Plant diversity darkspots for global collection priorities

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Summary:

- More than 15% of all vascular plant species may remain scientifically undescribed, and many of the >340,000 described species have no or few geographic records documenting their distribution. Identifying and understanding taxonomic and geographic knowledge shortfalls is key to prioritising future collection and conservation efforts.
- Using extensive data for 343,754 vascular plant species and time-to-event analyses, we conducted multiple tests related to plant taxonomic and geographic data shortfalls, and identified 29 global diversity darkspots (regions expected to lack most information about their species diversity and distribution by 2050). We defined priority regions for future collection according to several socio-economic and environmental scenarios.
- Our understanding of the global diversity and distribution of vascular plant species is estimated to remain incomplete and biased by 2050 under current collection patterns. Most plant diversity darkspots are found within biodiversity hotspots, except New Guinea. We identify the Philippines, Myanmar, Assam, Bangladesh, East Himalaya, Iran, Turkey, Colombia, and Peru, as global collection priorities under all environmental and socio-economic conditions considered.
- Our study provides a framework to accelerate plant species documentation for the implementation of conservation actions. As digitisation of the world's herbaria progresses, collection and conservation priorities may soon be identifiable at finer scales.

5-8 keywords: area prioritisation; biodiversity hotspots; conservation; geographic distribution; Linnean shortfall; species scientific description; sustainable development; Wallacean shortfall.

INTRODUCTION

Biodiversity is declining worldwide, posing a direct threat to planetary health (Díaz *et al.*, 2019). The recently adopted Kunming-Montreal Global Biodiversity Framework (GBF) aims to facilitate the implementation of biodiversity-positive actions across all of society to achieve the vision of "people living in harmony with nature" by 2050. In this context, plant scientists have a key role to play by providing essential data, tools and evidence to decision-makers through improved documentation and understanding of this vital facet of biodiversity. A major scientific milestone in this pursuit is the compilation of names and geographic distributions of nearly 345,000 taxonomically accepted vascular plant species by the World Checklist of Vascular Plants (WCVP; Govaerts *et al.*, 2021). The burning questions now are how many species remain to be scientifically described, and where and how to concentrate efforts to safeguard global plant diversity into the future (Pimm & Joppa, 2015).

In an attempt to categorise our knowledge limits, six biodiversity shortfalls have been described to characterise data gaps (Hortal *et al.*, 2015). Two of these shortfalls concern species' scientific descriptions and geographic distributions, commonly referred to as the Linnaean and Wallacean shortfalls, respectively (Hortal *et al.*, 2015). The Linnaean shortfall is assumed to be large, with >60,000 angiosperm species estimated to not have been scientifically named yet (Joppa *et al.*, 2011). Moreover, and in contrast to vertebrates (Moura & Jetz, 2021), little is known about the diversity and distribution of undescribed vascular plant species. Although WCVP provides comprehensive distribution data for most known species at a coarse resolution (i.e., "botanical countries"), major biases and gaps have been shown to nurture the Wallacean shortfall at a finer resolution (Meyer *et al.*, 2016). This in turn impedes thorough characterisation and understanding of the full geographic range of individual plant species and their diversity.

Assessing the magnitude and spatial variation of both the Linnaean and Wallacean shortfalls is thus key for developing collection strategies. Historical collections have been biased spatially by land accessibility, the density of taxonomists, and both environmental and socio-economic factors (Meyer *et al.*, 2016). However, there is no current measure of whether ongoing botanical surveys are being conducted in the places that need them most, or whether they accentuate biases in botanical knowledge (Geldmann *et al.*, 2016). It is also important to note that the classification, distribution, and ecology of plants are held extensively in non-western traditional knowledge systems, in which similar shortfalls may not necessarily be quantifiable at large spatial scales (Gardner *et al.*, 2022).

Nearly 40% of described vascular plant species are estimated to be threatened globally (Nic Lughadha *et al.*, 2020), and there is a risk that some may go extinct before being described (Roberts *et al.*, 2016). Biodiversity hotspots, originally defined as regions containing exceptionally high concentrations of rare and endangered plant species, were conceptualised as a means to identify priority areas for conservation (Myers *et al.*, 2000; Mittermeier *et al.*, 2011). However, biodiversity hotspots and other more recent mapping efforts (e.g., Jung *et al.*, 2021; Cai *et al.*, 2023) have given relatively little consideration for taxonomic and geographic knowledge shortfalls. This in turn has the potential to misguide conservation actions, as newly described species are more likely to be threatened than others (Roberts *et al.*, 2016), and a lack of species geographic data may result in both hotspot misidentifications (Meyer *et al.*, 2015) and inaccurate estimates of extinction risk (Morais *et al.*, 2013). While the use of an early version of WCVP has shown that biodiversity hotspots may be housing most undescribed plant species (Joppa *et al.*, 2011), a thoroughly updated and joint consideration of taxonomic and geographic shortfalls could point towards new perspectives for collection and conservation.

