity globally. It involves simultaneously sequencing the DNA of whole communities of taxa from a single sample. The predictions of several available studies using this method ranged from 1.5 to 6.3 million. One additional study had calculated species-richness data for the ten largest genera of fungi in soil including *Cortinarius* (14,375 species), *Cladophialophora* (15,968), and *Glomus* (7,610), which span three phyla. Comparison of those figures to the number of currently accepted species in each genus resulted in a factor of 80–115:1, with extrapolation giving a global estimate of 19.35 million species. However, adjusting for errors caused by various biases, the research team derived a global estimate of 2.28 million.

AT THE CURRENT RATE THAT SCIENTISTS ARE NAMING SPECIES, IT WOULD TAKE 750–1,000 YEARS TO FULLY DESCRIBE THE WORLD'S FUNGI.

The smooth cage fungus (*Ileodictyon gracile*) is saprotrophic, which means it lives and feeds on dead organic matter.

Although the original recent predictions of global fungal diversity ranged from 500,000 to more than 19 million, the results arrived at after scrutiny of the underlying data and methodologies appeared to coalesce around 1.5 million. However further corrections were required to account for the exclusion of some fungal groups. For example, using fungus:plant ratios may have overlooked fungi not associated with plants – such as those living on or in other fungi, insects or other animals. And the focus of metabarcoding on soil fungi could have neglected above-ground plant pathogens, endophytes, lichens, and arthropod-associated fungi. Moreover, both methods may have missed out fungi in aquatic and marine environments. When the research team made additional adjustments to account for these omissions, the global predictions emerging from the different approaches were surprisingly homogenous, at between 1.5 and 3.2 million, with a mean of 2.53 million. The scientists therefore proposed a revised range of 2–3 million, with a best estimate of 2.5 million, confirming fungi as the second largest kingdom of eukaryotes after animals (see Figure 1).

PROVIDING LIFE SUPPORT

Fungi underpin nearly all life on Earth, being vitally important to land plants, how ecosystems function and ultimately the whole of humanity. Mutualistic fungi improve the uptake of essential nutrients to plants (for example, mycorrhizal fungi form associations with plant roots, in which the plants provide the fungi with carbon and fats in exchange for water and mineral nutrients, such as nitrogen and phosphorus). And some ‘endophytic’ fungi, which live in plants without harming them, support their hosts by stimulating their immunity to pathogens and enhancing their stress resistance. Fungi are significant biomass decomposers of rigid natural polymers such as lignin, cellulose and chitin. And they are an increasingly valuable source of bioactive compounds, including antibiotics, immunosuppressants and statins for medicine.

For all these reasons, finding, naming and understanding the as-yet-undocumented 92–95% of fungi that exist out in the world is an urgent priority. At present, over 2,500 species of fungi are named as new to science each year; continuing at this current rate would require 750–1,000 years to name the remaining unknown species. Even accelerating this process by an order of magnitude to 25,000 new species per year, it would still take around a century. Currently, naming a new species requires a physical specimen – which is usually an organism encountered in the wild or cultured in a laboratory. However, such methods are likely to yield descriptions for only a fraction of the extant fungal diversity. New protocols are therefore needed that allow the naming of ‘dark taxa’ – those only known from their DNA sequence. The research team are therefore advocating a change to the way fungi are formally described, so that they can be classified based solely on molecular data.

The formal classification of fungi solely from environmental metabarcoding data would potentially make it viable for scientists to catalogue 50,000 new species per year, reducing the time needed to describe the remaining diversity to decades rather than centuries. As a first step, sequence data from type specimens (those used traditionally to formally name a species) would need to be produced to anchor names of all species already described. With that process completed, a researcher could compare DNA barcodes from a sample to established reference databases to find out whether or not a particular species was new to science. The vast collections of fungi already deposited in the world’s fungaria, such as at RBG Kew, are also a potential source of thousands of new species, which sequencing could reveal. Together, data from the type and non-type specimens could form the basis of a global framework for merging specimen-based and environmental sequence data.

Scientists could then comprehensively sample fungi from all habitats and regions around the world with relative ease, using this to further hone diversity estimates and better understand where fungi are distributed. This work has already begun in earnest. Recent global initiatives, such as the Global Lichen Hunt (a project to encourage the public to search for lichens in their backyards and upload their observations), FunAqua (aimed at building a global DNA-based inventory of aquatic fungal biodiversity in water and sediments) and FunLeaf (a citizen-science program to describe organisms associated with plant leaves), are filling in gaps in fungal biodiversity data from substrates other than soil. Meanwhile, the Sequence Read Archive, the largest publicly available repository of high-throughput sequencing data from all branches of life, contains about 150,000 environmental samples corresponding to fungal DNA, with many billions of individual DNA sequences – and this number is growing exponentially.

A NEW FUNGAL FRONTIER

Research has shown that one teaspoon of soil can contain hundreds of fungal species. So, alongside continuing to collect fungi using traditional methods, a focus on environmental sampling would speed up the collection of species from the field and the gathering of DNA sequence data. A concerted global effort could easily generate in excess of a million samples within a period of five years. ‘Employing a global terrestrial grid cover of 20 by 20 kilometres should enable us to cover most of the global fungal diversity,’ says Dr Robert Lücking, Head of Research and Curator for Fungi, Lichens and Bryophytes at the Botanical Garden of the Free University of Berlin, Germany. ‘The key challenges will not be scientific, but logistical – securing the required resources and permits, and forming equitable partnerships and collaborations to avoid duplicating effort and wasting resources. Once those hurdles are overcome, we will be well placed to accelerate the gathering of fungal specimens, and finally expand knowledge of the fungal kingdom to match the level of plants.’

This chapter is based on the following peer-reviewed publication:

Niskanen, T., et al. (2023). Pushing the frontiers of biodiversity research: Unveiling the global diversity, distribution and conservation of fungi. *Annual Review of Environment and Resources*. DOI: https://doi.org//10.1146/annurev-environ-112621-090937

SHOWCASING SPECIES NEW TO SCIENCE

In this chapter, we learn: how exploration and detective work have revealed thousands of species new to science since the start of 2020; how very large species can sometimes remain hidden; and why even widespread species of fungi are still being encountered by mycologists for the first time.

>8,600

SPECIES OF PLANTS AND

>10,200

SPECIES OF FUNGI SCIENTIFICALLY NAMED SINCE THE START OF 2020

Victoria boliviana, one of the species named as new to science in 2022, is now thriving at RBG Kew.

Hibiscus hareyae

Mauritiella disticha

The new plant species named since 2020 come in all shapes and sizes (clockwise from top left):

Hibiscus hareyae, from the coastal scrub of Tanzania, East Africa, is able to withstand particularly dry conditions.

Mauritiella disticha, a spiny-trunked fan palm, is restricted to just five sites in the Amazon basin.

Carpotroche caceresiae, a tree from rainforests in Nicaragua and Honduras, was named after Berta Isabel Cáceres Flores, one of 123 environmental activists assassinated between 2009–2016 in Honduras.

Aloe rakotonasoloi was named as new to science by botanists at RBG Kew's overseas office in Madagascar.

Dendrobium aurifex is one of 19 new tree-dwelling orchids found in 2020 from New Guinea.

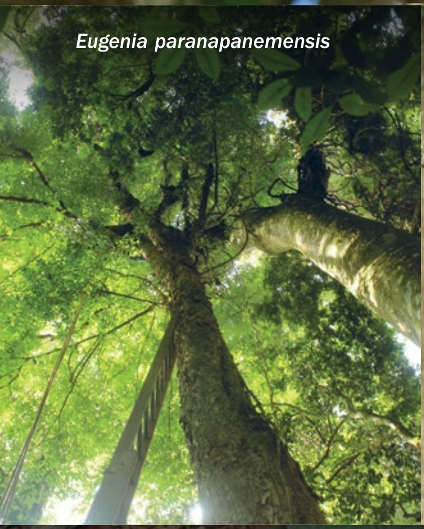
Saxicolella deniseae is one of several species of 'orchids of the falls' that have gone extinct due to dam construction.

Ipomoea aequatoriensis, a new species of morning glory, is a potential wild ancestor of the sweet potato.

Gomphostemma phetchaburiense is only known from a single cave site that is threatened by droppings from a nearby colony of rock pigeons.

Eugenia paranapanemensis inhabits one of the last surviving fragments of Brazil's Mata Atlântica rainforest, which is under threat from farming.

Tiganophyton karasense is not only a new species, but also hails from a new genus and family in the Brassicales order (which includes the cabbage and caper families). The species grows in extremely hot salt pans, hence its genus name *Tiganophyton* – 'frying pan plant'.



Eugenia paranapanemensis

Tiganophyton karasense

Carpotroche caceresiae

Gomphostemma phetchaburiense

Ipomoea aequatoriensis

Saxicolella deniseae

Dendrobium aurifex

Aloe rakotonasoloi

YOU MIGHT THINK A GLOBAL PANDEMIC WITH TRAVEL-RESTRICTING LOCKDOWNS MIGHT HAVE SLOWED THE RATE AT WHICH SCIENTISTS DESCRIBED AND NAMED NEW SPECIES OF PLANTS AND FUNGI. BUT THAT IS NOT THE CASE.

A PLETHORA OF PLANT SPECIES

Since the start of 2020, more than 8,600 plants have been named as new to science. While remote habitats are often the source of new plant species, novel additions also frequently arise from eureka moments in herbaria or even on social media, when taxonomists realise a specimen collected years ago has been wrongly placed on the tree of life, or that someone has posted a photo of a species they have never seen before. Having to stay at home during the pandemic gave time to work through backlogs of specimens and unfinished manuscripts, and kept the tally of global plant diversity rising.

The story of how *Victoria boliviana* came to be named in 2022 exemplifies how new species – even rather large ones – can sometimes hide in plain sight. A specimen of this giant Bolivian waterlily, which has leaves exceeding three metres across, had been stored in the Herbarium of the Royal Botanic Gardens, Kew (RBG Kew) for 177 years under the misnomer *Victoria amazonica*. The latter is one of two species that had been considered to be the only living representatives of the genus *Victoria*, the other being *V. cruziana*. It was only after RBG Kew waterlily expert Carlos Magdalena followed up a hunch that there might be a third species, that *V. boliviana* was found to exist. Magdalena grew the Bolivian waterlily from seed and noticed that prickles on the new plants were distributed differently to those on the other *Victoria* species growing at Kew Gardens. To complement Magdalena's horticultural work, his RBG Kew colleagues, Bolivian collaborators and a botanical illustrator then compiled and compared historical records, specimens from different herbaria and social media posts; made detailed botanical drawings; and conducted DNA sequencing to fill in more pieces of the puzzle. Through a multi-stranded piece of investigative work, they demonstrated that *V. boliviana* was new to science.

Identifying new species often involves elements of detective work. The species *Hibiscus hareyae*, which was named in 2020, was first encountered in the 19th century by British surgeon Dr John Kirk in Tanzania. He sent two similar herbarium specimens to Kew in 1874, one from Tanzania and one from Kenya, saying that he considered the plants to be variants of the same species. Joseph Hooker at Kew named both specimens as *H. schizopetalus* in 1880, filing the material in the Kew Herbarium. Dr Kirk collected additional specimens from Tanzania in subsequent years. After seeds of the Kenyan plant were grown in London in 1874, *H. schizopetalus* became widely cultivated. But when Australian hibiscus expert Dr Lex Thomson was perusing digital images of historic herbarium specimens, some 145 years later, he noticed that the Tanzanian plants had several major features not seen in the cultivated ones, and realised he had encountered a new species. With spectacular jagged crimson petals, and the ability to tolerate dry conditions, *H. hareyae* could soon join its cultivated cousin on garden-centre shelves.

'Taxonomy totally is detective work,' confirms Dr Martin Cheek, Senior Research Leader in Accelerated Taxonomy at RBG Kew. 'You might think you have a new species but you have to make sure that no one has described and named it before. You use all sorts of methods to try and track down specimens that might be the same plant and find out where those specimens were collected from – because often place names have changed. Sometimes it can take years to work out a plant's provenance because the names on herbarium specimens aren't on current maps, and you might have to go back into old journals that are no longer published or can be in different languages.' (See Box 1, overleaf.)

DISTINGUISHING FEATURES

Each group of plants has a set of features that vary and that taxonomists can use to differentiate one species from another. To be considered a new species, a plant's physical characteristics must set it apart from its closest relatives, or it must have significant differences in its DNA sequence (for cryptic species that look identical, this is often the only piece of evidence). In contrast to fungi, for which it has become standard to use DNA for describing new species, morphological characteristics, such as the shapes, sizes and colours of flowers, are still the mainstay of the scientific description of plant species. However, botanists often employ DNA techniques to resolve complex challenges around how species evolved, or to investigate 'polyploidy' – a mechanism in which whole plant genomes are duplicated and through which new species sometimes arise – or when unravelling the evolutionary relationships among organisms to find their positions on the tree of life (see Chapter 5).

Often a mixture of the two approaches is most informative. When researchers were using DNA techniques to study polyploidy in birch trees in 2021, they noticed that the specimens gathered from trees in one particular geographical area exhibited different genomic characteristics to those seen in material from other locations. Although the number of sets of chromosomes (thread-like structures of DNA and protein) within cells differed between the two sets of samples,

WHILE REMOTE HABITATS ARE OFTEN THE SOURCE OF NEW PLANT SPECIES, NOVEL ADDITIONS ALSO ARISE FROM EUREKA MOMENTS IN HERBARIA OR EVEN ON SOCIAL MEDIA.

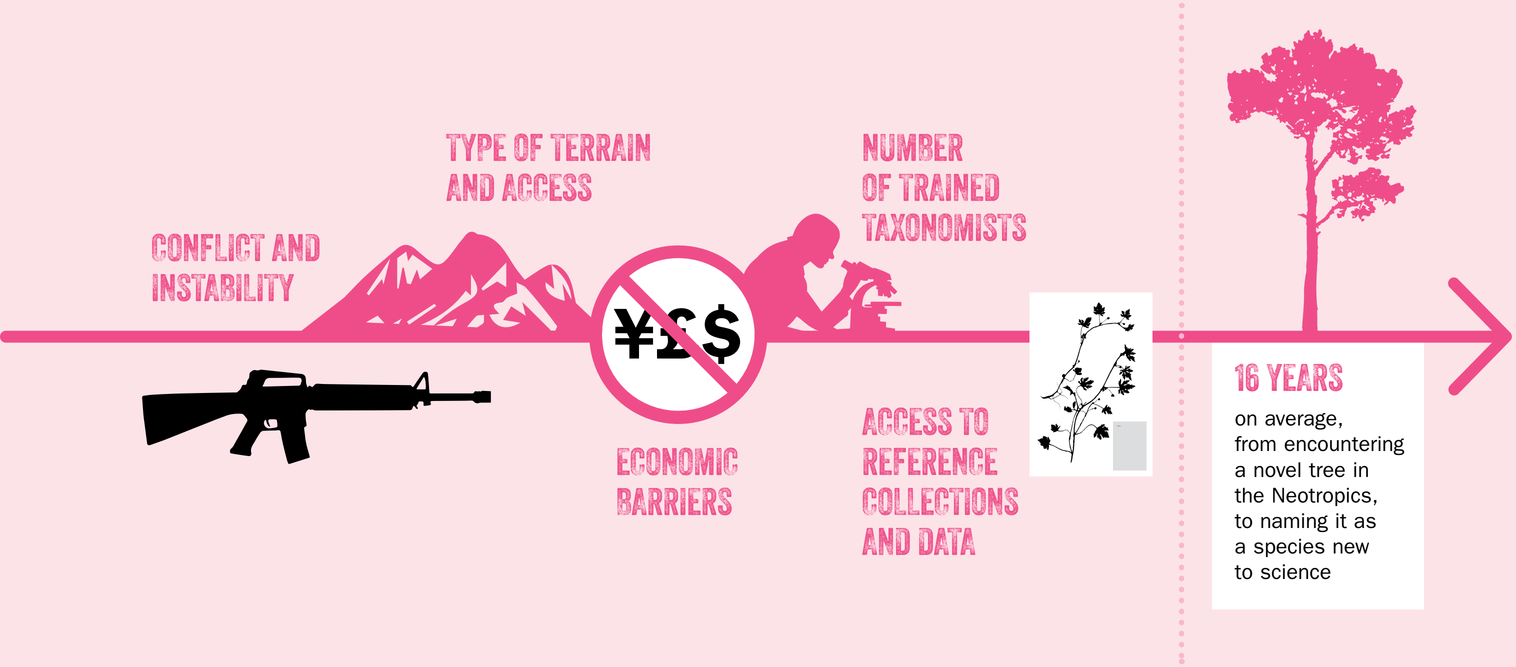
Between 1941 and 1960, Colombia yielded the largest number of tree species described as new to science in the Neotropics. However, from 1964 to 1965 no new species were described, as conflict hindered field research.

it was not clear from this alone whether the scientists had encountered a new species. RBG Kew's taxonomists were able to show there was sufficient morphological separation because the bark, trunk and catkins from one sample were different to those in the other. Dr Nian Wang, the lead biologist on the project named the new species *Betula buggsii*, after his supervisor Richard Buggs, Professor of Evolutionary Genomics at Queen Mary University of London and RBG Kew.

The person who describes a species as new to science also gives it a name. However, as it is frowned upon to name an organism after oneself, new plant species often immortalise the collector of the herbarium specimen, or the taxonomist's heroes, colleagues or loved ones. Alternatively, the name might reflect the plant's appearance, its habitat, how local communities refer to it, or where it grows. The names of new species reported from Ebo Forest in Cameroon in recent years help to record the struggle to conserve this highly biodiverse habitat. The forest, which makes up the Ebo Important Plant Area, and is inhabited by rare chimpanzees and gorillas, has already yielded more than 14 species new to science in recent years.

After the Cameroonian government announced plans to allow logging across a vast stretch of the forest in 2020, conservationists – including botanists from RBG Kew – voiced their concerns, and highlighted the area's unique biodiversity. Meanwhile, the local Banen people, who consider the forest their ancestral home, protested the decision with support from actor Leonardo DiCaprio, who raised awareness of the campaign on social media. This combined effort probably contributed to the President of Cameroon's decision to cancel the logging concession later in the year, although, without legal protection, the forest's future remains highly uncertain. Recent novel species from

BOX 1: Factors that affect the rate of species description



16 YEARS

on average, from encountering a novel tree in the Neotropics, to naming it as a species new to science

It takes 16 years, on average, from encountering a novel tree in the Neotropics – the tropical belt that stretches from Argentina to Mexico, including the Caribbean – to naming it as a species new to science. This is the main finding of a study that looked at how quickly new species were published within a group of just over 2,000 Neotropical trees. The region with the longest time lags was the central Andes (encompassing southern Ecuador, Peru, western Bolivia, and northern and central Argentina and Chile), while Chocó (western Colombia) had the shortest. By country, Peru had the longest time lags, and Haiti the shortest.

The Neotropics are particularly diverse, with around 23,000 known tree species alone. This means that there are many close relatives a potentially novel tree must be compared to, and contrasted with, to confirm its status as new to science. The authors of the study found that the time lag between collection and naming was lower when the same person had collected and named a species, or when field botanists had sent material to herbarium-based researchers as part of a specific collaborative research project. Conditions that extended the time lag included political instability and conflict, which can deter researchers from undertaking fieldwork in some areas due to safety concerns.

While 16 years sounds like a long time, the lag for some other plant groups can be as long as 40 to 50 years. With plant species going extinct at least 500 times faster than natural background rates, and predictions that this figure could rise to 10,000, there is an urgent need to speed up how new species are described and named. The study authors concluded that enhancing collaboration and training opportunities in Latin American countries, continuing and expanding field visits to collect material, and exploiting opportunities to use artificial intelligence and genomics in taxonomy would be critical to completing the inventory of the Neotropical flora.


Staurogyne yamokmehong


Streptocarpus malachiticola


Pseudohydrosme ebo


Acanthostachys calcicola


Hydnellum nemorosum

The new species named since 2020 come from all over the world, including the UK (clockwise from top left):

Staurogyne yamokmehong, is used by the Shan Ni people of Myanmar as a hormone regulator.

Streptocarpus malachiticola is a Cape primrose from the Democratic Republic of the Congo. Its name means 'growing on malachite' – malachite being a copper ore extracted from mines in the area.

Pseudohydrosme ebo, from Cameroon's Ebo Forest, flowers from an underground tuber when its leaves have died back.

Acanthostachys calcicola, a Brazilian bromeliad from the same family as the pineapple, is pollinated by hummingbirds.

Cortinarius heatherae, was spotted along a river beside Heathrow Airport, in the UK.

Chassalia northiana, one of 14 species of *Chassalia* named in 2021, honours the artist Marianne North, who painted the species in 1876 in Borneo.

Uvariopsis dicaprio, another newly named species from Cameroon's Ebo Forest, was named after actor Leonardo Dicaprio, after he supported a campaign to protect the forest from logging.

Cyanoboletus mediterraneensis is a small- to medium-sized bolete fungus. Parts of the mushroom turn intense dark blue when handled or damaged, a characteristic that unites species of the genus *Cyanoboletus* and gives it its name.

Philibertia woodii, a periwinkle from the Andean valleys in Bolivia, which may be of medicinal value, has egg-shaped, kiwi-like fruits that are edible when roasted.

Hydnellum nemorosum is one of a group of rare fungi that form mushrooms with teeth under their caps, in place of gills.


Philibertia woodii


Cortinarius heatherae


Cyanoboletus mediterraneensis


Uvariopsis dicaprio


Chassalia northiana

the area include the pink voodoo lily (*Pseudohydrosme ebo*), highlighting the forest itself; the magenta-and-white-flowered busy lizzie (*Impatiens banen*), honouring the Banen people; and *Uvariopsis dicaprio,* a four-metre tree of the ylang ylang family, which was named after DiCaprio.

LATE TO THE RESCUE

Sadly, many species – including *Uvariopsis dicaprio* – are already threatened with extinction by the time they are named as new to science (see also Chapter 9). The stunning, colourful bromeliad *Acanthostachys calcicola*, encountered on a forest-shaded limestone cliff in central Brazil in 2019, is likely threatened with extinction because only 25 plants were found, despite searches of the same habitat close by. Naturally exposed limestone areas often have unique flora but are at risk around the world from quarrying for construction materials.

The clearance of habitats for plantation agriculture is similarly a major threat to plants. The exploding firework flower (*Ardisia pyrotechnica*), a member of the primrose family from Borneo that was named in 2021, has already been assessed as Critically Endangered under International Union for Conservation of Nature (IUCN) criteria. Some species are even extinct by the time they become known to science, among them Denise's orchid of the falls (*Saxicolella deniseae*). Collected in 2018 by Guinean botanist Denise Molmou from a set of waterfalls on the Konkouré River of Guinea in West Africa, it is presumed extinct after a dam was constructed 30 kilometres downstream, flooding the area.