Sampling effort is shaped indirectly by a wide array of environmental and socio-economic conditions (e.g., poverty, security, climate, topography, levels of environmental protection; Mair, 2016). These factors can sometimes represent insurmountable barriers to botanists, potentially making regions with the largest taxonomic and geographic knowledge gaps unrealistic targets for collection efforts, especially when considered alongside the relatively limited resources available to botanical organisations. However, regional socio-economic and environmental contexts are rarely considered when quantitatively assessing areas for collection (and conservation) prioritisation (but see Meyer *et al.*, 2016). Accounting for regional opportunities and challenges is thus key to develop collection strategies that facilitate describing the most species possible, while also accounting for – and whenever possible helping to address – social and environmental issues of importance to civil society and botanists (Pascual *et al.*, 2021).

Here, we pursue the challenge of accelerating the description of plant diversity by assessing taxonomic and geographic shortfalls, using WCVP and the Global Biodiversity Information Facility (GBIF) as key data sources, and a suite of analytical methods. We specifically test (Q1) whether areas with the largest estimated taxonomic and geographic gaps overlap; (Q2) what attributes are most associated with the early description and geolocation of vascular plant species; and (Q3) whether global collection efforts of the previous decade have been concentrated in areas representing the largest expected shortfalls in the future. Inspired by the concept of “dark taxa” (DNA sequences not identified to the species level; Page, 2016), we

combine our estimates of taxonomic and geographic shortfalls to define plant diversity "darkspots" as areas housing most undescribed and poorly geolocated species, and assess (Q4) whether darkspots could become hotspots with increased taxonomic and geographic sampling efforts. Finally, we explore (Q5) a range of collection priority scenarios informed by a combination of key environmental and socio-economic drivers. Our results indicate substantial opportunities for revisiting plant collecting strategies to support the equitable conservation, sustainable use, and benefit sharing of the world's plant diversity in line with the GBF.

MATERIALS AND METHODS

We analysed historical and geographical patterns of description and geolocation of vascular plant species across *botanical countries* of the world, as defined by level 3 of the World Geographical Scheme for Recording Plant Distributions (WGSRPD; Brummitt, 2001). We used a time-to-event analysis (Moura & Jetz, 2021) to predict the number of vascular plant species remaining to be described and geolocated in each botanical country by the year 2050 (i.e., the year of the visionary goals of the GBF) as a function of several species attributes (i.e., climatic and geographic ranges, uses by humans, interest from taxonomists). Then, we identified areas where both Linnaean and Wallacean shortfalls coincide (Q1); and species attributes driving these patterns (Q2).

Subsequently, we used a skyline modelling approach (Gjesfjeld, 2020) to compute past description and geolocation rates through time in each botanical country. We then tested whether our estimates of the potential number of undescribed and non-geolocated species by 2050 are correlated with the collection rates of the previous decade across all botanical countries (Q3). Furthermore, we identified darkspots as areas containing the largest taxonomic and geographic shortfalls and assessed their (mis-)matches with known biodiversity hotspots (Q4). Finally, we characterised the socio-economic and environmental contexts of each botanical country using the United Nations' Sustainable Development Goals (SDGs) indicators and a Principal Component Analysis (PCA). We then identified priority botanical countries for both the description of new species and the geolocation of known species under nine scenarios accounting for regional opportunities and challenges (Q5).

Taxonomic and geographic data

WCVP (Govaerts *et al.*, 2021) is a comprehensive global database that collates and reconciles information about most known vascular plant species from peer-reviewed literature, authoritative scientific databases, herbaria and observations; all of which is then curated by expert reviews. We used it to retrieve information on species nomenclature, synonymy, year of first global scientific description (*sensu* Linnaean taxonomy; DuBay *et al.*, 2022), and geographic distribution at the botanical country level. Our study included only species with accepted names and excluded hybrids, resulting in a list of 343,754 vascular plant species. We obtained geo-referenced occurrence records for each of these species from the Global Biodiversity Information Facility (GBIF). Data was accessed through the Microsoft Planetary Computer (MPC) platform, a cloud computing environment with a catalogue of global spatio-temporal datasets (https://planetarycomputer.microsoft.com/; GBIF.org [01 March 2022] GBIF Occurrence Download, https://doi.org/10.15468/dl.nqbg5v).