'My own personal observation is that the number of threatened plants has gone up shockingly in recent years,' rues Dr Cheek. 'When I started out as a taxonomist 30 years ago, you wouldn't really even consider that a species you were publishing might go extinct; you just assumed it was going to still be around in the wild. Now, you might work out that you have new species and go and look for its natural habitat only to not find any at all. Then you use a time slider on Google Earth, and you can sometimes actually see images showing the habitat disappearing, and the dates, and that is very depressing. It is really important that we keep up with our work, as once we do put a name on a new species and carry out a conservation assessment of it, then resources can be allocated to protecting it.'

THE NEED TO FIND FUNGI

Like plants, fungi also face the risk of being lost before they have been found to exist. And with more than 90% of species yet to be described and named (see also Chapter 2), the search to find the species currently unknown to science is extremely urgent. Since the beginning of 2020, more than 10,200 fungal species have been described as new to science. While this is not an insignificant number, the speed at which new species are being added to known fungal diversity may be insufficient to keep up with the rate at which novel species are being lost. And sometimes, as is also true for plants (see Box 1), a long time can pass between a novel fungal species being encountered and receiving a name. For example, a rare tooth fungus spotted growing in moss under a sweet chestnut tree in Windsor Great Park, UK, in 2008, was only named as new to science – as *Hydnellum nemorosum* – in 2021. A DNA-based analysis revealed Windsor to be the only known site of the fungus in Britain, so it has already been proposed for inclusion on the IUCN Red List of Threatened Species.

EUROPEAN NEWCOMERS

The UK is proving to be a rich hunting ground for species of fungi that are new to science. In 2020, six new species of webcap toadstool mushrooms from the genus *Cortinarius* were uncovered, three in Scotland and three in England – including one on the boundary of Heathrow Airport. These kinds of fungi are ecologically important for supporting the growth of plants such as oak, beech, birch and pine, as well as for cycling carbon in woodlands and providing beneficial nitrogen to trees. Meanwhile, a species of white 'hedgehog' mushroom growing in the ancient beech forest of White Down, Surrey, UK, was named *Hydnum reginae* in 2022 to honour the late Queen Elizabeth II. It had been previously considered to be *Hydnum albidum*, a name originating from North America, but recent DNA analysis revealed US and European specimens to be different species. DNA technology also revealed a new species of Mediterranean bolete, *Cyanoboletus mediterraneensis,* in 2022. Encountered in northern Israel and Sardinia, Italy, it had previously been identified as the ink stain bolete *Cyanoboletus pulverulentus*, which is common in temperate Europe.

'Mycologists estimate that more than two million fungal species, or more than 90% of all fungi, remain to be described,' says Dr Tuula Niskanen, former Research Leader at RBG Kew and now Senior Curator at the Finnish Museum of Natural History, Helsinki, who described and named one of the new species of webcap toadstool mushrooms (*Cortinarius aurae*). 'Surprisingly, this figure does not only represent rare species but also many common ones, including those occurring in the UK. Fungi have remained such a mystery to us, compared to plants and many animals, because their cryptic lives mainly unfold hidden from our eyes and have been challenging to study with traditional techniques. Only in the last few decades, thanks to the widespread use of DNA-based techniques, have we started to understand the true diversity of this kingdom.'

For more information on species names, see ipni.org and indexfungorum.org

Box 1 was based on the following preprint:

Lujan, M., et al. (2023). Trials and tribulations of Neotropical plant taxonomy: Pace of tree species description. *bioRxiv.* DOI: https://doi.org/10.1101/2023.09.05.556231

THE UK IS PROVING TO BE A RICH HUNTING GROUND FOR NEW SPECIES OF FUNGI.

MAKING SENSE OF PATTERNS OF DIVERSITY

In this chapter, we learn: that trees dominate in the tropics, while herbs are more prevalent at higher latitudes; how temperature and rainfall have been important in the evolution of annual versus perennial plants; why large animals may be the reason larger fruits are found in Africa; and that pockets of fungal richness exist at both tropical and temperate latitudes.

Technology, including Light Detection and Ranging (LiDAR) that was used to create this image, is helping scientists gain ever more insights into plant diversity.

TREES ACCOUNT FOR

80%

OF BIOMASS IN NORTHERN EUROPE BUT ONLY 3% OF THE DIVERSITY

IT'S A CONUNDRUM THAT HAS VEXED SCIENTISTS FOR CENTURIES: HOW TO EXPLAIN WHAT DRIVES GLOBAL AND LOCAL PATTERNS OF BIODIVERSITY.

Simply defining diversity is the first challenge, as it can refer to the richness of species, the number of different evolutionary lineages present (see also Chapter 6), the genetic variation within species, the array of plant forms and functions, and so on. However, combining newly available datasets on species characteristics and distributions is helping to resolve some long-standing enigmas about the drivers of many kinds of diversity. Recent studies that examined influences behind patterns of plant form, life-cycle strategies, and the richness of plant and fungal species are particularly revelatory. Their findings suggest that multiple factors – from evolutionary history, to past and present climates, geology and even the presence or absence of animals – are implicated in shaping the plant and fungal diversity patterns we see across the Earth today.

MAPPING TREES AND HERBS

Plant species exhibiting similar combinations of characteristics in the way that they grow or reproduce are considered to have the same form. The term 'growth form' refers to their overall appearance or habit (such as tree, shrub or herb), while the term 'life form' references their perennating buds (the vegetative means by which plants survive unfavourable seasons or conditions – for example as aboveground buds or belowground bulbs) (see Figure 1). Such forms result from adaptations that species have made in response to the environmental conditions around them, so plants with the same life or growth form are not necessarily related. For example, South America's cacti and South Africa's succulent euphorbs belong to entirely separate plant families but some look very similar at first glance. This is due to similar adaptations to arid environments, such as thick swollen stems, and spines to deter animals. Although species with matching plant forms have long been grouped in ecological studies, and the concept underpins how biomes (for example, tropical rainforest) are sometimes defined, the question of how they contribute to global patterns of biodiversity has remained unanswered.

Scientists at the University of Göttingen, Germany, set out to quantify the contribution made by different plant forms to global plant diversity, and to explore the extent to which present and past climatic conditions, environmental diversity and evolutionary history underpin those patterns. They began by combining data from the World Checklist of Vascular Plants (WCVP), the Global Inventory of Flowers and Traits (GIFT) and a recently published plant epiphyte list to obtain a near-complete global checklist of life and growth form classifications, spanning 295,755 species. They then examined the proportions of different life and growth forms and mapped their distribution across botanical countries (see Chapter 1, Box 1). This confirmed, for example, that the dominance of woody perennials in tropical latitudes gives way to predominantly herbaceous floras in temperate and boreal regions. This trend follows the sharp decline in plant diversity observed from the tropics to the poles.

'In a lot of cases we already knew the patterns but they hadn't been quantified,' explains Dr Amanda Taylor, an ecologist at the University of Göttingen. 'But what was quite surprising, once we added numbers and percentages, was that while trees accounted for 80% of biomass in northern Europe, they only represented 3% of the diversity. What was also interesting was that in the tropics, where we have the highest diversity of trees, their regional contribution was comparable to that of other types of plant forms, such as herbs, shrubs, epiphytes and climbers. Often trees are used as a surrogate of biodiversity, but we found there are very few regions of the tropics where 'tree' is the dominant growth form. So, we need to see beyond the trees and consider other forms that contribute to biodiversity in these analyses, rather than just focusing all the time on trees.'

Next, the scientists examined factors that might be driving the spatial distribution of plant forms. This revealed that although evolutionary history has some influence, the observed patterns were primarily explained by the contemporary climate – principally temperature and precipitation. Evolutionary history appeared to be more influential in regions where certain plant forms were distributed among a few species-rich genera. For example, species in the genus *Aeonium*, most of which are succulent chamaephytes endemic to the Canary Islands, have diversified to thrive in arid steep and rocky habitats that are inaccessible to most other plant lineages, making them the most successful plant genus across the archipelago. The finding that terrestrial herbs constitute up to 90% of the plant diversity in temperate and boreal regions likely reflects the many mechanisms that herbs have evolved to withstand climate variations. These include using belowground organs, such as bulbs, to store energy and water during hard times, and staying dormant in the soil as seeds when conditions are inclement.

ANNUALS LIKE IT HOT

Another study that used the WCVP to investigate the evolution of life-cycle strategies found that temperature and precipitation were key in determining whether a flowering plant species reproduces annually or perennially. Analysis of 32 groups of flowering plants across eight climatic variables found temperature – particularly the highest temperature of the warmest month – to be the most consistent climatic factor in prompting flowering plants to evolve to be annuals. The authors proposed that the annual strategy is consistently favoured in areas prone to extreme heat, due to the ability of annuals to escape heat stress as seeds. In regions where extreme heat is uncommon or does not occur, annuals tend to be outcompeted by perennials.

'In this study, we were interested in testing whether there are consistent and general climatic drivers of life-history evolution,' explains Dr James Boyko, a postdoctoral researcher at the University of Michigan, USA, who led the study. 'We know that there are many patterns specific to particular clades [groups of organisms that stem from a common ancestor] in which an association between various

FIGURE 1: The diversity of plant growth and life forms

From the tropics to the Arctic, plant species have adapted to enable them to thrive in the environmental conditions around them. The result is the array of growth and life forms we see around the world today. Percentages represent the relative contribution each makes to global biodiversity patterns of growth or life forms.

Growth forms

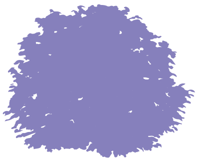
TREE

A perennial woody plant larger than a shrub (>10 m) and typically with a single, self-supporting trunk

16%

SHRUB

A perennial woody plant larger than a subshrub (0.50–10 m), smaller than a tree



28%

SUBSHRUB

A small shrub (<0.50 m) that is mostly, but not always, woody at the base

12%

HERB

A small herbaceous plant that never develops a woody stem

32%

EPIPHYTE

Grows non-parasitically on other plants, produces aerial roots

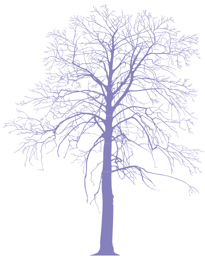
7%

CLIMBER

Woody or herbaceous plant that roots in the ground but is structurally supported by other plants

5%

Life forms



PHANEROPHYTE

Perennial plant that bears its perennating buds well above the surface of the ground

21%

NANOPHANEROPHYTE

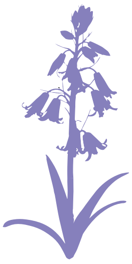
Any phanerophyte between 25 cm and 2 m in height; buds above soil level

20%

CHAMAEPHYTE

Subshrub and dwarf-shrub with buds on persistent shoots near the soil surface, max 25 cm above ground

15%



GEOPHYTE

Plant that survives unfavourable seasons in the form of underground storage organs

11%

HEMICRYPTOPHYTE

Plant having its overwintering buds located at or just below the soil

24%

THEROPHYTE

Annual plant that rapidly completes its life cycle in favourable conditions and survives unfavourable seasons in the form of seeds

9%

Adapted from Taylor et al. (2023)

measurements of temperature, precipitation, or seasonality are found, but how consistent are these drivers across all flowering plants? Unsurprisingly, most of the climatic variables we tested were not consistently associated with life-history evolution. However, for 31 of the 32 clades we examined, annual species preferred a higher maximum temperature of the warmest month. This was by far our most consistent finding, suggesting a general pattern that drives life-history evolution across the world's flowering plants.'

WHY AFRICA HAS BIG FRUITS

Current climate is not always the key driver of plant form, however. Scientists who wanted to understand why Africa hosts palms with larger fruits than elsewhere, such as those of the lala palm *(Hyphaene coriacea*), found that past climate change on the continent and the presence of large animals – megafauna – were likely to have been the key drivers behind this pattern. They proposed that a period of climatic cooling and drying that took place during the Miocene geological epoch from around 12 million years ago (Ma) prompted the expansion of savanna, a mixed woodland and grassland ecosystem in which trees are widely spaced forming an open canopy. This, coupled with the persistence of megafauna (which suffered extinctions elsewhere in the world from around 500,000 years ago), created a unique ecological opportunity for species with large fruits to evolve and spread. The cooling and drying was more pronounced in Africa than elsewhere, and the expansion of savanna at the expense of forest may have led to the co-evolution of large-fruited palms and large fruit-eating animals capable of dispersing the seeds, such as modern-day elephants and their ancestors.

'We looked for the botanical countries with the largest palm fruits we could find, and then we assessed whether the fruit sizes could be explained by coexistence with large mammals,' explains Dr Renske Onstein, Senior Researcher at Naturalis Biodiversity Center and Head of the Evolution and Adaptations group at the German Centre for Integrative Biodiversity Research. 'We did find a relationship between the two, and we also found that these large fruits occur in Africa in locations with open habitats and low canopy heights. You also find open systems in other places, but elsewhere there wasn't the relationship with the large fruits – it was really only in Africa where it seemed to be important. We think that is because of the interaction with megafauna that also occur in those open systems. So, it is a combination of things that led to Africa being quite special – and providing this unique evolutionary arena.'

PEAK DIVERSITY

Mountain chains also appear to create a unique signature when it comes to biodiversity – in this case species richness. Upland areas typically harbour greater biodiversity than lowlands, which is considered to reflect the wide diversity of habitats that exist in mountainous locations. For example, rock faces and scree at differing angles and orientations can receive vastly different levels of sunlight and protection from frost and other weather, increasing the number of microhabitats that different species can thrive in. However, it turns out that the wide array of habitats in mountains cannot, alone, explain the exceptional richness of plant species encountered in some upland areas.

One study investigated the relationship between habitat diversity and uplands both across the whole of Eurasia and within the Hengduan Mountains of southwestern China. It found that although habitat heterogeneity was able to account for much of the variation in plant diversity, the exceptionally high richness of seed-plant species in the Hengduan Mountains, which host more than 12,800 species compared with 4,000 in the European Alps, could be better explained when habitat diversity was considered in combination with climatic factors and rock type.

'The species richness of 41 out of 97 seed-plant families in the Hengduan Mountains exceeds that predicted by the Eurasian heterogeneity-to-richness relationship,' explains Yaquan Chang, an ecologist at ETH Zürich, who led the study. 'These "outlier" families are very interesting; when we zoomed in on them, we found that habitat diversity can explain around 50% of the variation of these families' richness. So, we can conclude that the habitat heterogeneity is the first-order process for determining species richness but that there are some other factors, such as mountain-building processes or the orientation of the mountain range and its location, that are needed to help determine the remaining biodiversity patterns.'

The shifting climate and geology of the Hengduan Mountains have created multiple plant habitats, barriers and thoroughfares within a relatively small area. Current climates range from cold and partly humid in alpine elevations, to dry and hot in deep valleys, while, on geological timescales, there has been much deformation, with movement along large faults fragmenting habitats and exposing different types of bedrock. It is possible that the complex forces of climate and geology acting on the mountains and their deeply incised, isolated river valleys may have contributed to the uplands becoming a biodiversity hotspot. In addition, the frequently disturbed, transient landscape, with opportunities for habitat creation and fragmentation (through, for example, soil erosion), would have created novel ecological niches that favoured the on-the-spot evolution of new species and their colonisation of nearby areas.

DIGGING FOR DATA IN THE SOIL

While knowledge of how plant diversity is distributed around the world has accumulated as botanists have worked down the centuries, understanding of the geography and drivers of fungal species richness has lagged behind. Until as recently as the last decade, data were mostly only available for readily collectable species, such as mushrooms, truffles, lichens and rusts, which meant that a large proportion of hidden fungal diversity, including species that lack or have inconspicuous fruiting bodies or produce them only rarely, was overlooked. However, the adoption of sophisticated DNA techniques is now enabling a more complete picture of fungi to be pieced together, transforming understanding of where these species are concentrated and what might be driving the observed patterns.

A newly published map, drawing on the latest research on soil fungi, shows that while some of the most species-rich areas are found in tropical forests and woodlands,

MULTIPLE FACTORS, FROM CLIMATE TO GEOLOGY TO INTERACTIONS BETWEEN ORGANISMS, HAVE SHAPED THE DIVERSITY WE SEE ON EARTH TODAY.

Scientists are exploring why China's Hengduan Mountains have such a rich flora.

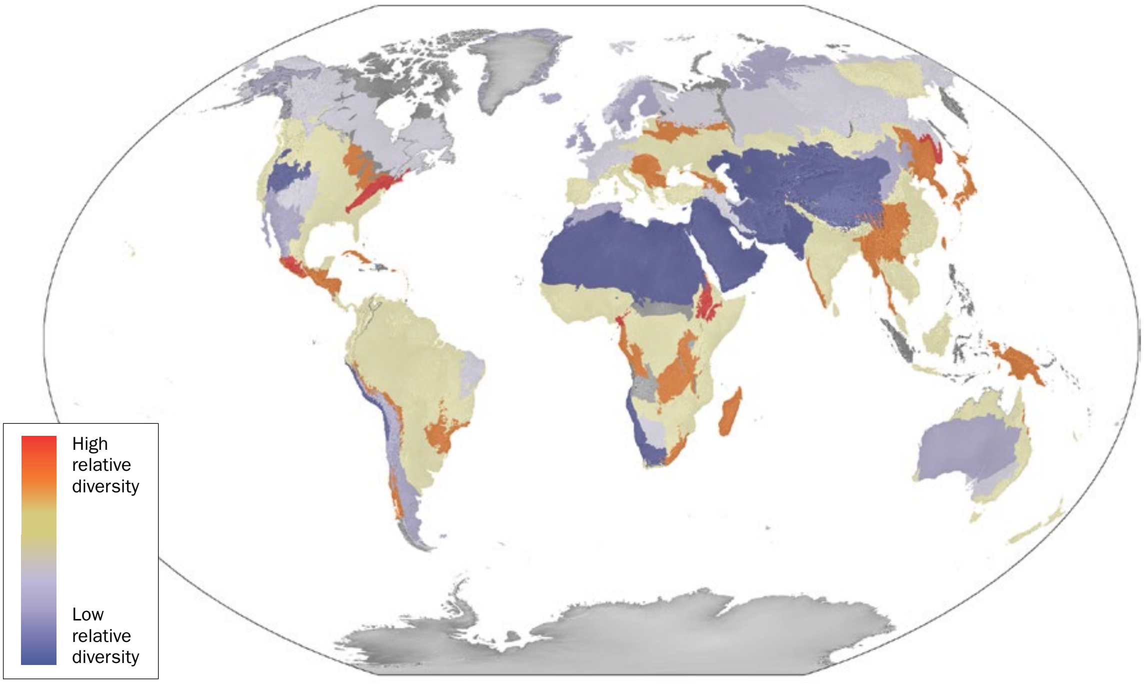
Plants have adopted a variety of life and growth forms to help them thrive on Earth.

Unravelling the science of climbing plants

An analysis of the WCVP dataset by researchers in Brazil and the USA found that there are at least 9,071 species of climbing plants in the Neotropics. Twining was the mechanism found in the largest number of species, whereas simple scrambling (simplest from an evolutionary point of view) was present in the largest number of families. The type of climbing mechanism was not found to have significantly affected the rate at which different climbing lineages diversified. Climbers appear to form a higher proportion of the flora in hot and wet biomes in Amazonia and Mesoamerica, occurring mainly in highly humid habitats such as tropical rainforests. This distribution is likely related to the anatomy of climbers, which invest a lot of resources in large crowns but not so much in supporting structures, and are more susceptible to drought and freezing. There are indications that the diversity of climbers in tropical areas may be underestimated, and this highlights the importance of collecting additional specimens from these areas.

FIGURE 2: Average global diversity of soil fungi

The map shows the average global species diversity of soil fungi based on predictions derived from DNA sequence data from soil samples. The scale runs from blue (low relative species richness) to red (high relative species richness). Some of the most species-rich areas in the world are in tropical forests and woodlands, but there are also pockets of high diversity in some temperate areas, such as North America and East Asia.



Adapted from Niskanen et al. (2023)

there are also pockets of high diversity at temperate latitudes (Figure 2). Among the main biomes of the world, forests such as in Cameroon and the Atlantic Forest in South America host the greatest diversity of soil fungi, but grasslands and tundra are also home to a significant number of species. Far fewer fungi grow in dry and cold areas, such as deserts and the polar regions. The drivers of fungal species richness vary from local to global scale and differ between the three main functional groups – saprotrophs that live on dead organic matter, pathotrophs that dwell in, and cause harm to, other organisms, and symbiotrophs that form mutualistic associations with other organisms. The environmental drivers include soil pH, climate (which also alters soil characteristics), the deposition of nitrogen from the atmosphere and habitat type. Saprotrophs and pathotrophs have the broadest distributional range, the latter aided by anthropogenic spread. Mycorrhizal fungi, which are symbiotrophs associating with plant roots, appear to have the narrowest climatic niche.

The naturalist Charles Darwin was among early scientists to wonder what influenced patterns of species diversity, having noted after his voyage on HMS *Beagle* in the early 19th century that species varied globally, locally and over time. Today, thanks to large global datasets and number-crunching technology, botanists are finally finding answers for plant species. Solving the conundrum of where fungal species are concentrated, however, and what drives those patterns is still its early stages. The hope is that rapid advances in fungal knowledge will soon illuminate similarities and differences across patterns of plant and fungal diversity. This will enable botanists and mycologists to work together to understand how these patterns are interrelated, and to unravel the implications of climate change and other threats on both to inform ongoing efforts to halt biodiversity loss.

This chapter is based on the following peer-reviewed publications:

Boyko, J.D., et al. (2023). The evolutionary responses of life-history strategies to climatic variability in flowering plants. *New Phytologist*. DOI: https://doi.org/10.1111/nph.18971

Chang, Y., et al. (2023). Phytodiversity is associated with habitat heterogeneity from Eurasia to the Hengduan Mountains. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19206

Niskanen, T. et al. (2023). Pushing the frontiers of biodiversity research: Unveiling the global diversity, distribution and conservation of fungi. *Annual Review of Environment and Resources.* DOI: https://doi.org//10.1146/annurev-environ-112621-090937

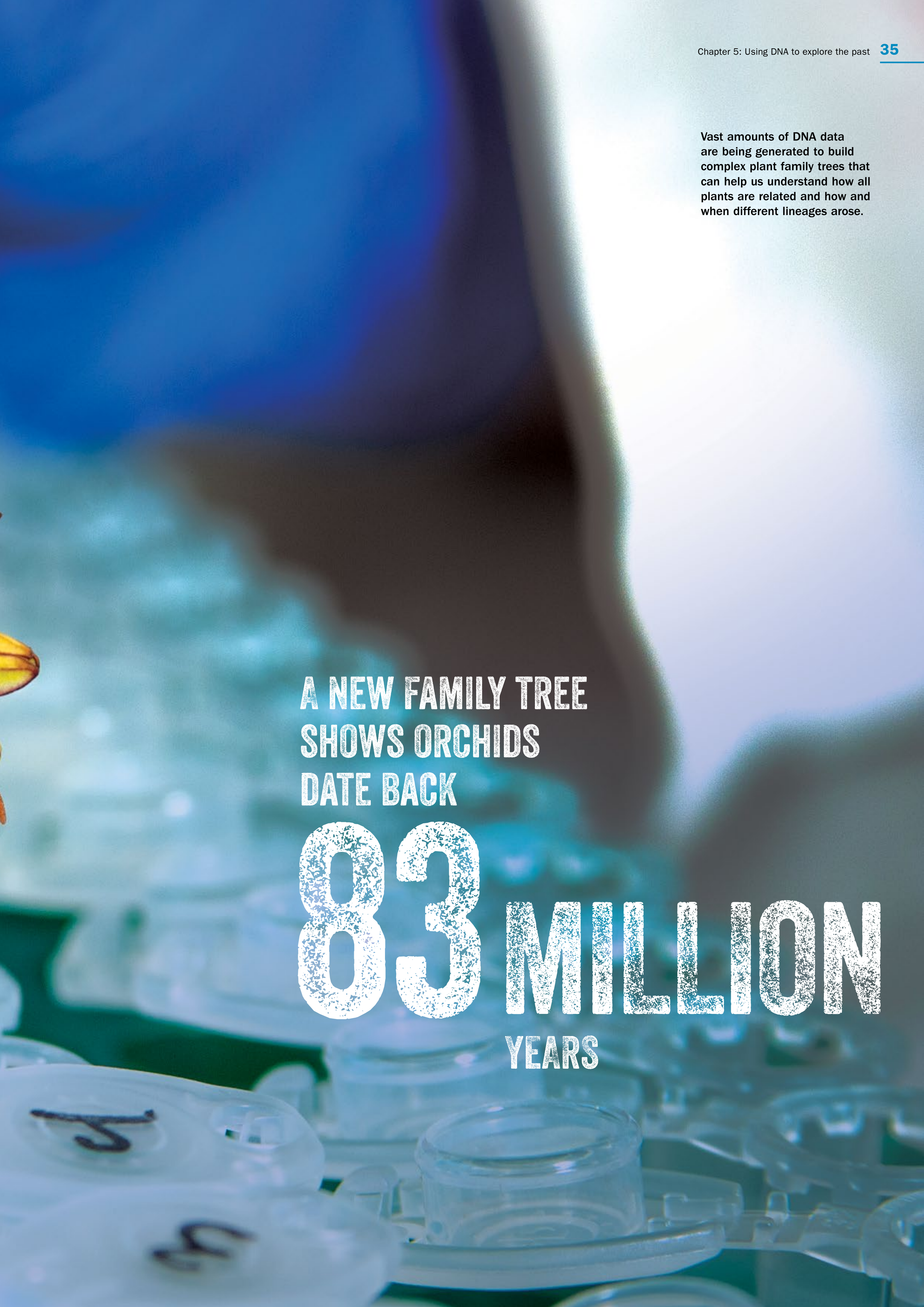
Sperotto, P., et al. (2023). Climbing mechanisms and the diversification of neotropical climbing plants across time and space. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19093

Taylor, A., et al. (2023). The contribution of plant life and growth forms to global gradients of vascular plant diversity. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19011

Wölke, F.J.R., et al. (2023). Africa as an evolutionary arena for large fruits. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19061

USING DNA TO EXPLORE THE PAST

In this chapter, we learn: that the first orchids originated when dinosaurs walked the Earth; how figworts evolved on lands that are now in southern Africa; why cycads are not as widespread as they once were; and that rice and pineapples share ancient roots.



Vast amounts of DNA data are being generated to build complex plant family trees that can help us understand how all plants are related and how and when different lineages arose.

A NEW FAMILY TREE SHOWS ORCHIDS DATE BACK 83 MILLION YEARS

PLANT DIVERSITY CAN BE LIKENED TO A KALEIDOSCOPE. THE PATTERN OF SPECIES WE SEE ON EARTH TODAY IS JUST A FLEETING MOMENT WITHIN A CONSTANTLY CHANGING SEQUENCE OF EVENTS.

Scientists wanting to know what led to current patterns of plant distribution are using genomic and geographical data to help them peer back into the past. By sequencing the DNA of plants, and mapping where wild species grow today, they are slowly building more and more detailed evolutionary trees. Not only is this revealing which plants are most closely related to each other, it is also helping to explain where and when species originated and how they spread across the globe. Here we show how novel approaches are overturning thinking on orchids, resolving riddles around figworts and uncovering some long-lost secrets of cycads and sedges.

Before the development of DNA technology, botanists relied on the outward appearance of plants and internal features, such as their anatomy and chemistry, to try to determine how species were related based on shared or divergent characteristics. They often presented these data in the form of a branching tree. Founded on the idea that all living organisms share a common ancestor, the approach was useful but problems arose where similar features appeared in unrelated plants.

As genetic technology evolved, botanists started to reconstruct evolutionary history based on the DNA sequences of plant species, this time building trees that reflected their molecular make-up. Some used these two approaches together to compare patterns and help resolve ambiguities. Although improvements in sampling and in how relationships are inferred are still needed, sequencing data are today enabling more comprehensive evolutionary trees to be constructed, with the ultimate goal of constructing the ‘tree of life’, depicting how all living things are related.

PLOTTING A VAST FAMILY TREE

A study undertaken by scientists at the Royal Botanic Gardens, Kew (RBG Kew) and global collaborators sought to better understand the evolutionary history of orchids by developing an evolutionary tree for the family (Orchidaceae). This was no small undertaking, as orchids are an incredible evolutionary success story, today representing almost a tenth of all known flowering plant species on Earth. Some 30,000 species exist, within almost 750 genera, spread across every continent except Antarctica. They include the vanilla orchid (*Vanilla planifolia*), source of the iconic

Researchers investigated how orchids originated and spread around the world. This tiger orchid (*Grammatophyllum multiflorum* var. *tigrinum*) is only found in the wild in the Philippines.

ice-cream flavour, the bee orchid (*Ophrys apifera*), which has a flower resembling a female solitary bee that dupes male bees into pollinating the plant, and *Bulbophyllum nocturnum*, which blooms at night and closes its flowers during the day.

'I have always been puzzled by where orchids come from,' explains Dr Oscar Pérez-Escobar, Research Leader in Accelerated Taxonomy at RBG Kew. 'There is a fundamental tool that we can use to answer that question, which is a phylogenetic tree, or phylogeny, showing how organisms are related to each other. Once we understand the relationships, we can try to understand where orchids come from, and to infer, for example, whether the ancestor of orchids had blue or red or black flowers, or whether they lived on trees or on the ground. Through the years, as we've produced more phylogenies, some studies have come close to answering that question but many of those have been based on very, very limited sampling. Obviously, compiling a complete phylogeny of 30,000 species is a gargantuan task. So, I thought, why don't we gather all the robust data we have. So, we did – and we produced the largest-ever phylogeny for the orchid family.'

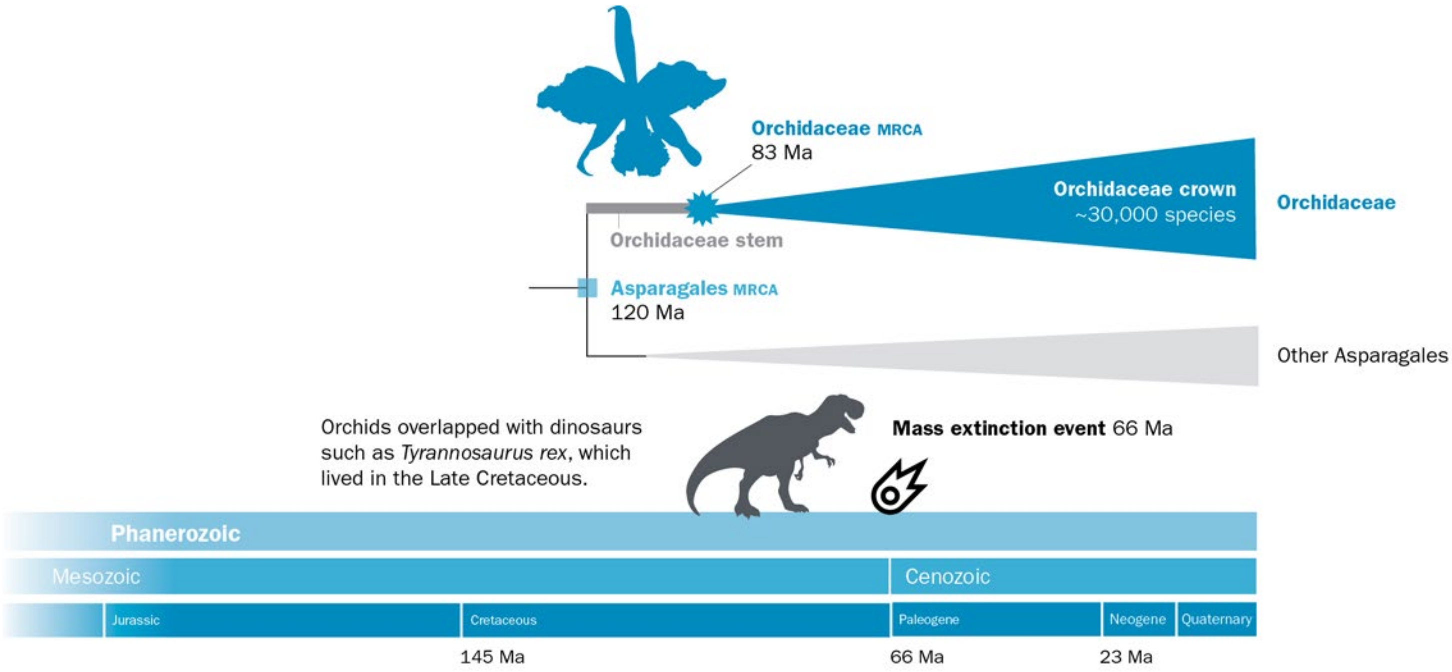
The orchid family is divided into five subfamilies: Apostasioideae, Cypripedioideae, Epidendroideae, Orchidoideae and Vanilloideae. Subfamilies are further divided into tribes, which in turn are divided into subtribes and then split further into genera and then species. Dr Pérez-Escobar and colleagues combined a variety of data to develop their evolutionary framework for the orchids, beginning with two datasets. The first, from the RBG Kew Plant and Fungal Trees of Life (PAFTOL) project and the Genomics for Australian Plants Consortium, was derived from high-throughput sequencing, which enables millions of DNA fragments to be sequenced at once. This provided detailed coverage of the genome (the full complement of DNA found in an organism) for all five orchid subfamilies, 17 of 22 tribes, 40 of 49 subtribes, 285 of 736 genera and 448 species. The second came from Sanger (traditional) sequencing data for only two genes but from 1,921 species, approximately 7% of all known orchid species.

The researchers used the first dataset to develop a backbone for the orchid family, which enabled them to understand how the subfamilies, tribes, subtribes and genera were related. The relationships among subfamilies and tribes generally agreed with those found in other recent studies. The Sanger data, with greater detail at the finer levels, yielded trees for the different genera, which were then grafted onto the PAFTOL backbone.

The team then used a method called 'molecular clock dating' to estimate the ages of the different clades (groups of species believed to comprise all the descendants of a common ancestor). Mutations in DNA sequences underpin the evolution of new species and accumulate over time. This enables scientists to estimate dates for the main branching events in a phylogenetic tree. Clades have two components, a crown and stem (see Figure 1). The crown group comprises the most recent common ancestor of all

FIGURE 1: A date with the dinosaurs

How long have the orchids been around? Probably longer than you think. This simplified phylogenetic tree shows the position of the family in relation to other members of the same plant order (Asparagales). The crown group contains all known orchids, which diverged from their most recent common ancestor (MRCA) 83 million years ago (Ma) (Orchidaceae MRCA denoted by ✸). The stem group contains the extinct ancestors of the orchids. Orchids diverged from all other families of the Asparagales 120 Ma (Asparagales MRCA denoted by ■). This places orchids at least as far back as the Late Cretaceous, before the age of the dinosaurs came to an end.



Adapted from Pérez-Escobar et al. (2023)

known species in the group and all of its descendants, while the stem encompasses the extinct taxa that are more closely related to the crown group in question than to any other living group. By calibrating their evolutionary tree with information from previous studies based on reliably dated fossils, the team were able to position the orchid clade in time. They estimated a 'crown age' for the orchid family of around 83 million years and a 'stem age' of around 120 million years.

This work showed that the most recent common ancestor of today's orchids lived during the Late Cretaceous, a geological epoch during which Earth was much warmer than today, and major continental landmasses that had once formed a supercontinent called Pangea were pulling away from each other. Using geographical data from the World Checklist of Vascular Plants (WCVP), the Global Biodiversity Information Facility (GBIF) and the RAINBIO mega-database, the scientists then investigated a suggestion from earlier research that orchids originated in lands that today form Australasia. Their findings indicated that, instead, the ancestor of all orchid species first originated in Laurasia. This was the more northerly of two landmasses that had previously formed Pangea (which broke away to eventually form modern-day North America, Greenland, Europe and northern Asia). Further results from the molecular clock dating indicated that most of the diversity in orchid species alive today originated during the last five million years.

The scientists next used the geographical data to explore patterns of species richness and to find out where new species were arising at the fastest rates. This revealed that the highest concentrations of orchid species were in the Neotropics (the tropical belt that stretches from Argentina to Mexico, including the Caribbean), although parts of Australia, New Guinea, Madagascar and South Africa also exhibited high species richness. Along with the Neotropics, these regions were once part of Gondwana – the landmass that had previously been connected to Laurasia to form Pangea. This would suggest that after originating in the northern hemisphere, orchids spread southwards and underwent bursts of speciation (the evolution of new species).

A surprising finding was that high rates of speciation did not always coincide with species-rich locations. For example, while southern Mesoamerica (comprising the Costa Rican and Panamanian moist and seasonal forests) exhibits outstandingly high levels of species richness and was found to have the highest speciation rates, Southern Australia exhibited low rates of speciation despite being rich in orchid species. It is possible that Australia's elevated species diversity may have accumulated at a slower pace and over longer timescales, possibly as a result of the region having a more stable landscape and climate than Mesoamerica.

'One reason for this finding may be that Australia has existed for a very long time, as have some of the biomes there,' says Dr Pérez-Escobar. 'That is in contrast to Central America and the northern Andes, which are known to have more dynamic and recent geological histories. For example, the northern Andes is one of the most diverse places and because of the way the Andes originated – through a very dynamic process where the mountains rose relatively quickly in geological terms – many environments became rapidly available for orchids to colonise, and that promoted speciation in a much faster way. Exploiting these opportunities is what has led to orchids being such a large plant family today.'

RESOLVING A TAXONOMIC 'HODGEPODGE'

You might think that botanists would find it much easier to understand the origin and diversification of a plant family with far fewer species than the Orchidaceae. But untangling relationships between the 2,000 species that make up the figwort family (Scrophulariaceae) has proven to be no less of a challenge. In inferring relationships by examining external characteristics, such as the shape of stamens and the arrangement of sepals and petals in flowers, past taxonomists had inadvertently grouped together species derived from more than one common evolutionary ancestor. Genetic techniques subsequently identified eight tribes of figworts, but these relationships lacked a firm phylogenetic footing, preventing scientists from understanding the family's origins and evolutionary history.

A new study sought to reconstruct the evolutionary history of the family both geographically and through time, and to use this to explain differences in distribution and diversity patterns among living clades. The scientists began by sequencing DNA from almost all figwort genera (84%), encompassing the eight previously defined tribes and three genera that had been unplaced in the classification. Then, using molecular clock dating and modelling, the team explored the origins and global spread of figworts. The work indicated that several previous classifications were incomplete and would need updating. Overall, the study pointed to the existence of two major lineages: the first comprising 11 genera and 340 species (17% of known species), and the second comprising 24 genera and 1,700 species (83%).

The biogeographical modelling suggested the figwort family evolved some 66 million years ago (Ma) on the former Gondwanan landmasses that, by then, had separated and were on their way to the current positions of modern Africa, South America, Madagascar and Australia. This point in geological time marks the boundary between the Cretaceous and Paleogene periods, when three-quarters of plant and animal species (including the dinosaurs) went extinct, reducing competition and enabling new lineages to emerge. Of the two major figwort clades, the smaller began

MOST OF THE ORCHID SPECIES ALIVE TODAY ORIGINATED DURING THE LAST FIVE MILLION YEARS.

The deep history of grasses and their relatives

Important crops such as rice, maize, sorghum and pineapple hail from the large order of flowering plants called Poales. Comprising 14 families and just over 24,300 species, it encompasses the grasses, rushes, sedges, pipeworts and bromeliads. In the most comprehensive evolutionary study of the order to date, a team led by scientists from Masaryk University, Czech Republic, Texas A & M University, USA, and the University of Cape Town, South Africa, combined data from the World Checklist of Vascular Plants on species names and distributions, with data on preferences for open or closed habitats (such as prairie or forest, respectively) and evolutionary history.

The team found that the shared ancestor of the Poales evolved 120 million years ago in the western part of the ancient continent of Gondwana. The families we see today evolved early on in the order's evolutionary history, each spreading out from discrete locations. However, despite the distance between them, some families appear to have evolved in parallel, with repeated evolution of traits enabling species to colonise open and closed habitats at different times, rates and latitudes.

The grass family (Poaceae) and the sedge family (Cyperaceae), which make up around 74% of species richness in the order, provide an example. Both originated in the Late Cretaceous on either side of the widening Atlantic Ocean but dispersed and evolved in parallel to achieve cosmopolitan distributions. In all tropical regions, the grass family diversified first in closed habitats before lineages began appearing in open landscapes. In contrast, in northern temperate regions, sedges from open-habitat lineages diversified first. Investigating how Poales species evolved can help us to understand the ancient origins of crops that millions of people rely on for sustenance every day.

The order Poales has achieved global dominance largely through parallel evolution in open habitats, like this Malagasy grassy ecosystem.

Cycads, such as the *Encephalartos woodii* pictured here, are cone-bearing plants with a long evolutionary history.

WITH 68% OF CYCADS TODAY AT RISK OF EXTINCTION, THEY ARE THE MOST THREATENED ORDER OF PLANTS.

to diversify around 60 Ma in southern Africa, then continued in Madagascar around 40 Ma, with later divergence taking place in the Americas and Australasia around 24 Ma.

‘Interestingly, the more species-rich lineage exhibited a different pattern,’ says Dr Tamara Villaverde, Assistant Professor at Universidad Rey Juan Carlos, who led the study. ‘The six tribes of this clade diverged in isolation in southern Africa from around 63 Ma, with subsequent migration events out of Africa more recently. With this solid framework showing how and when the present diversity of the family arose, we can explore further questions to gain insights into the biology and ecology of this fascinating plant family.’

INVESTIGATING THE DEEP PAST

Even plant groups with far fewer species than the orchids and figworts can be hiding complex evolutionary histories, stretching far back into deep time. The order Cycadales is one such group. Cycads are ancient seed plants which, together with the conifers, ginkgos and gnetophytes, make up the gymnosperm clade that we see today. Unlike the flowering plants (angiosperms), gymnosperms reproduce via ‘naked seeds’ that are not enclosed in fruits. The cycads mostly have stout, woody trunks and a crown of palm-like, spiky evergreen leaves. Today, there are only around 370 species, but they were once a far more diverse group. Botanists have long understood they were an ancient lineage but knew little about their origin and geographical range.

A project undertaken by scientists at institutions in Austria and France developed a phylogenetic framework for the cycads, by combining molecular data for currently existing species with leaf-shape data from both living plants and fossils of extinct plants. The study found that cycads originated in the Carboniferous geological period (360 Ma to 300 Ma) at high latitudes on the northern part of Pangea (Laurasia), when the supercontinent was still intact. They then expanded south onto the southern region of the landmass (Gondwana) in the Jurassic, from around 200 Ma. Global cycad diversity is thought to have reached its pinnacle some 25 million years later in the Middle Jurassic.

‘The inclusion of fossil data in the phylogenetic framework allowed us to unveil patterns that would otherwise be hidden,’ says Dr Mario Coiro, a postdoctoral researcher at the University of Vienna, who led the study. ‘For example, we found that the latitudinal range of cycads has narrowed in the last 15 million years. We only realised that cycads evolved and expanded at much higher latitudes in the past when including fossil diversity in the picture; we would have completely missed this if we had only analysed species alive today.’

The research revealed that from the Jurassic until the end of the Cretaceous (66 Ma), cycads expanded into all continents, aided by now-vanished land bridges connecting South America to Antarctica, Antarctica to Australia, and Greenland to North America and Europe. The team found that Greenland and Antarctica played a crucial role as the source of many lineages in their positions as geographical crossroads between the major landmasses. Geological events such as the opening of oceans or the uplift of mountains appear to have also been important in the formation of new species, as populations were split apart. And a succession of cooling events that took place from 66 Ma could have driven high-latitude cycads to extinction and shifted the distribution of the group to more tropical and subtropical latitudes.

It is clear that alongside the origin and spread of new lineages, extinction has been a key feature throughout the deep and recent history of the cycads. Today is no different, with 68% of species at risk of extinction, making them the most threatened order of plants.

CONNECTING PAST AND PRESENT

Plant lineages often contain many extinct species – representing gaps in their family trees – particularly those that evolved in the long-distant past. However, as the studies outlined here demonstrate, amassing genetic and other information from living species and fossils, and combining it with spatial data, can help to create skeletal family trees that can be added to in future. By creating these frameworks, botanists are able to move back and forth in time through the evolutionary kaleidoscope. This is enabling them to see how plant diversity patterns on Earth’s surface shifted, as different plant lineages spread under favourable conditions and retreated under inclement ones. And it is helping them to make important new connections between species’ distributions in the past and those evident today.

This chapter is based on the following peer-reviewed publications and preprints:

Coiro, M., et al. (2023). Reconciling fossils with phylogenies reveals the origin and macroevolutionary processes explaining the global cycad biodiversity. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19010

Elliott, T.L. et al. (2023). Global analysis of Poales diversification – parallel evolution in space and time into open and closed habitats. *bioRxiv*. DOI: https://doi.org/10.1101/2023.09.14.557735

Pérez-Escobar, O., et al. (2023). The origin and speciation of orchids. *bioRxiv*. DOI: https://doi.org/10.1101/2023.09.10.556973

Villaverde, T., et al. (2023). Phylogenomics sheds new light on the drivers behind a long-lasting systematic riddle: the figwort family Scrophulariaceae. *New Phytologist*. DOI: https://doi.org/10.1111/nph.18845

WHY EVOLUTION MATTERS FOR SAVING BIODIVERSITY

THERE'S MORE THAN ONE WAY TO DEFINE DIVERSITY

In this chapter, we learn: the role evolution plays in shaping species' characteristics; why we should consider plant form and function when planning conservation measures; and that current Biodiversity Hotspots might not be the only places we need to conserve.