We used exact-matching to link species names in GBIF's taxonomic backbone to species in our WCVP list. We only kept names that matched directly with an accepted name or through homotypic synonymy. We used the metadata information provided by GBIF and functions from the *CoordinateCleaner* R package (Zizka *et al.*, 2019) to exclude fossil occurrence records, records with common georeferencing mistakes, records with coordinates close to botanical institutions and GBIF headquarters, and duplicated records based on longitude, latitude and year of collection. We removed all records outside each species' native range according to WCVP. Our final dataset included >121 million occurrence records for 249,521 vascular plant species (c. 70% of our list of species retrieved from WCVP) across 449 families and 363 out of 369 botanical countries. For each species, we then extracted the year of collection of the first record found within each botanical country.

Species-level explanatory variables

We considered eight variables that could affect the time to the description of a new species and the time to the geolocation of a species already described: annual mean temperature (AT), annual precipitation (AP), temperature seasonality (TS), precipitation seasonality (PS), elevation (E), range size (RS), taxonomic activity (TA) and number of uses by humans (USE). For further details about the selection and compilation of these variables, please see Supporting Information (SI) Methods **S1a**.

To avoid collinearity issues in further modelling efforts, we detected highly correlated pairs of predictors (i.e., with a Pearson correlation coefficient higher than 0.7) and excluded the one of the pair with the greater Variance Inflation Factor (VIF; Zuur *et al.*, 2010). As such, we excluded AT and all remaining predictors were then centred at their sample means and scaled by their sample standard deviations within their respective botanical country to help improve the inference of model parameters.

Future taxonomic and geographic shortfalls

We fitted two parametric proportional hazard (PH) regression models with two different response variables: (i) the number of years between 1759 (i.e., six years after Linnaeus' first edition of Species Plantarum and one year after the publication of Linnaeus' 10th edition of Systema Naturae) and the description of species *i* ($T_{i,desc}$), and (ii) the number of years between the description of species *i* and its first recorded occurrence point in botanical country *k* ($T_{k,i,geoloc}$). For both models, we only considered species descriptions and geolocations up to the year 2021. We did not fit any model for Antarctica because it contained observations for only three species.

Since the year of geolocation is not available for all records, $T_{k,i,geoloc}$ is considered *censored* (i.e., partially observed), which has been accounted for to allow for valid estimation of the model parameters (Hosmer *et al.*, 2008) (see Supporting Information (SI) Methods **S1b**).

We used the Stan probabilistic programming language (Carpenter *et al.*, 2017) through the *rstanarm* package (Goodrich *et al.*, 2020) to fit these models in a Bayesian framework, using $T_{i,desc}$ and $T_{k,i,geoloc}$ as response variables, AP, TS PS, E, RS, TA and USE as explanatory variables and the default Hamiltonian Monte-Carlo (HMC) sampler (Hoffman & Gelman, 2014) (for more details about the models' parameterisation see SI Methods **S1c**). We ran three chains with 15,000 iterations, discarding the first 5,000 iterations as warm-up, leaving 10,000 iterations as posterior samples. We assessed convergence using trace plots and the Gelman-Rubin diagnostic statistic (Gelman & Rubin, 1992), where values < 1.1 indicate adequate convergence.

The goodness of fit of both models was assessed using an integrated Brier score (iBS), which quantifies predictions accuracy over a given time period (see SI Methods **S1d**). iBS=0 indicates perfect accuracy of the model's predictions, while iBS=1 indicates perfect inaccuracy.

We used the posterior samples of the models' parameters to generate proportions of species remaining to be described and geolocated by the year 2050 for each botanical country (for more detail about the procedure, see SI Methods **S1e**).

We used the predicted proportion of species remaining to be described to estimate the potential number of species awaiting scientific description by the year 2050 as follows:

$$N_k^* = N_k^{tot} - N_k$$

$$N_k^{tot} = \frac{N_k}{Prop_k}$$

$$\frac{N_k}{N_k^{tot}} = Prop_k$$

where, N_k^* denotes the number of species remaining unknown by 2050 in botanical country k, N_k^{tot} and N_k denote the total and currently known number of species in k, respectively, and $Prop_k$ denotes the aforementioned expected proportion.

To determine the potential number of species still awaiting geolocation by 2050, we calculated the number of species expected to occur in each botanical country according to WCVP, but with no valid occurrence records, then we multiplied this number by the expected proportion of species non-geolocated in 2050.