The Wollemi pine (*Wollemia nobilis*) is part of an ancient lineage, with only two other living genera in its family (Araucariaceae).

AROUND THE WORLD, MYRIAD LIFEFORMS HAVE EVOLVED TO DEPEND ON EACH OTHER IN COMPLEX WAYS. THIS BIODIVERSITY, AT SCALES FROM SINGLE GENES TO ENTIRE ECOSYSTEMS, IS ESSENTIAL FOR OUR EXISTENCE.

Plants, in particular, provide us with food, materials, medicines and more. They regulate important planetary cycles that provide us with the air we breathe and water we drink, and contribute to our overall well-being. If we are to safeguard life on Earth, we must end the current extinction crisis in which plant species are dying out at least 500 times faster than before humans existed. But with limited time and resources, we need to know how best to conserve biodiversity to keep ecosystems diverse and functioning, while preserving species with the greatest potential for use by future human populations.

TAKING EVOLUTION INTO ACCOUNT

Conservation efforts to date have tended to focus on locations hosting many different species – particularly regional endemics not found anywhere else – with threats from human activities such as deforestation or land clearance also taken into consideration. To this end, scientists have identified 36 global Biodiversity Hotspots, areas hosting exceptional concentrations of endemic species that are also under threat from habitat loss. These Hotspots are often used to prioritise areas for conservation. However, in recent decades, researchers have begun to measure biodiversity in other ways, including by calculating ‘phylogenetic diversity’, a measurement that considers the distinctiveness of species resulting from their evolutionary history and position on the tree of life, the family tree of all living things.

According to this measure, the most diverse floras or faunas are those that comprise many species that are distantly related to each other, thus representing many different evolutionary branches. Preserving such diverse communities of species makes it more likely that we will conserve the range of genes, forms and functions that make up healthy and resilient ecosystems and have the highest potential for use by humans. However, a new study has shown that hotspots of phylogenetic diversity differ from areas previously identified as Biodiversity Hotspots, which suggests we may need to widen the scope of conservation efforts going forward.

‘We wanted to know, if you put the plant tree of life on a map, where is most of the diversity going to be?’ explains Dr Wolf Eiserhardt, Associate Professor at Aarhus University, Denmark, and Honorary Research Associate at the Royal Botanic Gardens, Kew (RBG Kew). ‘Then along came this amazing opportunity when the World Checklist of Vascular Plants [WCVP – see Chapter 1] published distributions for all plant species. It gave us the chance to learn where most branches of the tree of life are actually found on the map. Our findings show that phylogenetic diversity is more evenly spread around the globe than species diversity, so we can’t get away with focusing conservation attention on a limited number of localised areas.’

Species richness is simply a count of the individual species that grow within a particular geographical area. By contrast, phylogenetic diversity is measured as the sum of the length of all the branches on the tree of life that connect a set of species back to their common ancestor. One way to think of it is as a summary of the amount of evolutionary history connecting all the species in the area in question.

The form and function of a plant species is a product of its evolutionary history. Each species exhibits a suite of characteristics – based on its underlying genetic make-up and responses to its environment – which endows it with particular traits, such as whether it is woody, the type of fruits it bears and its capacity to tolerate different environmental conditions. Closely related species that only diverged from one another recently usually exhibit many of the same characteristics, while a species found alone on a single, long evolutionary branch, such as the ‘living fossil’ the Wollemi pine (*Wollemia nobilis*), is more likely to contain traits, or combinations of traits, not present elsewhere.

If something changes in an ecosystem – say, drier conditions ensue – a habitat containing diverse plants that have evolved independently from one another over a long time period might have a greater spectrum of features to draw on to help it tolerate the new conditions than one containing species that have diverged relatively recently. In this way, diverse evolutionary histories underpin an ecosystem’s resilience to environmental change. And greater diversity equates to a wider array of features that might benefit humanity in future, too. So, conserving diversity of plant form and function is critical to all life on Earth.

‘Species aren’t all the same, and how much they count towards the diversity of form and function in an ecosystem depends on how closely related they are,’ explains Dr Eiserhardt. ‘That was the original motivation for coming up with phylogenetic diversity as a measure of biodiversity. Species are often “redundant” in an evolutionary sense. In other words, if you have ten species that are really close relatives that have had hardly any time to diverge in terms of form and function, then that is a very different situation to having ten species that all diverged tens of millions of years back and have had plenty of time to accumulate different characteristics, which, today, underpin their various forms and ecological functions and the way they behave in their ecosystem.’

WHY NOT ALL HOTSPOTS ARE EQUAL

The scientists behind the new study sought to map the distribution of plant phylogenetic diversity, find out how it related to species richness and understand how it might best be conserved. They began by matching species from a recently created phylogenetic tree of seed plants with the WCVP to derive a dataset of 330,527 species. They then calculated diversity indices for each country – or close equivalent – using botanical countries (see Chapter 1, Box 1). They first measured the number of species recorded per botanical country (species richness) and the number of unique species in each (species endemism).

Many plant species found atop Venezuela's tepuis evolved in isolation and are not found anywhere else in the world.

RESEARCHERS MEASURE BIODIVERSITY IN DIFFERENT WAYS, INCLUDING BY CONSIDERING THE DISTINCTIVENESS OF SPECIES RESULTING FROM THEIR EVOLUTIONARY HISTORY.

The island of Madagascar hosts many unique species on distinct evolutionary branches.

DIVERSE EVOLUTIONARY LINEAGES UNDERPIN AN ECOSYSTEM'S RESILIENCE TO ENVIRONMENTAL CHANGE.

After that, they summed the length of all the branches related to members of a particular botanical country to calculate phylogenetic diversity, and calculated the endemism of this phylogenetic diversity as the total amount of branch length found only in a particular country (see Figure 1).

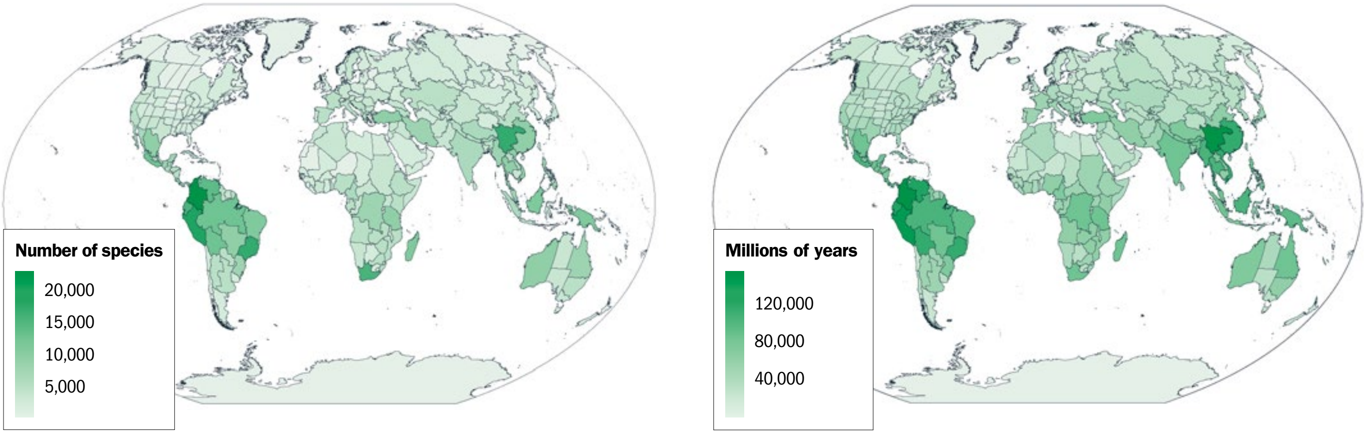
The next step was to delineate hotspots for the four variables. The scientists did this following two approaches. First, they identified the top ten botanical countries for species richness, species endemism, phylogenetic diversity and phylogenetic diversity endemism. Then they identified each country's contribution to each of these variables. This second approach involved using a 'greedy algorithm' that first took the botanical country with the highest diversity value then sequentially added botanical countries, at each step choosing the one that added the most diversity – was most complementary – to the total diversity in the set. This identified the minimum number of countries that together contained the maximum amount of diversity in as small an area as possible. The set of ten countries that jointly maximised this cumulative diversity for the four variables was then identified. To explore the environmental characteristics of the delineated hotspots, the researchers calculated the extent to which each botanical country encompassed different biomes, namely: tropical rainforest, temperate forest, taiga or boreal forest, desert, tundra, grassland and savanna.

The findings showed that phylogenetic diversity was more evenly distributed across the globe than species richness. In addition, more than twice as many botanical countries were needed to represent 50% of global phylogenetic diversity than to achieve the same for species richness (see Figure 2, overleaf). This can be explained by the fact that as a sampling area was expanded, new species were added, but as they were geographically near to those already sampled, they were more likely to be their close relatives than be complementary to them. This result highlights the risks of focusing purely on species richness when prioritising areas for conservation.

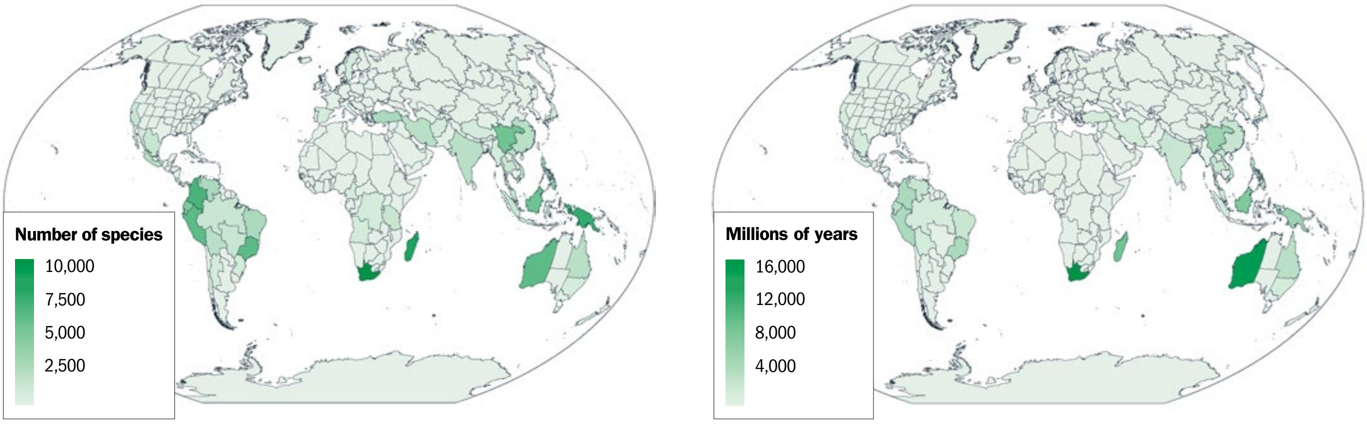
FIGURE 1: Different ways to measure diversity

Four aspects of diversity were examined in the new study: species richness; species endemism (uniqueness); phylogenetic diversity; and phylogenetic diversity endemism. Traditionally, conservation has focused on species richness and endemism. However, phylogenetic diversity, which takes account of evolutionary history, is a more effective measure of capturing diversity and ensuring ecosystems remain resilient. The maps show that phylogenetic diversity is more evenly distributed across the globe, so current conservation priorities may need to be rethought to ensure critical biodiversity is not lost.

Species richness **Phylogenetic diversity**



Species endemism **Phylogenetic diversity endemism**



Adapted from Tietje et al. (2023)

Another interesting revelation was that, when it came to representing global diversity, hotspots selected for cumulative phylogenetic diversity outperformed those selected for having the highest absolute phylogenetic diversity. For example, the botanical countries with the highest absolute phylogenetic diversity included clusters of adjacent countries in north-western South America and continental Asia. But several of those countries did not contribute sufficiently to cumulative phylogenetic diversity to be considered hotspots, instead remaining outside of the top ten for this calculation. Countries in sub-Saharan Africa and Australasia also needed to be included to maximise cumulative phylogenetic diversity.

The different positions of species on the tree of life help to explain this redundancy. Although countries in north-western South America individually have high phylogenetic diversity, being neighbours they tend to contain the same branches of the tree of life – and so they are not all essential when maximising cumulative phylogenetic diversity, and, by extension, wealth of form and function. In contrast, some African and Australasian countries that individually have lower phylogenetic diversity host different branches of the tree of life, and thus contribute more to cumulative phylogenetic diversity. For example, the sub-Saharan island nation of Madagascar, having been isolated from other landmasses over a very long period of time, has evolved many distinct evolutionary branches that have given rise to diverse species that are not closely related to species living elsewhere. The findings around cumulative phylogenetic diversity indicate that not only is it insufficient to use species richness for prioritising areas for conservation, but that focusing only on absolute phylogenetic diversity also risks failing to conserve the full global set of form and functionality of seed plants.

The findings related to environmental characteristics were also illuminating. They showed that regions of high absolute phylogenetic diversity included large expanses of tropical rainforest but typically also included other forest types, such as tropical dry forests and temperate forests. The hotspots derived from maximising cumulative phylogenetic diversity were also mostly forested but additionally encompassed more open, non-forested biomes. An example is the Cape Provinces region of South Africa, which is exclusively covered by open biomes (at the scale used in this study) and hosts more than 10,000 species that are unique to the area. This means that while the tropical rainforest is, on its own, the most phylogenetically diverse biome, other biomes are required to represent the entirety of form and function that has arisen in modern plants as they have evolved.

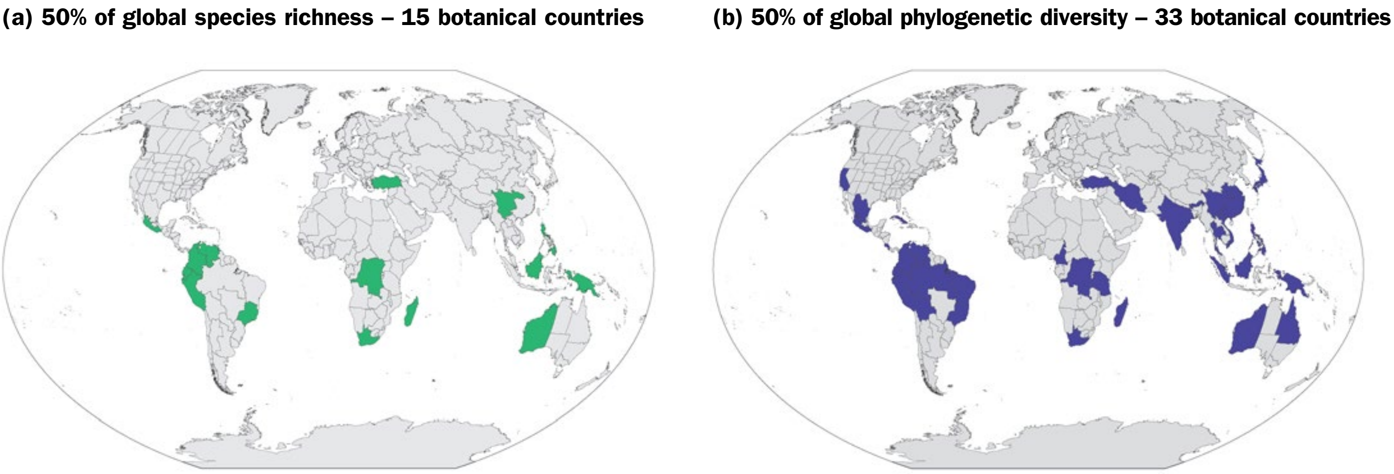
'There is a bit of a craze about the Neotropics, with a lot of literature recently pointing out how the region is the most biodiverse place on Earth and really important to protect,' explains Dr Eiserhardt. 'That is true and there are other important places as well if you look at just the absolute number of species. But the point is that just looking at the absolute number of species, or even absolute measures of phylogenetic diversity, is going to lead you down the wrong track because you will end up protecting more of the same rather than something that is complementary to a place that you have already protected. If you are interested in maximising cumulative phylogenetic diversity, you need a wider geographical representation.'

This chapter is based on the following peer-reviewed publication:

Tietje, M., et al. (2023). Global hotspots of plant phylogenetic diversity. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19151

FIGURE 2: Capturing different aspects of diversity

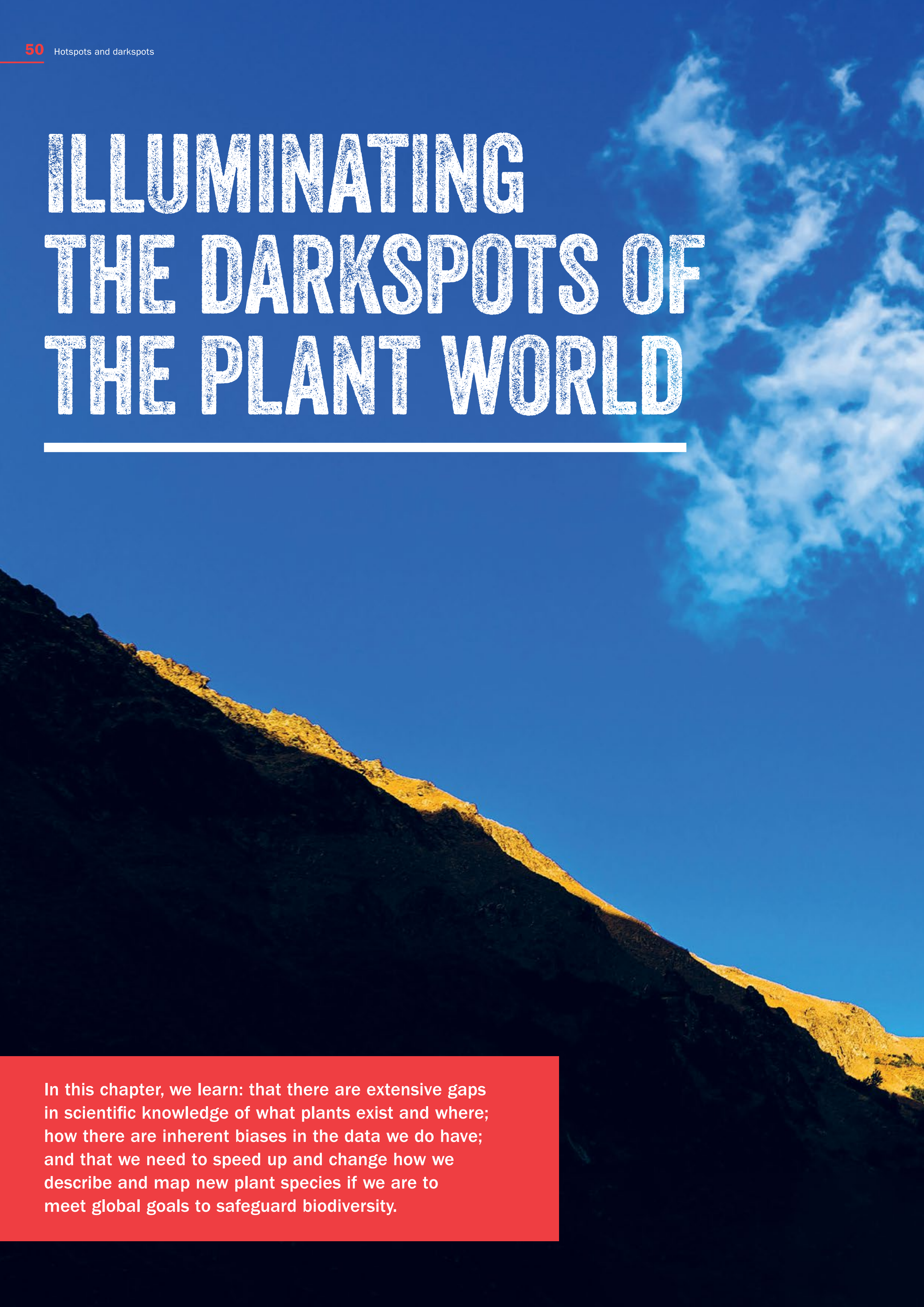
Maps showing the minimum number of botanical countries needed to capture 50% of global species richness (a) and phylogenetic diversity (b). To capture 50% of phylogenetic diversity, global conservation efforts would need to focus on more than twice the number of botanical countries than if focusing on species richness – 33 compared to 15.


(a) 50% of global species richness – 15 botanical countries

(b) 50% of global phylogenetic diversity – 33 botanical countries

Adapted from Tietje et al. (2023)

South Africa has an exceptionally diverse flora, including many plant lineages that arose before the fragmentation of the ancient supercontinent of Gondwana. An example is the Proteaceae family, which includes the sugarbushes (*Protea*).



ILLUMINATING THE DARKSPOTS OF THE PLANT WORLD

In this chapter, we learn: that there are extensive gaps in scientific knowledge of what plants exist and where; how there are inherent biases in the data we do have; and that we need to speed up and change how we describe and map new plant species if we are to meet global goals to safeguard biodiversity.

32

PLANT DATA DARKSPOTS HAVE BEEN IDENTIFIED WORLDWIDE

Iran is one of six plant diversity darkspots located within temperate Asia.

THEY ARE THE DARK MATTER OF BOTANY – PLANT SPECIES THAT ARE YET TO BE SCIENTIFICALLY NAMED, DESCRIBED AND MAPPED BUT WHICH ARE ESTIMATED TO MAKE UP 15% OF THE WORLD'S FLORA.

As well as being part of the global web of biodiversity that helps to sustain life on Earth, plants could yield nutritious foods, medicines, timber and other useful materials. With 77% of undescribed species predicted to be threatened with extinction (see Chapter 9), the race is on to find and conserve them. But how do scientists allocate limited resources to looking for uncharted plants – and prioritise those most at risk – without knowing where in the world this unknown diversity is hiding?

A project undertaken by the Royal Botanic Gardens, Kew (RBG Kew) and partners sought to solve this conundrum by shining a light into the 'dark' corners of the natural world. The scientists began by predicting the number of species per botanical country (see Chapter 1, Box 1) that currently remain unnamed and unmapped. This involved identifying areas where both taxonomic and geographical data were lacking – 'darkspots' – and examining why certain species may have been scientifically described and mapped ahead of others. Next, they looked at where the darkspots coincided with the 36 global Biodiversity Hotspots – previously defined areas with a particularly rich and unique flora that are also under threat from exceptional habitat loss. Finally, they considered how socio-political and environmental factors might influence botanical exploration, as a guide for shaping future strategies to track down, describe and conserve the 'missing' species.

'Resources to undertake new botanical expeditions or to digitise existing collections are limited,' explains Dr Samuel Pironon, Research Leader at RBG Kew and Modelling Scientist at the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC). 'So, we need to prioritise collection efforts. Knowing where there are most species remaining unnamed and unmapped, of which many are likely to be threatened, is crucial in this context. Understanding where the unknowns are concentrated could also help us refine our estimates of priority areas for conservation.'

The study aimed to address two major gaps in data related to biodiversity. The first is the shortfall between the number of species that exist and those formally described by scientists, while the second reflects the paucity of knowledge on the geographical distributions of species. The lead modeller for the project, Ian Ondo, Programme Officer at UNEP-WCMC and Senior Spatial Analyst at RBG Kew, estimates that the shortfall in plant descriptions is substantial, with potentially tens of thousands of flowering plant species yet to be scientifically named – although the uncertainty is high and varies hugely among regions. And while the World Checklist of Vascular Plants (WCVP) now provides distribution data for most known species at the level of botanical countries, these data are widely absent at finer resolutions within countries, where major biases and gaps exist. Comprehensive data are also lacking for plant traits (see Box 1).

Understanding how much these shortfalls vary is key to developing targeted collection strategies to unearth new plant species from the wild and to document known species in new places. The latter is especially crucial to helping us understand where species grow, their rarity, the limits of temperature and rainfall they can tolerate, and their risk of extinction. Meanwhile, some currently unknown occurrences of species might represent genetically distinct populations with unique properties.

FINDING THE KNOWN UNKNOWNS

The researchers used the WCVP, the Global Biodiversity Information Facility (GBIF) and other online resources to identify the plant species currently known to exist, the year they were first collected in each botanical country, and their patterns of distribution. WCVP is a comprehensive, expert-curated global database of known vascular plant species (see Chapter 1), while GBIF is an international online portal that provides open-access data about all types of life on Earth. Using these resources, the researchers derived a dataset comprising occurrence records for around 250,000 vascular plant species, across 363 of 369 botanical countries and 450 plant families. This formed the basis for their analysis.

The team began by examining historical and geographical patterns of descriptions of vascular plant species to predict how many species remain to be scientifically described. The vast majority of botanical countries were predicted to contain fewer than 50 remaining unknown species. However, a much larger shortfall in plant descriptions was predicted for the Asia-Tropical and South America continental regions, with some botanical countries there predicted to still house hundreds of species unknown to science. The outlook was similar for Turkey, Madagascar and China South-Central. Large gaps in distribution data were also forecast for other parts of the world. Thousands of known species were still missing geographical records across most continents, with Myanmar, the Indian state of Assam, Colombia and Vietnam missing data for more than 4,000 species each.

The research also showed that the size of a species' range strongly influenced gaps in both description and distribution data. Species with a large range were most likely to be described before those with a small range.

SOME COUNTRIES IN TROPICAL ASIA AND SOUTH AMERICA ARE PREDICTED TO HOUSE HUNDREDS OF SPECIES UNKNOWN TO SCIENCE.

BOX 1: Focusing in on traits

On top of data shortfalls in our knowledge of what species grow where, an analysis by scientists from the USA, Australia, Denmark and the UK has revealed that there are also gaps and global biases in what we know about plant traits. Traits are measurable characteristics, such as leaf size or seed mass, and are a result of species' long-term interactions with their environment and with other organisms. They drive the functioning of terrestrial ecosystems. Using taxonomic and geographical data from the World Checklist of Vascular Plants, the team found that despite a massive amount of available trait data, our knowledge remains far from complete. As with the other shortfalls described in this chapter, it is also spatially biased, with data coverage higher in the Global North. Furthermore, it is disproportionately collected from regions with high levels of human disturbance, which may bias the results of studies using these data. Global effort is crucially needed to collect more, and balanced, data on plant traits if we are to understand how ecosystems worldwide function and how they may respond to climate change, potentially affecting the functioning of the whole biosphere. And we must gather these data with haste: trait data coverage is particularly low in tropical regions, which may already be approaching climatic thresholds beyond which irreversible change to ecosystems may occur.

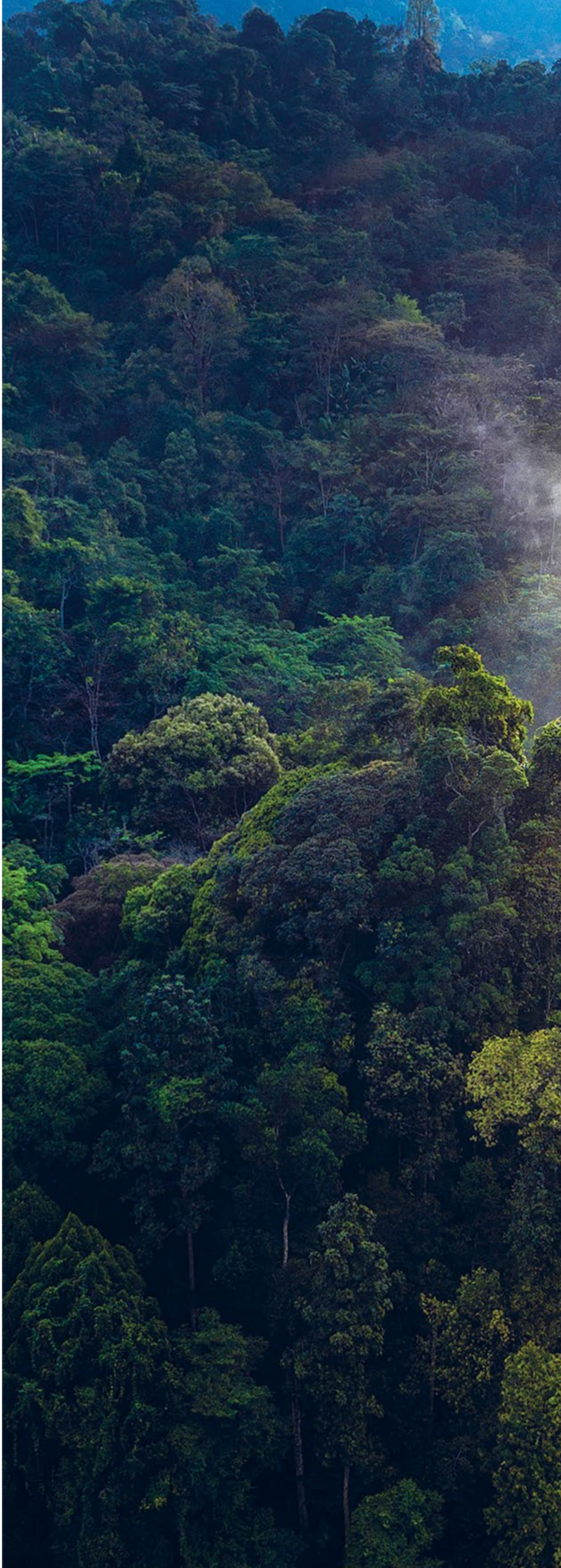
This was not surprising, given that people are more likely to spot plants growing across a wide region than those limited to small areas. In terms of the distribution, in earlier periods of botanical exploration, the larger the species' range, the longer it took for its occurrence to be recorded in all the botanical countries in which it grew – in other words for its complete distribution to be mapped at this scale. Today, the distributions of most large-range species are well known but there are still many small-range species remaining to be documented. Other findings were that those species described early on tended to have a high number of human uses. When the team examined the collection patterns for the last decade (2010–2019), they found that current botanical collection methods were more effective at overcoming the distribution data shortfall than the data gap in naming and describing plants.

'Many species that are not yet described by science, are in fact well known by indigenous communities,' explains Dr Kiran Dhanjal-Adams, postdoctoral researcher at RBG Kew. 'And species extinctions and cultural extinctions are inextricably interlinked. With the Kunming-Montreal Global Biodiversity Framework [GBF] highlighting the importance of indigenous and local communities in conservation, we have the basis for strengthening partnerships and increasing our capacity to describe species in a way that can help raise conservation interest and funds to support local communities, as well as shedding light on darkspots.'

BLACK HOLES IN THE DATA

The researchers next looked for where taxonomic and geographical knowledge gaps overlapped. Overall Colombia, New Guinea, and China South-Central had the greatest combined descriptive and geographical data shortfalls globally, in decreasing order. By continent, New Caledonia and Fiji had the greatest combined shortfall for the Pacific; Western Australia and Queensland for Australasia; New Guinea and Vietnam for Asia-Tropical; China South-Central and Turkey for Asia-Temperate; Madagascar and Cape Provinces for Africa; Albania and Yugoslavia (former) for Europe; Mexico Southwest and Mexico Southeast for North America; and Colombia and Peru for South America. The team generated a 'darkspot score' between zero and one for each botanical country, with zero representing the smallest taxonomic and geographical knowledge gaps, and one the largest. The global vascular plant diversity darkspots were then defined as those botanical countries with the highest darkspot scores. The cut-off point for adding countries to the darkspot shortlist was when the combined land area of the darkspots matched the extent of the 36 global Biodiversity Hotspots, to allow for comparisons to be made.

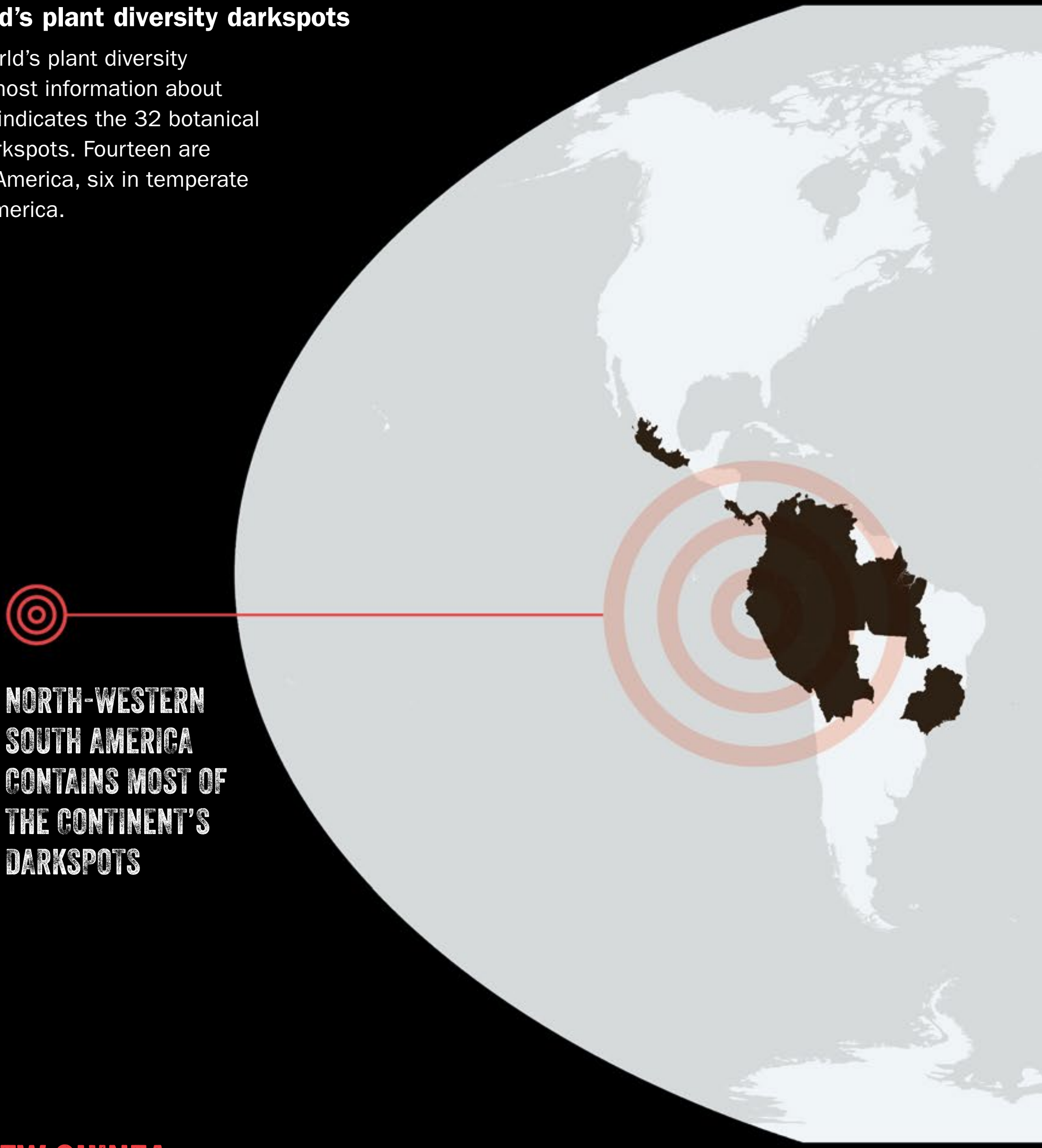
This work revealed the existence of 32 darkspots (see Figure 1). Fourteen of them spanned large parts of the Asia-Tropical region (Myanmar, Assam, Philippines, Vietnam, Bangladesh, New Guinea, India, East and West Himalaya, Thailand, Sumatera [Sumatra], Laos, Malaya [Peninsular Malaysia] and Borneo). Nine were in South America (Colombia, Peru, Venezuela, Bolivia, Brazil North, Brazil Southeast, Ecuador, Costa Rica and Panama). Six were located in the Asia-Temperate region (China South-Central, Turkey, Iran, Uzbekistan, China Southeast and Tadzhikistan [Tajikstan]).



MANY SPECIES THAT ARE UNKNOWN TO SCIENCE ARE, IN FACT, WELL KNOWN TO INDIGENOUS COMMUNITIES.

FIGURE 1: Pinpointing the world's plant diversity darkspots

This map shows the location of the world's plant diversity darkspots (regions estimated to lack most information about plant diversity and distribution). Black indicates the 32 botanical countries defined as plant diversity darkspots. Fourteen are within tropical Asia, nine within South America, six in temperate Asia, two in Africa, and one in North America.



NORTH-WESTERN SOUTH AMERICA CONTAINS MOST OF THE CONTINENT'S DARKSPOTS

TOP 2 KNOWLEDGE GAPS

COLOMBIA

NEW GUINEA

Colombia:
The largest knowledge gaps on plant diversity and distribution occur in Colombia.

New Guinea:
New Guinea comes second in terms of knowledge gaps and is also the only country not to overlap with the current global Biodiversity Hotspots.

Adapted from Ondo et al. (2023)

14 OF THE 32 GLOBAL PLANT DIVERSITY DARKSPOTS ARE IN TROPICAL ASIA

MADAGASCAR AND CAPE PROVINCES HAVE THE GREATEST COMBINED DATA GAPS FOR AFRICA.

32

32 DARKSPOTS

COLOMBIA, BORNEO, ECUADOR, INDIA, MYANMAR, NEW GUINEA, PERU, THE PHILIPPINES AND TURKEY SHOWED UP CONSISTENTLY AS GLOBAL PRIORITIES.

Two were in Africa (Madagascar and Cape Provinces) and one in North America (Mexico Southwest). The 32 darkspots overlapped to a very large extent with the 36 Biodiversity Hotspots, with the exception of the island of New Guinea. Conversely, there were a large number of hotspots not identified as darkspots in the analysis, particularly in the Pacific, Australasia, North America, Africa and Europe continental areas.

GETTING THE PRIORITIES RIGHT

To assess how socio-political and environmental factors might influence plant-collecting priorities, the researchers defined nine scenarios based on trade-offs between the darkspot score, income group and level of environmental protection (as defined by the United Nations Sustainable Development Goals indicators). These showed that different botanical countries came into focus as priorities under the various scenarios. For example, when prioritising botanical countries with low-income levels, Afghanistan, Pakistan, Sudan and Angola became global priorities. When prioritising those places with low levels of environmental protection, Tibet became a global priority. The botanical countries of Colombia, Borneo, Ecuador, India, Myanmar, New Guinea, Peru, the Philippines and Turkey showed up consistently as global priorities across all scenarios. These locations can be considered to have a high potential for describing and mapping new species. The scenario-based framework can provide further guidance for examining trade-offs between income and environmental protection when planning plant collecting outside of these nine obvious target areas in future. It can also be used in conjunction with regional studies on knowledge gaps, for example on Mesoamerica (see Box 2).

BUSINESS AS USUAL IS NOT ENOUGH

Overall, the work indicated that if recent trends in scientifically describing and mapping new plant species continue, current botanical collection may be insufficient to completely document the geographical distribution of all vascular plants in the near future. This would prevent the visionary goals of the GBF – to safeguard and sustainably use biodiversity – from being achieved. And while the current Biodiversity Hotspot classification is regarded as a useful framework to guide biodiversity scientists and conservationists, the new research findings show that the Hotspots alone are not enough to inform collection priorities. Rather, in parallel with the findings outlined in Chapter 6, they indicate that considering plant diversity darkspots in conjunction with Hotspots would be a better approach going forward.

New Guinea is a case in point. When the global Biodiversity Hotspot classification was developed in 2000, it recognised that New Guinea was rich in unique species but, as at least 70% of its original vegetation was intact, it did not consider the island to be sufficiently threatened to be included as a Biodiversity Hotspot. However, with the conversion of land to agriculture increasingly affecting the region, the currently unknown species it hosts – as highlighted through its darkspot status – may become threatened or go extinct before they have been described and mapped.

'The way we are documenting biodiversity is not commensurate with the time we have left and the challenges we are facing,' says Prof. Alexandre Antonelli, Director of Science at RBG Kew. 'Business as usual is not good enough. Worldwide, we have to be more effective. I'm particularly excited about our findings because my colleagues at RBG Kew and other collections-based institutions around the world need to know where the scientific community should work to accelerate the scientific description of species and to record where they occur. The framework we present here provides a road map for how we can achieve this by adopting inclusive approaches that benefit local stakeholders, strengthen capacity and generate globally valuable knowledge. It can help ensure that by 2050 we have identified all the hotspots of biodiversity and that there are no darkspots left.'

This chapter is based on the following peer-reviewed publications and preprint:

Maitner, B., et al. (2023). A global assessment of the Raunkiæran shortfall in plants: geographic biases in our knowledge of plant traits. *New Phytologist*. DOI: https://doi.org/10.1111/nph.18999

Ondo, I., et al. (2023). Plant diversity darkspots for global collection priorities. *bioRxiv*. DOI: https://doi.org/10.1101/2023.09.12.557387

Ramírez-Barahona., et al. (2023). Assessing digital accessible botanical knowledge and priorities for exploration and discovery of plant diversity across Mesoamerica. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19190

> THE WAY WE ARE DOCUMENTING BIODIVERSITY IS NOT COMMENSURATE WITH THE TIME WE HAVE LEFT AND THE CHALLENGES WE ARE FACING.

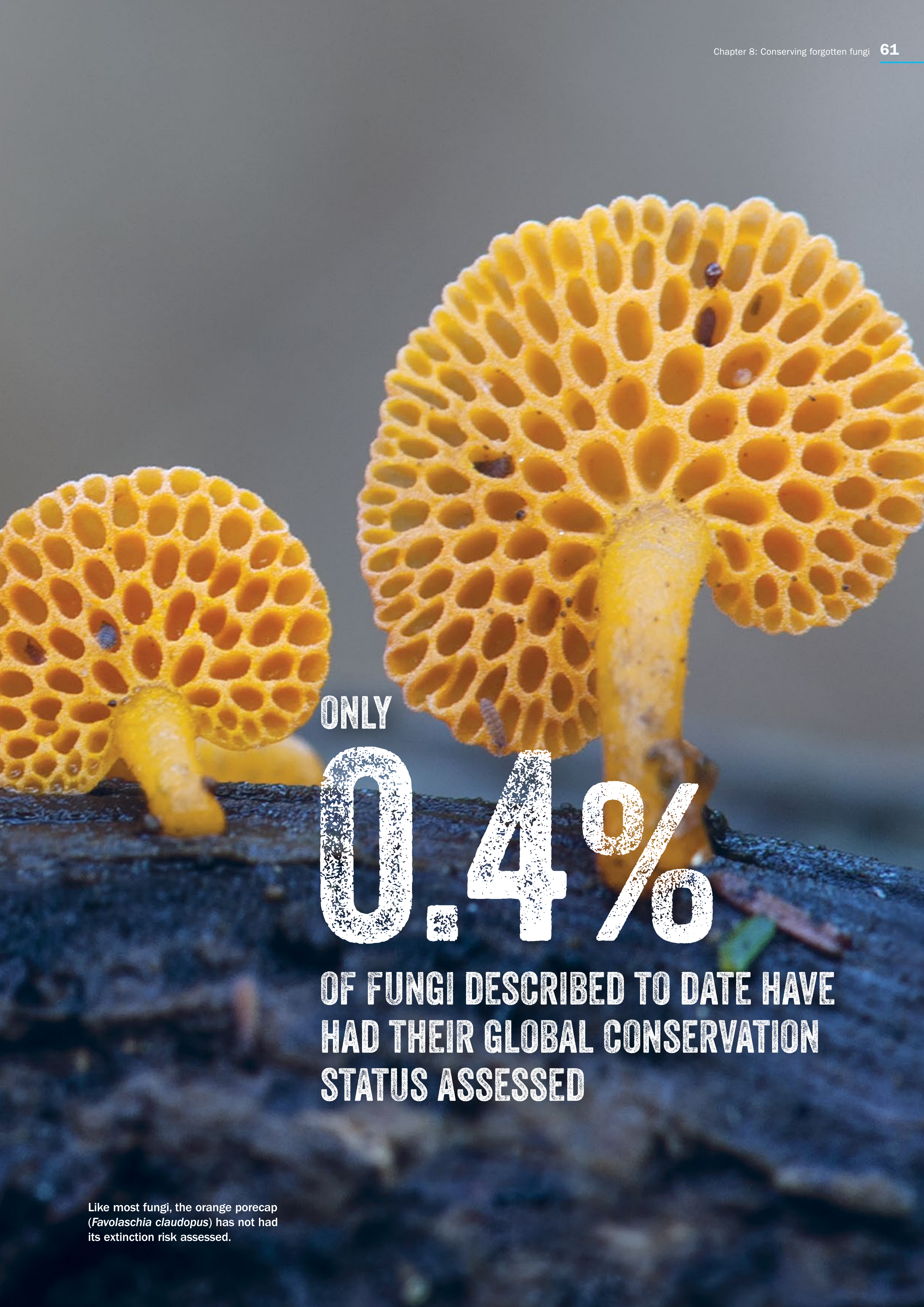
BOX 2: Gaps and priorities in Mesoamerica

Mesoamerica, the continental region stretching from Mexico to Panama, is exceptionally rich in plant species. Yet a case study from the National Autonomous University of Mexico that used the WCVP as a framework to look at digital data availability for plants in Mesoamerica reported knowledge shortfalls. The researchers found evidence for poor data coverage in three dimensions: spatial, temporal and phylogenetic. In examining 3,578,777 occurrence records for 32,522 Mesoamerican plant species, they uncovered incomplete geographical coverage, the absence of recent occurrence records and low phylogenetic representation. Gaps were notable in Central Mexico, Guatemala, Honduras and Panama. Such shortfalls limit the usefulness of digitally available occurrence data, and hamper research on evolutionary history, conservation and species dynamics under human disturbances. Mesoamerica has also experienced one of the highest deforestation rates in the world, and data to support the conservation of biodiversity are therefore crucial. The authors of the study hope that highlighting regional data deficiencies can be used to target renewed surveying, collecting, digitisation, sequencing, research, conservation and monitoring in future.

Scientists have identified notable gaps in plant data from Guatemala.

CONSERVING FORGOTTEN FUNGI

In this chapter, we learn: that assessing the conservation status of elusive fungi is challenging but possible; how Nordic nations are leading the way in conserving fungi; why we need new protocols for classifying fungi; and how citizen scientists may be fungi's best friends.



ONLY

0.4%

OF FUNGI DESCRIBED TO DATE HAVE HAD THEIR GLOBAL CONSERVATION STATUS ASSESSED

Like most fungi, the orange porecap (*Favolaschia claudopus*) has not had its extinction risk assessed.

HOW DO YOU WORK OUT WHICH FUNGI TO CONSERVE WHEN >90% OF THE SPECIES ESTIMATED TO EXIST ON EARTH ARE YET TO BE FORMALLY DESCRIBED? IT MAY SOUND TOO CHALLENGING TO CONTEMPLATE BUT A DEDICATED FUNGAL CONSERVATION MOVEMENT IS GATHERING PACE, COMMITTED TO PUTTING THE DATA THAT ARE AVAILABLE TO GOOD USE AND TO COLLECTING YET MORE.

So far, this effort has led to 625 fungi being assessed for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, of which 352 (56%) are considered to be globally threatened or near threatened. While this means that only 0.4% of the fungi described to date have had their global conservation status assessed – equating to 0.02% of those estimated to exist (see Figure 1, overleaf) – it is a starting point on which mycologists can build as naming, classifying and assessing fungi intensifies.

A FUNGAL AWAKENING

The IUCN Red List of Threatened Species has long charted the global conservation status of plants and animals, becoming recognised as the gold standard for assessing extinction risk. Making a conservation assessment involves using IUCN criteria to classify species as: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern or Data Deficient, either globally or within a particular country or region. As recently as 2003, only two species of fungi had made it on to the global Red List. However, after the Global Fungal Red List Initiative was launched, mobilising scientists and fungus enthusiasts to propose at-risk species to prioritise for assessment, the number began to rise. It is expected to exceed 1,000 by the end of 2023.

The first national Red Lists for fungi were developed in the late 1980s after reports of declines in lichens (partnerships between fungi and algae or bacteria, or both) and macrofungi (those that produce visible fruiting bodies, such as mushrooms and brackets). Today, some 58 countries have official or unofficial national Red Lists, Red Data Books, or corresponding tallies of conservation values for macrofungi. Meanwhile, at least 17 have the equivalent for lichens. Altogether, more than 20,000 species of fungi (including lichens) have been assessed at national level, mostly in the northern hemisphere. The drive to increase the number of globally Red-Listed species is also helping to highlight substantial threats to fungi in countries without national Red Lists, many of which occur in highly biodiverse regions. Officially documenting species in this way can draw authorities' attention to rare or declining species in their midst and potentially encourage them to conserve them.

Although not legally binding, Red Lists are recognised as representing the best available knowledge of species' status and trends, and can be used as the basis for legal protection. Currently, national fungal Red Lists are being used to identify the best areas and habitats to conserve, guide forest- and land-management protocols and legislation, and inform action plans for conserving species. In Fennoscandia and Denmark, fungal Red List data are guiding numerous conservation-management efforts; in Chile, the first country to include fungi in environmental legislation, they are informing forest-protection measures; and in Australia, New Zealand and the USA they are starting to be incorporated into conservation actions.

The assessment of extinction risk for any organism on a Red List – whether fungus, plant or animal – is based on the size and extent of its population and an evaluation of trends, such as a significant decline in numbers. For many fungi, as with most insects and numerous plants, directly calculating population size is challenging. In recent decades, efforts by mycologists, surveys (such as those carried out to identify and prioritise areas of conservation interest), targeted citizen-science initiatives focused on locating threatened species, and to some extent new DNA techniques, have greatly increased knowledge of fungal distributions and their ecologies. This has made it possible to estimate fungal populations based on the extent and quality of associated habitats, host plants and substrates.

'Early on, some mycologists claimed that we knew too little to make assessments because species often grew unseen as mycelia [underground networks of fungal filaments] for many years, and only popped up at unpredictable intervals,' says Professor Anders Dahlberg, of the Swedish University of Agricultural Sciences in Uppsala, who co-initiated the drive to get more fungi included on the global IUCN Red List. 'But I disagree. We know quite a lot about many species, particularly common ones and those with specific habitat requirements or conspicuous sporocarps [fruiting bodies]. If we know a species is mostly occurring in old-growth forests, we can estimate that 90% to 95% of all occurrences are there, and if there is a loss every year of 1% of those forests to logging, then we can surmise for an assessment that the fungi may be lost at the same rate. It's a bit like planning a holiday. You can do it with a little or a lot of knowledge and the more precise you can be, the better you can pre-plan your trip. The process of making conservation assessments for fungi is similar.'

Attempts to undertake population analyses for assessing fungal species, have nonetheless faced challenges.

INFORMATION PRESENTED ON GLOBAL AND NATIONAL RED LISTS SUGGESTS THAT CURRENT THREATS TO FUNGAL SPECIES LARGELY MIRROR THOSE FACED BY ANIMALS AND PLANTS.

The green elfcup (*Chlorociboria aeruginascens*) is commonly seen in the UK on decomposing wood.

Mycologists are still uncertain, for example, about how long fungi live, the conditions they require to form mycelia, which species have spore banks and what their significance is for those that do, and whether fungal species are generalists or specialists regarding the partnerships they form. However, the Red List methodology makes provision for this by including an estimate of the uncertainty level of data submitted. This can be revised as more becomes known about a species.

THREATS IN COMMON

Information presented on global and national Red Lists suggests that current threats to fungal species largely mirror those faced by animals and plants. The main threat comes from land-use changes that modify natural systems, such as conversion to forestry, agriculture or residential and commercial development. For example, in parts of Europe, declining areas of older natural forest and expanded timber production are leading to less deadwood and fewer old trees being available for fungi to populate. And semi-natural grasslands have been lost or degraded through inappropriate grazing regimes, tree planting, reseeding and the increasing use of fertilisers. Many fungi require such low levels of soil nitrogen that their diversity is also threatened by the deposition of airborne nitrogen pollution emitted by combustion engines. This is particularly problematic close to cities; in the Netherlands, annual nitrogen deposition of as much as 20 kilograms per hectare (kg/ha) has been recorded, much higher than the pre-industrial level of 1–3 kg/ha.

Climate change is having detrimental impacts too. With the overwhelming majority of fungal diversity directly dependent on plants – whether as beneficial partners, decomposers or parasites – climate-related habitat change that harms plants in turn affects their co-existing fungi. Shifts in temperature and moisture levels can also directly affect fungi. Meanwhile, the over-collection of economically valuable fungi is a risk for some species, such as the caterpillar fungus (*Ophiocordyceps sinensis*), from the Himalayas, which has been used in traditional Chinese and Tibetan medicine.

As relatively immobile and often long-lived organisms, fungi benefit from many of the actions taken to conserve plant and animal species, such as protecting sites and sustaining ecological processes within threatened habitats. However, the Red List assessments show that the degradation of some ecological settings particularly affects fungi. Conserving fungal diversity and function therefore also calls for targeted management practices. These include preserving mature trees to serve as species reservoirs, maintaining supplies of deadwood in forests, and keeping grasslands nutrient-poor. Enacting such specific practices supports and strengthens conservation in general, while ensuring that habitats required by threatened fungi can be identified, prioritised for conservation and protected.

This is already happening, although so far in very few countries. For example, in the Nordic nations, fungi of conservation interest have been considered alongside priority animals and plants when delineating protected areas since the 1990s. In Sweden, the Swedish Forestry Act calls for deadwood to be left after harvesting, while the Forest Stewardship Council (FSC), an international non-profit organisation that promotes the responsible management of woodlands, goes further by requiring that new deadwood resources be created. Specifically, FSC certification demands that for every hectare, two wind-felled trees are retained and three high stumps or girdled trees are created during clear-cutting. In the UK, Sites of Special Scientific Interest (SSSIs) must be managed in a way that conserves the special features of the site, with each SSSI having a list of operations that cannot be carried out without consent. The Down Farm waxcap grassland SSSI in the UK, where fruiting bodies of 42 species of fungi have been recorded, has 28 restricted operations, from ‘cultivation’ and ‘mowing or cutting vegetation’ to ‘the application of manure, slurry, silage liquor, fertiliser and lime’. In Chile, after the popular edible mushroom *Butyriboletus loyo* was assessed globally as Endangered, measures were taken to ensure wild harvesting practices were more sustainable.

STRENGTHENING FUNGAL CONSERVATION

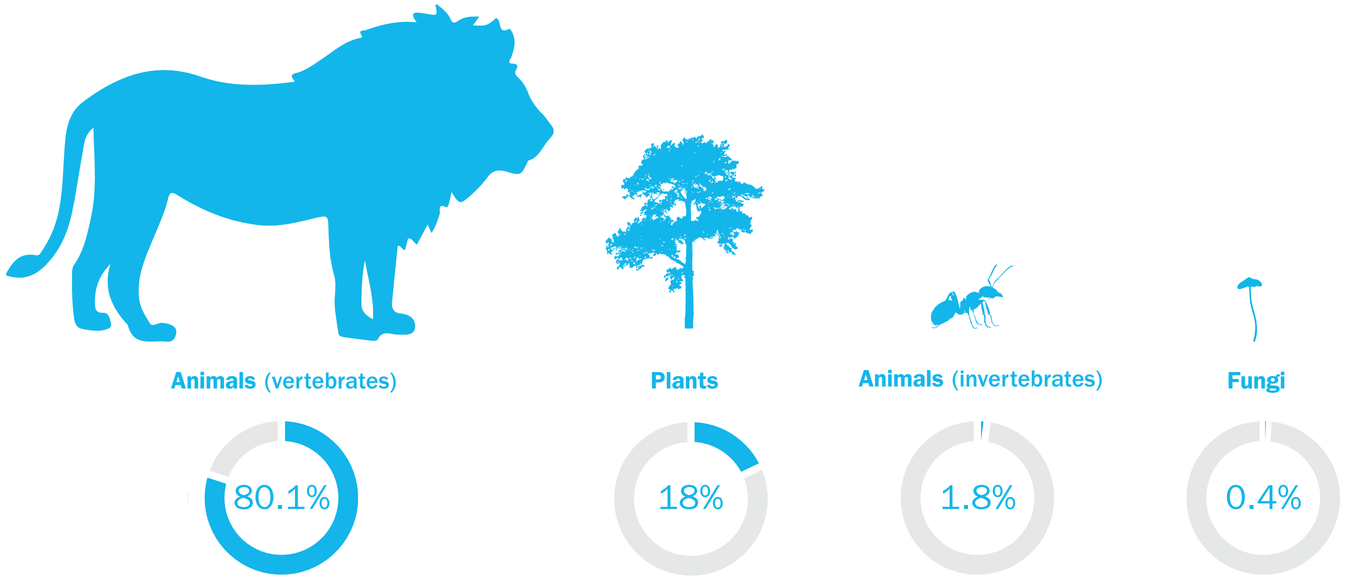
Professor Dahlberg and other scientists who reviewed the current state of fungal conservation, are calling for a two-pronged approach to prevent the decline and strengthen the protection of fungi. First, they propose that fungal conservation efforts are integrated with those to safeguard plant and animal life, and that conservation of these three kingdoms – flora, fauna and funga – is coordinated between protected areas and among countries. Second, they are calling for areas of particular conservation importance for fungi to be formally protected, with targeted management actions identified, designed and executed both inside and outside of those areas. Inside, this could include maintaining habitats to meet the particular requirements of a threatened species, while outside it might involve leaving deadwood and retaining areas of unfertilised grasslands to increase diversity.

While the scientists consider *in situ* conservation of fungi in their natural settings should be the priority, they believe that the increasing number of severely threatened habitats may call for complementary *ex situ* methods. Unlike with plants and animals, where seeds are banked and living collections of species are maintained in botanic gardens or zoos, *ex situ* conservation of fungi is still rare. Some species can be cultured, which usually involves growing them on an artificial substrate in a laboratory. Given that 40% of fungal diversity is made up of culturable fungi living on

MANY FUNGI REQUIRE SUCH LOW LEVELS OF SOIL NITROGEN THAT THEIR DIVERSITY IS THREATENED BY THE DEPOSITION OF AIRBORNE NITROGEN POLLUTION FROM COMBUSTION ENGINES.

FIGURE 1: Percentage of currently described species with IUCN Red List assessments

The number of IUCN Red List assessments for different groups of organisms varies widely. The icons for the four groups below are arranged in decreasing order, by the percentage of currently described species that have been assessed for extinction risk. Vertebrate animals are by far the most comprehensively assessed group, with IUCN Red List categories for 80.1% of known species. At the other end of the scale, we know almost nothing about fungi, with Red List assessments covering only 0.4% of currently described species (and only 0.02% of those estimated to exist).



Adapted from Niskanen et al. (2023)

dead or decaying matter, there is great potential for *ex situ* conservation – both in culture facilities and on collections of deadwood. Around 20,000–25,000 species could potentially be cultured from existing specimens held in over 800 collections around the world. Nevertheless, only 25 of the globally threatened or near threatened species are held in culture collections, highlighting a need to unite conservation aims with collecting ambitions in future.

‘Just as a germinating fungal spore accelerates its growth as it develops into a fully networked system of living filaments, the proliferation of the online network of fungal conservationists has now pushed the number of fungal species globally assessed using IUCN Red List criteria from 56 [the number cited in our 2018 *State of the World’s Fungi* report] to 625 over the last five years,’ explains Dr Martyn Ainsworth, co-author of the 2018 report. ‘This is good progress to celebrate, but it is frustrating at the same time. The reality is that we are still at the germination stage when it comes to thinking about the required levels of effort, scaling-up and automation that will be required if we are to prioritise global fungal diversity for conservation action in a timely manner.’

For the growing fungal conservation movement to continue to gain momentum and be effective, it will need more mycologists, the support of citizen scientists, and greater funding. More research on the best ways to meet the ecological requirements of threatened fungi will be vital, as will new approaches, such as using satellite imaging to understand changes in land cover. Preserving and propagating non-culturable fungi, including symbiotic species that cannot live without their evolutionary partners, may also call for novel methods. Going forward, scientists will be well placed to monitor diversity and trends in fungal populations by combining DNA ‘metabarcoding’ – already in use for identifying known and unknown species from environmental samples and helpful for tracking common and abundant fungi – with traditional manual searches for fruiting bodies of rarer species.

As new species are identified, named and placed on the fungal tree of life in the coming months and years, conservation mycologists can set their sights on ensuring that threatened species are preserved for posterity, along with the plants and animals they share habitats with. For now, while efforts to fill the large gaps in our knowledge of fungal diversity are ongoing, an additional priority is to raise awareness among the public, scientists and politicians of the vital roles that fungi play in supporting the environment, and the benefits they bring to humanity.

By inspiring and engaging an army of enthusiasts who can help shed additional light on where and how fungi live, citizen-science projects and media such as popular science books, TED Talks, documentaries and podcasts may help to conserve fungi as much as the expansion of scientific approaches and knowledge.

This chapter is based on the following peer-reviewed publication:

Niskanen, T., et al. (2023). Pushing the frontiers of biodiversity research: Unveiling the global diversity, distribution and conservation of fungi. *Annual Review of Environment and Resources*. DOI: https://doi.org//10.1146/annurev-environ-112621-090937

WHY WE ALL NEED TO TAKE EXTINCTION SERIOUSLY

In this chapter, we learn: how scientists predicted the extinction risk of all flowering plants for the first time; that three in four of the plant species yet to be described are likely to be at risk of extinction; and why the world's flora could become homogenised, with potential impacts on ecosystems and people.

45%

OF FLOWERING
PLANT SPECIES
ARE AT RISK
OF EXTINCTION

Extinction is a natural process, but pressures on plants are greater than ever.

IN AN IDEAL WORLD, WE WOULD KNOW THE EXTINCTION RISK OF EVERY PLANT SPECIES AND PRIORITISE CONSERVATION ACTIONS ACCORDINGLY.

But making assessments for all known species – which involves gathering information on variables such as population size and threats from human activities – is a considerable challenge for botanists with limited resources. Now, for the first time, scientists have used models to predict the extinction risk of every flowering plant species and identify the uncertainty level of each prediction. The findings can be used to fast-track high-risk species for assessment, helping to ensure that plants on the brink of extinction come under the protection of conservation policies. With other research suggesting that the loss of threatened species could bring about a homogenised global flora – potentially with the loss of distinctive ecosystems and the services they provide – conserving biodiversity is a concern for us all.

'We know what the symptoms of extinction risk are – narrow range, human impacts and, for some plants, life-history traits, such as how they grow and reproduce – so we can use this information in a model to try to predict the likelihood of extinction for plants that have yet to be assessed,' explains Dr Steven Bachman, Research Leader in Species Conservation at the Royal Botanic Gardens, Kew (RBG Kew). 'It is not the same as carrying out a Red List assessment, which is the gold standard for assessing the extinction risk of a species, but it does give you an indication. We had done this before for plant groups with good data, but the key difference now is that we have the World Checklist of Vascular Plants [WCVP], which has given us the opportunity to apply these models to every species. So, we used this method to look at species-level assessment across all flowering plants – which make up the majority of plants – and also calculated the degree of uncertainty around each of our predictions. Our findings indicate that 45% of flowering plant species are potentially threatened with extinction.'

GETTING THE MEASURE OF EXTINCTION

To begin their analysis, the scientists cross-referenced plant species included in the latest classification of flowering plants, and species on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with the WCVP. They arrived at a dataset of 328,565 wild flowering plant species, 60,231 of which had had their extinction risk assessed. Species assessed for the IUCN Red List are assigned to the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern or Data Deficient. After removing species assigned to the two extinct categories and grouping Data Deficient species with the unassessed species, the team were left with a robust dataset of 53,512 assessed species to use as the basis for modelling the predictors of extinction risk.

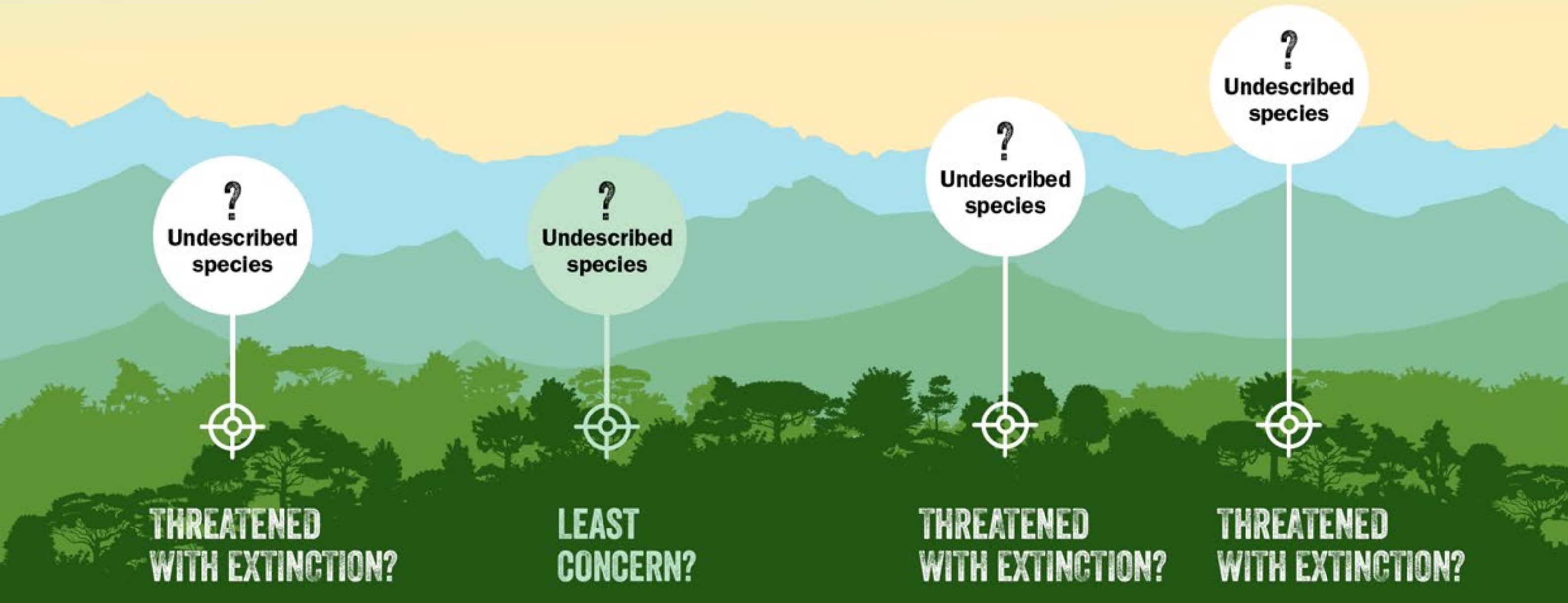
Five tried-and-tested indicators of extinction risk were selected for the analysis. These were: the number of botanical countries (see Chapter 1, Box 1) in which a species was present; evolutionary relatedness (as some research suggests closely related species may be more likely to have similar levels of extinction risk than species selected at random across the tree of life); plant form, such as woody perennial or annual; human footprint (including land-use change); and biomes, such as tropical rainforest, desert and grassland. The researchers added year of description for each species as an extra extinction predictor, based on new work indicating that recently described plants are more likely to be threatened with extinction (see Box 1). For the purpose of the study, species categorised as Least Concern or Near Threatened were grouped as 'non-threatened', and species categorised as Vulnerable, Endangered or Critically Endangered were combined as 'threatened'.

Using their derived dataset of 53,512 Red-Listed species, the scientists trained a tailor-made, probability-based model to predict the extinction risk of all unassessed or Data Deficient flowering plant species. The findings indicated that epiphytes – plants that grow on other plants, such as many bromeliads and orchids – were the most threatened plant form, while those with an annual life cycle were the least threatened. Among the largest plant families (with at least 3,000 species), the most threatened were: Piperaceae, which includes black pepper (*Piper nigrum*) – 60% of species threatened; Gesneriaceae, including the African violet (*Saintpaulia ionantha*) and several other important horticultural species – 58%; Bromeliaceae, containing the pineapple (*Ananas comosus*) – 56%; Orchidaceae, the orchid family – 56%; and Araceae, a source of important crops such as taro (*Colocasia esculenta*) – 55%. Species from tropical or sub-tropical climates were found to be more threatened than those originating in temperate or desert climes.

The six groups of extinction risk predictors were represented in the models by 85 individual indicators. Of these, the number of botanical countries in which a species was present was by far the most important single predictor of extinction risk. Global patterns in the species predicted as threatened broadly reflected those based on the current IUCN Red List. And, as with observed data, islands and archipelagos such as Hawaii, Madagascar, New Caledonia, Borneo and the Philippines emerged as hotspots of predicted threatened species. When the indicators were considered in their groups, the importance of human footprint, year of description, biome and evolutionary relatedness became more apparent (see Figure 1, overleaf). Of the 4,505 species categorised on the Red List as Data Deficient, the model predicted that 71% (3,212 species) are threatened, of which 77% were predicted with high certainty.

IN THE LARGE PLANT FAMILY PIPERACEAE, WHICH INCLUDES BLACK PEPPER (*PIPER NIGRUM*), 60% OF SPECIES WERE PREDICTED TO BE THREATENED.

3 IN 4 OF THE WORLD'S UNDESCRIBED PLANT SPECIES ARE LIKELY TO BE AT RISK OF EXTINCTION.



BOX 1: Presumed threatened unless proven otherwise

Scientists at RBG Kew are calling for all newly described plant species to be presumed threatened with extinction unless proven otherwise. Their proposal is based on the findings of a study they undertook that showed 77% undescribed plant species are likely threatened with extinction, and that the more recently a species has been described, the more likely it is to be threatened.

'We have observed more and more that newly described species are only known from a single location, or are really uncommon with very narrow ranges, so we decided to quantify this for the first time,' says Dr Eimear Nic Lughadha, Senior Research Leader in Conservation Assessment and Analysis at RBG Kew.

Scientists estimate that as many as 100,000 species of vascular plants are still to be described and named as new to science. If so, the new study findings would indicate that at least 75,000 of these are likely to be threatened with extinction. And at the current rate of species description, it could take 40 years to name all new species, by which time many could have already gone extinct.

To be formally protected, species must be noticed, described and assessed either for the IUCN Red List of Threatened Species or a similar inventory of risk. Species that have not yet been the focus of this process are likely to be overlooked in conservation prioritisation and action planning.

'Being assessed, particularly as Endangered or Critically Endangered literally changes the fate of a plant, as once its extinction risk is known, it can be prioritised for conservation,' confirms Dr Nic Lughadha. 'If adopted, our recommendation could aid in the protection of many tens of thousands of undescribed, threatened species, which, otherwise, may be lost before they are ever known to science.'

Extinction risk for newly described species

Observed proportion (red bars) and predicted probability (yellow line) of threatened species by the year in which they were described. (Adapted from Brown et al., 2023a)

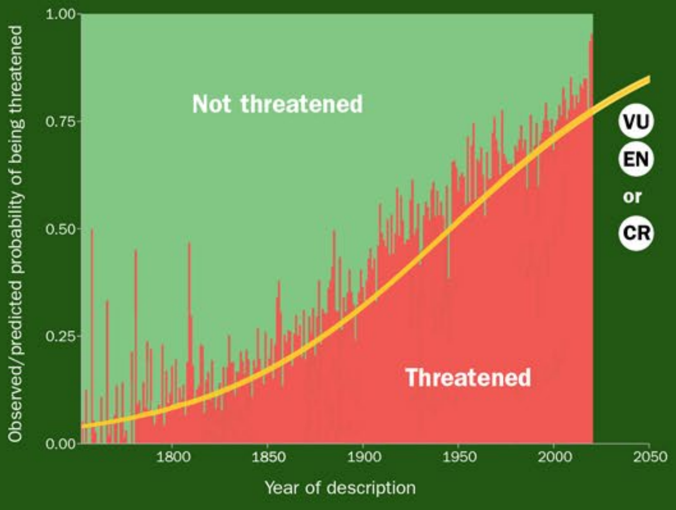
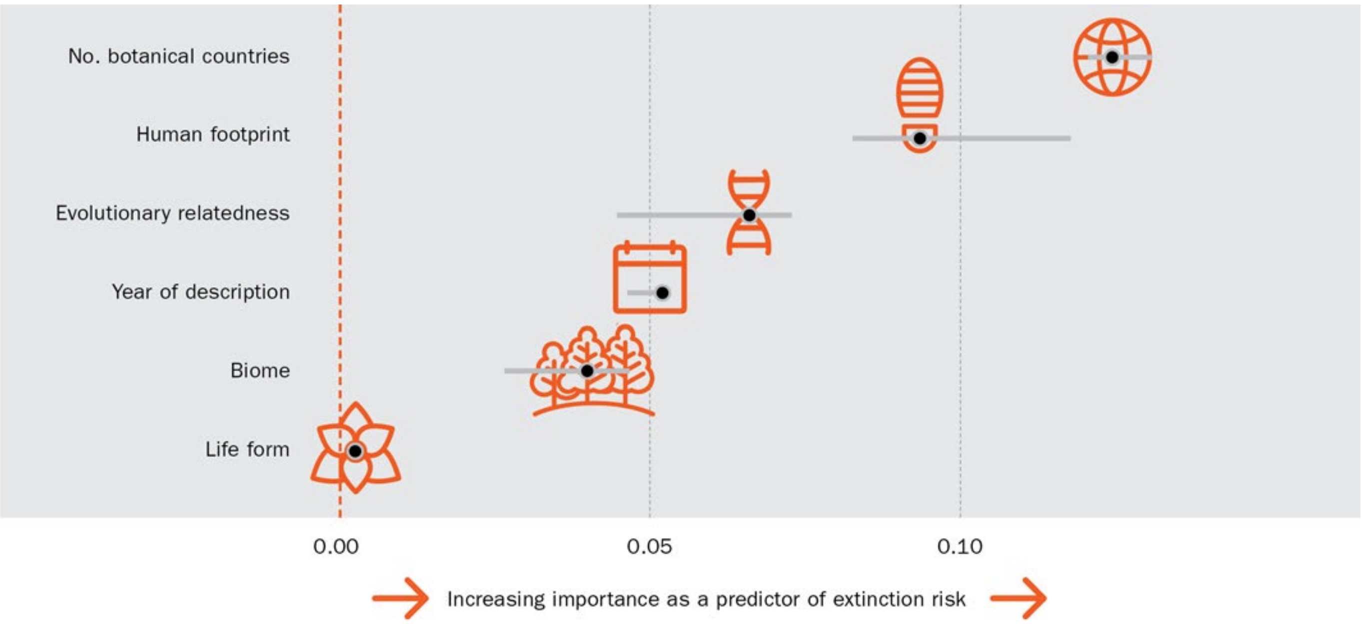


FIGURE 1: Predictors of extinction risk

The figure shows the six main types of predictors in the study and their importance, with grey bars to indicate the magnitude of uncertainty of the estimate. Eighty-five individual predictors were grouped into six classes: number of botanical countries, human footprint, evolutionary relatedness, year of description, biome (tropical forest, desert etc.), and plant life form (woody perennial, annual, epiphyte etc.).
The number of botanical countries a species occurs in (an approximation for how widespread it is) and human footprint (the degree of threat from human activities) were the top two predictors of extinction risk.



Adapted from Bachman et al. (2023)

'We hope that these findings can be used to say, "These are the species that are predicted threatened and haven't been assessed yet, and we are confident that they are good predictions, so we think that these should be priorities for full Red Listing",' explains Dr Bachman. 'Then either we develop a project to assess these species or we encourage other people to carry out these assessments. On the other side, we have the species that we are highly confident are not threatened. We have developed some tools in-house to fully automate those "Least Concern" assessments, so as soon as we understand a species is not threatened, we can automate the process of generating a near complete assessment that is enough to tick all the boxes for the IUCN and get it published as Least Concern on the Red List. By quickly dealing with these non-threatened species, we can focus our energy on the threatened ones.'

A BOTANICAL CRYSTAL BALL

As well as paving the way to speeding up conservation assessments, the extinction risk predictions are shedding light on what the future world might look like if we fail to save threatened plants. Specifically, RBG Kew scientists used the predictions to examine the role of threatened species in maintaining the world's 'phytogeographical regions' (phytoregions). These are regions of the world defined on the basis of having largely distinct assemblages of species. Some phytoregions are the result of hundreds of millions of years of geological, climatic and evolutionary processes and can even be traced back to the break-up of the ancient supercontinent Pangea, which, over time, gave rise to the current arrangement of continents seen today.

Human introductions of plant species to areas where they do not grow naturally are known to be changing the make-up of global phytoregions, but studies to date have been hampered by incomplete or biased data that have likely underestimated the contribution of extinction to this shift. To evaluate the impact arising from the loss of species either documented as, or likely to be, threatened, the researchers simulated extinction at different threat levels. They then mapped phytoregion boundaries for various scenarios of introductions and simulated extinctions, and compared these to today's phytoregions. The findings showed that the impacts of simulated extinctions included changes to the global phytoregional structure ranging from minor to extensive.

THE NUMBER OF BOTANICAL COUNTRIES IN WHICH A SPECIES WAS PRESENT WAS BY FAR THE MOST IMPORTANT SINGLE PREDICTOR OF EXTINCTION RISK.

The brook wakerobin (*Pseudotrillium rivale*) and its chromosomes (inset). Endemic to southern Oregon and northern California in the USA, it has a large genome (nearly ten times bigger than the human genome) and is listed as Vulnerable on the IUCN Red List of Threatened Species.

BOX 2: Large genomes may signal trouble for flowering plants

A flowering plant species' risk of extinction is related to the size of its genome – the full set of DNA in its cells. This is the main finding of a study led by RBG Kew in collaboration with institutions in the UK, Spain and the Czech Republic. It found mean genome size to be significantly and positively correlated with extinction risk, meaning that species with large genomes are more likely to be listed as threatened on the International Union for Conservation of Nature Red List of Threatened Species. This could provide insights into underlying drivers of extinction risk.

The study collated data on genome size and extinction risk for a representative sample of 3,250 flowering plants. They analysed these data alongside plant life form, endemism (whether a species is unique to a particular area) and climate variables. This revealed that the positive correlation between genome size and extinction risk was a feature of herbaceous but not woody species.

A further study by many of the same authors, led by scientists at Masaryk University, Czech Republic, examined the global distribution of plants by genome size and range size; the latter being a known indicator of extinction risk. The findings of this work revealed that, first, species with large ranges have small genomes but those with small ranges can have any genome size. And second, that the smallest genome sizes occur in the tropics, with size increasing generally towards the poles. However, genome size decreases again from temperate to Arctic regions in the northern hemisphere (a pattern not repeated in the southern hemisphere).

These studies indicate that genome size may have physiological links to range size and extinction risk, indicating new avenues for further research.

THE LOSS OF THREATENED SPECIES COULD SUBSTANTIALLY AFFECT GLOBAL PHYTOREGIONS, WITH A KNOCK-ON EFFECT ON EVOLUTIONARY AND ECOLOGICAL PROCESSES AT ALL SCALES.

'Humans are changing biodiversity patterns at the very highest levels, and quite a lot of those changes are leading to homogenisation,' explains Dr Matilda Brown, Conservation Science Analyst at RBG Kew. 'By carting species around the world and losing unique threatened species, we are making regions that were once really distinct much more similar, so we are blurring the edges of our global biogeographical regions – phytoregions for plants and zooregions for animals. A lot of previous work has focused on introductions of invasive species, and where extinctions have been considered, researchers have either just used the available Red List data or extinction risk predictions for a subset of species, so have missed out a big chunk of species that are likely to be threatened.'

BLURRING THE BOUNDARIES

The scenarios showed that when only plant introductions and extinctions of species already assessed as threatened were considered, the impacts on phytoregions were small. However, when the researchers also included the extinction of species predicted to be threatened in their simulations, the effect was far greater. When extinctions were limited to those species currently assessed as, or predicted to be, Critically Endangered, the shift remained relatively small, but the loss of other threatened species led to greater change. The scenarios indicated that if species likely to be Endangered or Vulnerable to extinction were also lost, then the global structure of today's phytoregions could be disrupted, leading to a more homogenised global flora than at present. It is the first evidence that the loss of threatened species could substantially affect global phytoregions, with a knock-on effect on evolutionary and ecological processes at all scales. While the chances of this happening are small, the work clearly illustrates the importance of conserving threatened plant species for maintaining the structure, distinctiveness and functioning of the world's ecosystems.

'We've demonstrated that threatened species are holding the phytoregional structure together, and that if we leave out data-poor species, which are more likely to be threatened, then we will wildly underestimate the effect that extinctions will have,' says Dr Brown. 'The worst-case scenario is that no matter where you go in the world, there is no sharp distinction between regions. We have introduced species making regions more similar – for example, the flora of New Zealand is now more similar to Europe than it is to Australia – but then we also have potential extinctions making regions less unique, so that in the extreme worst case-scenario, there's just one global phytoregion. We're not saying that will happen but, until now, it wasn't thought to be even theoretically possible. Everyone assumes that even worst-case extinctions wouldn't have that much of an effect – but our work indicates that they could, and that the consequences could be far-reaching.'

AN ISLAND LABORATORY

The island of St Helena in the South Atlantic gives a window on to what could happen at the global scale. Once an important stopping point for ships travelling between Europe and Asia, it has a large introduced flora of more than 350 species. Of its 90 native plant species, 50 occur nowhere else, and just under half have been assessed as threatened on the IUCN Red List. Most of St Helena's non-unique native species are shared with countries in the sub-Saharan African phytoregion, so St Helena was once part of this realm. Under a scenario in which introduced species were considered together with extinctions of species already assessed as, or predicted to be, endangered, a far more even distribution of shared species arose between phytoregions. The change was so great that St Helena no longer had a distinct affinity with the sub-Saharan African region but was considered to be part of the northern or Afro-Asian phytoregions.

'People aren't taking extinction seriously enough,' says Dr Brown. 'Because extinction stories are usually about obscure species, in places people have never heard of, and when they ask, "What is x species useful for?", we say, "Well, we don't know, and now it's extinct we'll never know". Those stories are never going to get through to people who don't care and who think extinction is not going to affect them. People often think they're not going to be affected by events happening somewhere else. We wanted to show that extinction is being underrated and underestimated, and that we need to do something about it.'

This chapter is based on the following peer-reviewed publications and preprints:

Bachman, S., et al. (2023). Extinction risk predictions for the world's flowering plants to support their conservation. *bioRxiv*. DOI: https://doi.org/10.1101/2023.08.29.555324

Brown, M.J.M., et al. (2023a). Three in four undescribed plant species are threatened with extinction. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19214

Brown, M.J.M., et al. (2023b). Re-evaluating the importance of threatened species in maintaining global phytoregions. *New Phytologist*. DOI: https://doi.org/10.1111/nph.19295

Bureš, P., et al. (2023). The global distribution of angiosperm genome size is shaped by climate. *bioRxiv*. DOI: https://doi.org/10.1101/2022.12.05.519116

Soto Gomez, M., et al. (2023). Genome size is positively correlated with extinction risk in herbaceous angiosperms. *bioRxiv*. DOI: https://doi.org/10.1101/2023.09.10.557053

CHAMPIONING UNIQUE PLANT SPECIES

In this chapter, we learn: that ten nations host 55% of species that grow in only one country; how wealth is no predictor for the priority a country gives to assessing the conservation status of its unique species; and that Brazil, Australia and China are the top three countries hosting the highest number of species that grow nowhere else.

Australia has a wealth of unique plant species, like this heath-leaved banksia (*Banksia ericifolia*).

THERE ARE A STAGGERING

221,399

PLANTS THAT ARE UNIQUE
TO A SINGLE COUNTRY

THEY SHOULD BE A SOURCE OF NATIONAL PRIDE – THE PLANTS THAT ARE UNIQUE TO THE COUNTRIES THEY OCCUR IN. THERE ARE A STAGGERING 221,399 OF THESE PLANTS, KNOWN AS COUNTRY ENDEMICS, WHICH MEANS THEY GROW IN A SINGLE NATION AND ARE FOUND NOWHERE ELSE IN THE WILD.

Some are extremely rare – such as the Critically Endangered Menai Strait whitebeam, *Sorbus arvonensis*, a tree that only grows on a small section of shore in North Wales in the UK. Others, such as Armenia's *Ribes armenum*, are the wild ancestors of important crops, in this case the blackcurrant. Given that their ranges are often small, they may be particularly affected by habitat destruction and climate change. Therefore, it is important for nations to understand the extent to which the unique species they host are threatened with extinction and to incorporate this information into national conservation strategies. However, a new study shows that fewer than half of the world's endemic species have had their extinction risk assessed, let alone been placed at the heart of a country's efforts to save its biodiversity.

'Endemic species form the basis for many international agreements,' says Rachael Gallagher, Associate Professor in Plant Conservation and Ecology at Hawkesbury Institute for the Environment, Western Sydney University, Australia, who led the study. 'For example, under the Convention on Biological Diversity, signatory countries must write National Biodiversity Strategy and Action Plans – and endemic species are a major focus of these. Plus, there are statutory requirements in a lot of countries for species to have protections put in place – such as the Environment Protection and Biodiversity Conservation Act here in Australia and the Endangered Species Act in the USA – and species found nowhere else on Earth are obviously pretty strong targets for conservation in those, too. But overall, we found that 58% of all country-based endemic species have no conservation assessment, amounting to 127,643 species.'

FINDING SPECIES MOST AT RISK

Conservation assessments provide key information on the population sizes and ranges of species, how their extent has changed over time, and their exposure and sensitivity to threats. Such information is needed for governments to develop plans to conserve and recover threatened species and fulfil their environmental legislative requirements. The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is often viewed as the gold standard for risk assessments, enabling species to be assigned to the categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern or Data Deficient. These and the digitally available results from other systems and standards used to assess conservation status, including regional and national assessments, are combined in a single database called ThreatSearch, hosted by Botanic Gardens Conservation International.

Dr Gallagher was motivated to investigate how many species endemic to particular countries had had their conservation status assessed after observing that the centres of diversity for many plant families lay within the boundaries of individual nations and that, therefore, the legislative responsibility for those species rested in the hands of particular governments. She and her colleagues felt that there might be a relationship between how wealthy a nation was, or the level of threat from human activities in that country, or simply the richness of unique species there, and the number of endemic plants assessed for their extinction risk. If so, global resources could potentially be directed at nations with limited assessment capabilities.

To test their hypotheses, the scientists took as their starting point spatial information in the World Checklist of Vascular Plants (WCVP). They aligned this as closely as possible to the borders of sovereign states, to arrive at 179 countries (or close equivalents, such as the island of New Guinea, where an exact match could not be achieved). Using data on endemic species from the WCVP, they assessed, for each of these nation units: the richness (number) of endemic species; the proportion of endemic plants with an extinction risk assessment included in the ThreatSearch database; the country's wealth, derived from the Inequality-adjusted Human Development Index (IHDI); and the level of threat it faced from human activities, as derived from the Global Human Modification of Terrestrial Ecosystems (GHM) database.

Of the nations assessed, 173 hosted at least one endemic species; the remaining six had none. As of July 2022, 42% of species (93,756) had a risk assessment included in ThreatSearch. The top ten countries with the highest total number of endemics were: Brazil, Australia and territories, China, South Africa, Mexico, Madagascar, New Guinea, USA (including Puerto Rico and other island territories), Colombia, and Peru (see Figure 1, overleaf). Diversity of endemic species in these countries accounted for 55% of the total endemic species richness globally. When ranked by the percentage of country endemics relative to other plants, Australia came out top (88%), followed by Madagascar (82%), and New Zealand and territories (69%). In some cases, countries may have used alternative taxonomic systems to the WCVP to classify their endemics, or their conservation assessment data were not available online or were too cursory to be included in ThreatSearch, and these and other factors can influence the figures. For example, while China and South Africa were identified in this study as having high proportions of their endemic flora assessed (at 71% and 87%, respectively), under local taxonomic systems both countries have, in fact, reported complete national assessments of their endemic flora.

The completion of threat assessments varied widely, from extremely low (less than 5% in 20 countries) to comprehensive (greater than 80% in 12 countries). On average, the rate of endemic assessment was low (34%), with some floristically diverse countries – including Australia

Brazil, which encompasses vast swathes of rainforest, hosts more unique plant species than any other country.

GLOBALLY, 58% OF ALL PLANT SPECIES THAT ARE UNIQUE TO A SINGLE COUNTRY HAVE NO THREAT ASSESSMENT.

and territories, Brazil, Mexico and Madagascar – close to or below average. Nations with fewer than 100 unique species generally had low levels of completed assessments. Among them were countries with endemics from a range of genera, such as Saudi Arabia, which hosts 87 endemic species in 43 genera but had assessed the conservation status of only one species. Completing assessments in these countries should be relatively inexpensive and achievable, particularly where resources and knowledge can be shared via international networks. Others had endemic species restricted to a few genera that are the subject of disagreements over their taxonomic classification, such as *Rubus*, *Taraxacum*, and *Hieracium* species occurring in high-latitude countries of the northern hemisphere, and many others, including *Genista*, in the Mediterranean region. Lineages in these genera typically reproduce asexually and readily hybridise, so there are differing views on the delimitation of species, which in turn affects the number of endemic species recognised. They can also be very difficult to tell apart, which can hinder work to establish their true distributions – an important part of conservation assessments.

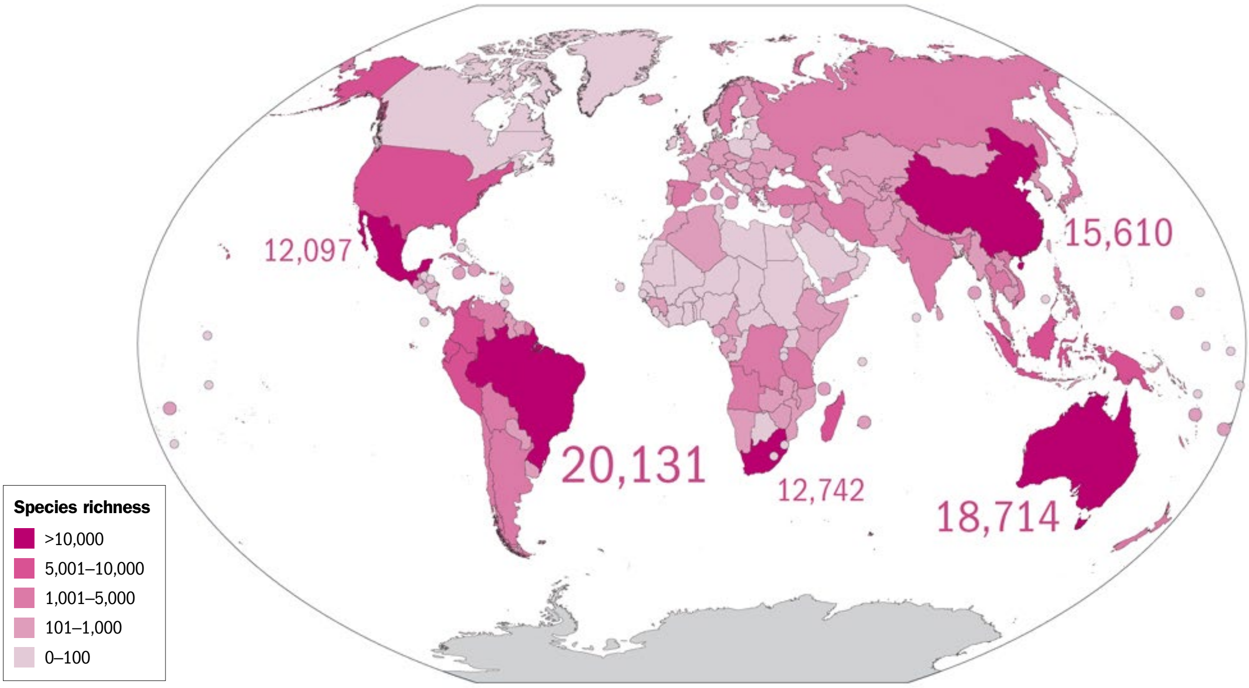
SIZE DOESN'T MATTER

Larger countries, on average, had higher numbers of endemic plant species, but some similar-sized countries supported vastly different numbers of endemics. For example, Canada and the USA, which both cover approximately 9,500,000 km^2, had 68 and 8,830 endemics, respectively. Meanwhile, Nigeria had 76 endemics versus Venezuela's 3,531, despite both extending to 900,000 km^2. Conversely, countries of different sizes exhibited similar numbers of endemic plant species in several cases. Examples include Cyprus (9,081 km^2), Ukraine (602,430 km^2), the Seychelles (514 km^2) and Switzerland (40,742 km^2), which all had around 100 endemic species. On average, island nations had two orders of magnitude more endemic plant species per km^2 than continental countries. Given that many islands are offshore components of nation states that are largely continental – such as Hawaii (USA) and Christmas Island (Australia) – some potential areas of notable species richness and endemicity may have been masked when these islands were amalgamated with continental land areas.

Somewhat surprisingly, the scientists found that a country's progress towards completing assessments for all its endemic species was unrelated to its wealth. For example, Burundi, ranked as having the world's 7th-lowest IHDI, had assessed 34 of its 38 endemics (89%), while some high-income nations, such as Japan (18th-highest IHDI) and Australia (10th-highest) had performed less well. The proportion of endemic plant species with an extinction risk assessment in a country could not be predicted by its endemic species richness, the IHDI, or the GHM metric on threat from human activities. National differences in political systems, varying levels of importance assigned to environmental issues, and the availability of external support could explain the lack of notable relationships. The high proportion of completed assessments in China, Italy, and South Africa – which all have high numbers of endemic species – demonstrated that having

FIGURE 1: The richness of endemic plants and levels of extinction risk assessments, by country

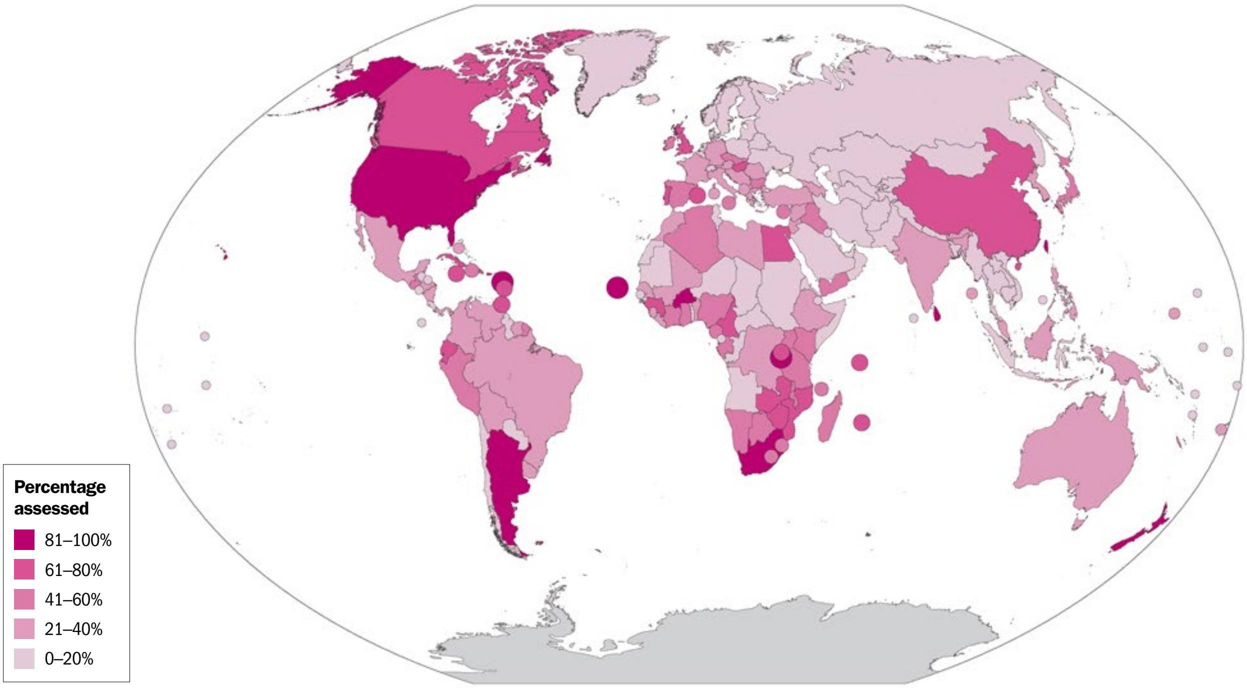
(a) Endemic plant species richness mapped by countries and their territories, with the exact number given for the five countries that have more than 10,000 unique plant species. Smaller countries and territories are depicted by circles.



Adapted from Gallagher et al. (2023)

This spot in North Wales, UK, is the only place you can find the Critically Endangered Menai Strait whitebeam (*Sorbus arvonensis*) in the wild.

(b) Percentage of endemic species in each country that have had their extinction risk assessed. Burkina Faso, Sri Lanka, Burundi, New Zealand, South Africa, Argentina and the USA have assessed >85% of their flora, according to ThreatSearch. Smaller countries and territories are depicted by circles.



Adapted from Gallagher et al. (2023)

This striking species, *Echium wildpretii* is endemic to the Canary Islands, mostly growing around Mount Teide in Tenerife.

large numbers of unique species need not impede progress in making conservation assessments.

‘The findings are good and bad, but the fact that an economic indicator like the Human Development Index doesn’t predict how many endemic species you have assessed is a real testament to low-income countries,’ says Dr Gallagher. ‘That has partly come about through initiatives run by the Royal Botanic Gardens, Kew, which has provided funding for and trained people in other parts of the world to carry out extinction risk assessments. Also, I know that in South Africa, which includes the Cape Floristic Region of extreme diversity and endemism, there is a sense of camaraderie and care about the flora among botanists. They split it into different groups and said, “I’ll do this group if you do that group”. It’s been a case of putting their nose to the grindstone and getting it done. Meanwhile, in China, which funds biodiversity research via the Chinese Academy of Sciences, assessing extinction risk to all its flora is seen as a primary task that must be done, and resources are committed for doing it.’

ACCELERATING PLANT CONSERVATION

Plants are fundamental to terrestrial and aquatic ecosystems, as well as underpinning many human livelihoods. *The Global Strategy for Plant Conservation 2011–2020* aimed to provide ‘an assessment of the conservation status of all known plant species, as far as possible, to guide conservation action’, but a substantial shortfall in threat assessments remains. As of 2020, only 28% of all known plant species had been recorded as having any kind of conservation assessment, and as of 2022 only 18% of known plant species had IUCN Red List assessments. Using machine learning to analyse the vast datasets of plants and their threats, such as from herbarium specimens and remotely sensed images, could help to speed up the assessment process. Without a comprehensive list of at-risk species, governments simply cannot prioritise and take effective action to conserve biodiversity.

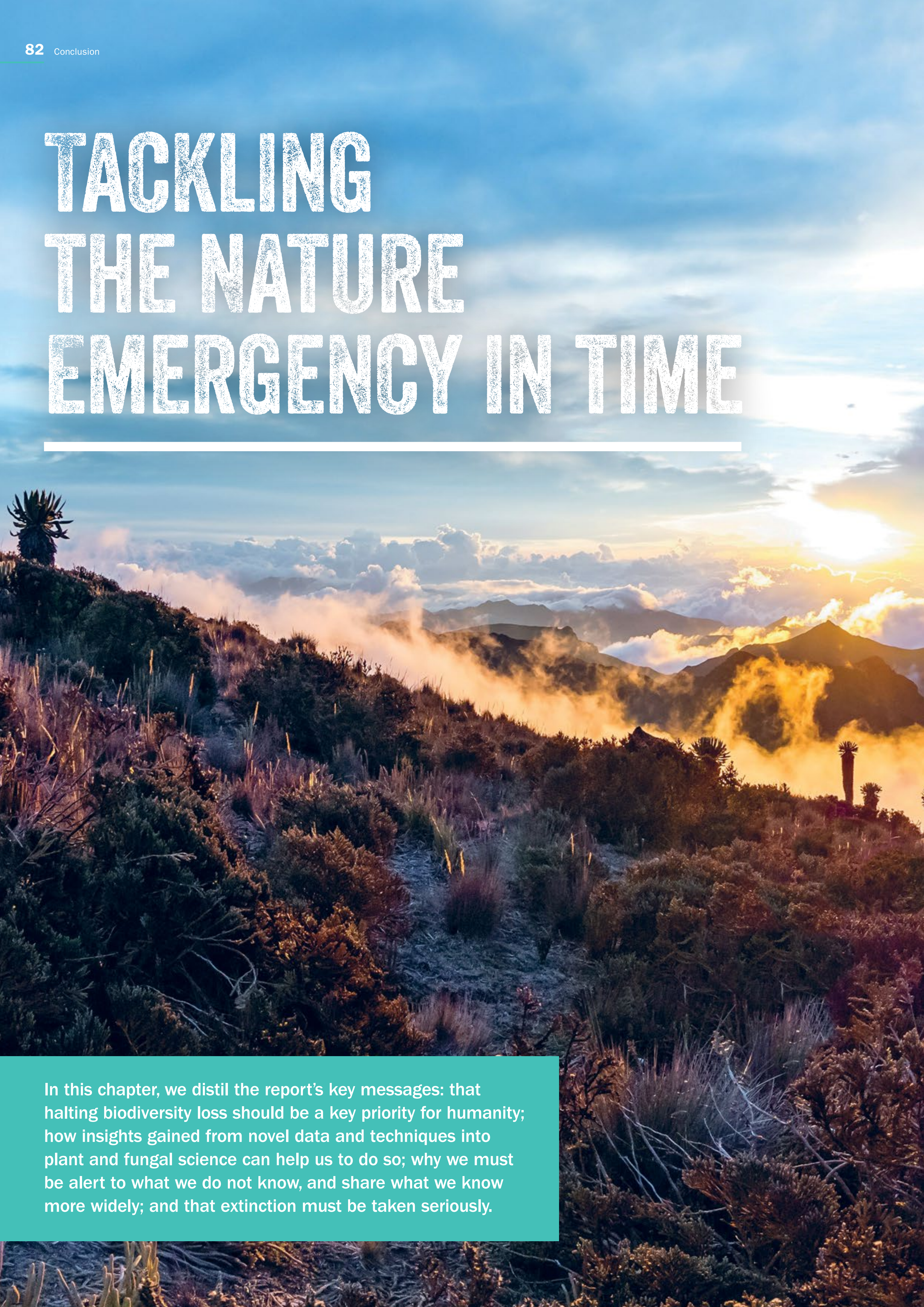
Efforts to assess plant species are gathering pace, however. For example, the Global Tree Assessment, an initiative of Botanic Gardens Conservation International and the IUCN Species Survival Commission Global Tree Specialist Group, has resulted in 80% of tree species being assessed. The initiative, which began in 2015 and aims to have all tree species assessed for the IUCN Red List, has so far found that 31% of tree species are at risk of extinction, paving the way for these to be better protected. It has also designed and implemented a rapid assessment methodology for trees of low conservation concern that are widespread, occur in multiple countries, and are well represented in botanical collections. Similar systematic approaches to making conservation assessments are needed to underpin national strategies for non-tree species (see also Chapter 9).

‘Applying an approach similar to the Global Tree Assessment would be fantastic,’ says Dr Gallagher. ‘It could be applied by focusing on countries that are prioritised based on the number of endemics they have and their rate of assessing them. It could potentially be applied first through a conservation assessment training programme for botanic gardens’ staff, who often undertake the taxonomic work that underpins such assessments. But it would also be really nice to raise awareness of endemics generally, perhaps by encouraging children and their parents to come up with common names for unique species that don’t have them at the moment, or to draw them. Showing people about the beauty and benefits that come from their unique national flora can help to engage them about the wonder of plants – and could also help generate much-needed philanthropic support to fund more extinction assessments – which, after all, is the first step towards conserving biodiversity.’

This chapter is based on the following peer-reviewed publication:

Gallagher, R.V., et al. (2023). Global shortfalls in threat assessments for endemic flora by country. *Plants, People, Planet*, 1–14. DOI: https://doi.org/10.1002/ppp3.10369

WITHOUT A COMPREHENSIVE LIST OF SPECIES AT RISK, GOVERNMENTS SIMPLY CANNOT PRIORITISE AND TAKE EFFECTIVE ACTION TO CONSERVE BIODIVERSITY.



TACKLING THE NATURE EMERGENCY IN TIME

In this chapter, we distil the report's key messages: that halting biodiversity loss should be a key priority for humanity; how insights gained from novel data and techniques into plant and fungal science can help us to do so; why we must be alert to what we do not know, and share what we know more widely; and that extinction must be taken seriously.

Plants and fungi form the building blocks of our habitable Earth; we lose them at our peril.

WE HAVE ONE LAST CHANCE TO SAVE THE BIODIVERSITY WE ALL DEPEND ON

IT IS IMPERATIVE THAT WE TAKE ACTION TO TACKLE THE CURRENT NATURE CRISIS, FOR THE SIMPLE REASON THAT ALL LIFE ON EARTH DEPENDS ON BIODIVERSITY.

The resources and services that nature provides – from food to fresh water – have arisen through eons of ecosystem-building by microbes (including fungi), plants and animals, and their interactions with geochemical processes. Because we are currently degrading ecosystems, releasing greenhouse gases into the air and polluting water resources at such a rapid rate, we risk destabilising the global equilibrium that these evolutionary processes have established. Effectively managing the plants and fungi that form the building blocks of our habitable planet is key to halting wider biodiversity loss and restoring Earth's ecosystems to full function.

UNDERSTANDING EVOLUTION'S PATTERNS

Acting as effective environmental stewards requires us to first know what it is we are managing. Thanks to the newly available taxonomic and geographical data in the World Checklist of Vascular Plants (WCVP) and groundbreaking work by mycologists to understand the global diversity of the vast fungal kingdom, we are beginning to form a better idea of what species there are and 'what grows where, and why', particularly with regards to wild plants. For example, the research presented in this report confirms current climate to be the key driver behind how wild woody and herbaceous plants are distributed across Earth's surface, with implications for how trees, shrubs and herbs will shift under human-induced climate change. But other factors, such as geology, past periods of climate change, and evolutionary history, including the animals with which plants co-evolved, are also demonstrated to be major influences on where we find plants exhibiting particular life and growth forms.

As we have also highlighted, using genomic techniques to build evolutionary trees for plants and fungi, and combining these with geographical and geological data, is enabling scientists to delve deeply into the underlying history that shaped the patterns of species distribution we see today – and also to predict how they might respond when new opportunities or pressures arise. This work has shown, for example, that, although the highly diverse orchid family originated 83 million years ago in the northern hemisphere, a substantial proportion of the species we see across Earth today arose through rapid bursts of speciation within the past five million years, concentrated within the southern hemisphere. New insights have emerged about the complex history of cycads and figworts, too, and such work is being carried out all over the globe on other plant families and different groups of organisms. Expanding this global effort further using ever-advancing technologies will, eventually, enable us to understand the entire tree of life.

CONSERVING OPTIMAL DIVERSITY SPOTS

Being able to interpret species distributions through the lens of their evolutionary history is enabling scientists to think afresh about the best ways to manage plants and fungi now and in the future. One important insight that has been reinforced in this report is that focusing conservation actions only on areas with the highest number of species per area is suboptimal. We need to expand the use of sophisticated approaches, including those that also take into account evolutionary history. For example, considering the number of branches of the tree of life represented in an area, alongside species richness, is critical when prioritising sites for conservation. Ecosystems with lots of distantly related species that have evolved over a long period of time are more likely to have a wider array of traits, which can give them greater resilience to environmental change. So, ensuring we save these species can help us to minimise biodiversity loss.

OVERCOMING DIVERSITY DATA DARKSPOTS

When addressing how to optimise conservation approaches for plants, we must not only be mindful of what we know but also what we do not (yet) know: the darkspots of diversity. This is because there are inherent and pervasive biases and data gaps within plant description and distribution data. These have arisen due to historical legacies of how plant science developed over time and across different parts of the world; the choices botanists have made around what species to collect and from where; the uneven distribution of wealth and expertise; and issues of physical access and associated logistical challenges. This report has identified shortfalls in plant descriptions from tropical Asia and South America, and in plant distribution data across most continents, with large gaps in Myanmar, the Indian state of Assam, Colombia and Vietnam. It has also shown that trait data, vital for understanding how ecosystems function, is also incomplete and spatially biased in favour of the Global North.

The most species-rich areas are often located in low- and middle-income countries; Brazil, China, Colombia and Mexico all rank in the top five countries for the number of plant species. If data biases are to be filled, then such botanically important nations need access to all the available taxonomic data. But a decade after the botanical community adopted electronic publication, with the aim of making plant diversity information more accessible, a study by researchers from the Royal Botanic Gardens, Kew, Meise Botanic Garden, Belgium, and the Natural History Museum, London, revealed it had yet to make a real difference in the open availability of this information. The study found that 41% of new species publications between 2012 and 2021 were in literature that remained undiscoverable by electronic means – due to works being published in hard copy only, or to a lack of identifying data making it challenging to search for, retrieve and re-find records. In addition, only 23% were published in open-access literature.

The authors of the study called for journals that publish primary biodiversity information to consider extending current waivers of open-access publishing fees to comprehensively include all low- and middle-income countries. They also highlighted the need to accelerate the mobilisation of specimen metadata and images from collections in botanically

All species, including this desert rose (*Adenium obesum*), have a part to play in the functioning of ecosystems.

BEING ABLE TO INTERPRET SPECIES DISTRIBUTIONS THROUGH THE LENS OF THEIR EVOLUTIONARY HISTORY IS ENABLING SCIENTISTS TO THINK AFRESH ABOUT THE BEST WAYS TO MANAGE PLANTS AND FUNGI NOW AND IN THE FUTURE.

Being effective environmental stewards requires us to know what it is we are managing, but accessing biodiversity can be challenging.

diverse countries, to help build taxonomic capacity where it is needed most.

The data gaps inherent in fungal collections are even greater than those hindering botanical research. Nonetheless, the updated estimate for the number of fungal species of 2.5 million that we report gives us a glimpse of the grand challenge to find, name and describe all those species – to achieve a step change in progress towards understanding their biological interactions, ecological roles and potential uses by humankind. Using business-as-usual methods to do so would take centuries, hence the outlined proposal to adopt a new method for finding and identifying fungi that capitalises on the rapid processing power of genetic technologies until physical specimens can be found, and cultured or preserved for further studies.

Likewise, new approaches to biodiversity conservation and ecosystem management that explicitly incorporate the protection of threatened fungi are needed. In some cases, where plants and fungi grow together, it makes sense to align fungal conservation strategies with those of plants. However, the differences in plant and fungal distribution patterns, captured in the new map presented in this report, mean some fungi will also need targeted conservation efforts, and should be considered independently when designating protected areas. Fungal conservation will also require specific actions to be taken, such as to prevent or limit the input of nutrients to species-rich grasslands, in which many threatened fungi thrive.

FORECASTS FOR SAFEGUARDING BIODIVERSITY

Understanding extinction is critical to conserving biodiversity, but unless we increase the current rate of scientific naming, we are in danger of losing species before they have been described. Research in this report has provided, for the first time, an estimate of the risk of extinction for each flowering plant species, along with the uncertainty associated with that prediction. While automated predictions using machine learning are no substitute for the established process of making detailed conservation assessments, and thereafter adding those species to the International Union for Conservation of Nature's Red List of Threatened Species, such predictions can help botanists prioritise species that should be urgently assessed.

If we are to safeguard biodiversity in order to keep Earth's crucial systems functioning, everyone must play their part. Citizen scientists are already helping experts to fill in gaps in fungal knowledge, but there is potential to engage people more with the natural world by highlighting the unique plants that almost every country has. An enthused and motivated populace is needed to provide a new generation of planetary stewards. Meanwhile, the findings from this report, informed by robust new plant and fungal data, provide clarity for scientists on what drives the patterns of biodiversity we see on Earth today and, with it, fresh understanding to inform better conservation decisions. The glimpse of what could happen if we lose too many species – a homogenised global flora and ecosystems unable to provide the resources we need – underlines the urgency of halting biodiversity loss, sustainably managing ecosystems and re-stabilising planetary systems while we still can.

This chapter is a summary of the peer-reviewed publications and preprints cited in the preceding chapters of the report, with the addition of the following:

Nicolson, N., et al. (2023). Global access to nomenclatural botanical resources: Evaluating open access availability. *Plants, People, Planet*. DOI: https://doi.org/10.1002/ppp3.10438

Taking action for a biodiverse planet

State of the World's Plants and Fungi 2023 is co-released with a collection of papers published by *New Phytologist* and *Plants, People, Planet*, titled 'Global Plant Diversity and Distribution'. Data and information on fungi comes from a review of global fungal diversity in the *Annual Review of Environment and Resources*. The research in these publications provides a robust, evidence-based foundation for the report, which is launched in tandem with an international hybrid symposium at RBG Kew from October 11–13, 2023: 'Tackling the Nature Emergency: Evidence, gaps and priorities'. The report, along with discussions and workshops at the symposium, will shape the way for a declaration outlining specific actions to be taken to galvanise research and collecting effort as we work together to deliver on the goals of the Kunming-Montreal Global Biodiversity Framework and tackle the Nature Emergency head on.

AN ENTHUSED AND MOTIVATED POPULACE IS NEEDED TO PROVIDE A NEW GENERATION OF PLANETARY STEWARDS.

RBG Kew's education programme is helping to inspire young people to become guardians of biodiversity.

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