To facilitate comparison between botanical countries of different areas, we generated a second set of predictions rescaled to a fixed area of 10,000 km^2 following (Brummitt & Lughadha, 2003) (SI Fig. S1-S6 and SI Fig. S8-S17).

Effect of species characteristics

We extracted and exponentiated the regression coefficients of our PH models from each botanical country to obtain hazard ratios (HRs) for each predictor variable. If HR=1, there is no effect of predictor variable *p*, if HR>1, an increase in *p* increases the chance of a species being described or geolocated, and if HR<1, an increase in *p* decreases this chance. Therefore, HRs allow to assess how and how much each species individual characteristic influences their description and geolocation.

Past collection efforts

We used the software LiteRate (Koch *et al.*, 2020) to fit a piecewise-constant model and jointly infer the rates of description and geolocation and the number and temporal placement of shift points (Silvestro *et al.*, 2019; Gjesfjeld, 2020). The method uses a reversible-jump Markov chain Monte Carlo (rjMCMC) and its output can be used to obtain marginal rates through time that account for model uncertainty (Silvestro *et al.*, 2019).

As inputs, we used the date of first scientific description and earliest geolocation in each botanical country. Species expected to be present in the botanical country according to WCVP but not found in our GBIF occurrence data were considered not yet geolocated. We used a Poisson-death process to estimate the rates of species description (expected number of newly described species per year) and first geolocation within a botanical country (expected number of newly geolocated species per year among those already described).

We ran the analyses for each botanical country for 1.2 million rjMCMC iterations, sampling every 1,000 iterations. After assessing the convergence of the chains and excluding the first 20% of the samples as a burn-in, we averaged marginal rates across the period 2010-2019 (avoiding data collection biases caused by the COVID-19 pandemic). Mean collection trends from 2010-2019 were then correlated with data gaps predicted for 2050 for both species description and geolocation using Kendall's correlation in R package gpubr v.0.4.0.

Darkspots and hotspots

To identify (mis-)matches between global biodiversity hotspots and the Linnaean and Wallacean shortfalls, we first obtained the geographic distribution of the 36 biodiversity hotspots from Hoffman (2016). To identify darkspots, we rescaled our Linnaean and Wallacean shortfalls estimates between 0 and 1, and summed their values to calculate a "darkspot score" ranging between 0 (i.e., smallest taxonomic and geographic knowledge gaps) and 2 (i.e., largest taxonomic and geographic knowledge gaps). To avoid arbitrary cut-offs and allow for a direct surface comparison, we categorised darkspots as botanical countries exhibiting the highest darkspot scores and a total cumulative land area equivalent to that of the 36 biodiversity hotspots.

Collection priorities

To characterise the average socio-economic development state of each botanical country, we used indicators monitoring progress towards all 17 SDGs from https://sdgs.un.org/goals. These relate to factors potentially impacting botanical expeditions, such as infrastructure and accessibility, security, access to vital resources, poverty, social inequalities, partnerships, levels of education and protection of the environment. Given the SDG data is unavailable at sub-national scale, we assigned national values to botanical countries representing regions within countries.

The SDGs are all interlinked; therefore, we used a Principal Component Analysis (PCA) to summarise the variation in all SDG indicators across botanical countries. The first two Principal Components (PCs) explained 66.63% of the variance in the data (SI Fig. S2), and were used to determine our collection prioritisation scenarios. PC1 (hereafter, “income group”) reflected variation in indicators associated with SDGs 1-13 and 16-17, and PC2 (hereafter, “environmental protection”) was mainly associated with variation in SDGs 14 and 15.

We assume that botanical countries with high income and infrastructure will have a large potential to document their floras using their own resources. In contrast, prioritising botanical countries with lower income and a high potential for undescribed plant diversity can be used to highlight areas where the global community may need to join forces to support the country’s poverty alleviation, capacity building and funds, which are all likely required in order to achieve a full documentation of their floristic diversity. Similarly, prioritising botanical countries with low environmental protection can be used to highlight regions where species may be at higher risk of extinction, and have the potential of being lost if not described soon. Finally, prioritising botanical countries with high environmental protection may highlight areas where species remaining to be described and/or geolocated face fewer threats and are therefore present in higher numbers and easier to sample. There may also be more capacity and resources available for collecting plant data to inform and improve protected area management.

Our baseline scenario (Scenario 1) ranks botanical countries by the magnitude of taxonomic and geographic knowledge gaps without accounting for each region’s specific socioeconomic and environmental characteristics. We then defined Scenarios 2-9 based on the darkspot score and possible combinations between our baseline and the two extremes of the socioeconomic and environmental variables (i.e., prioritising collections based on income group and/or environmental protection or not, and if so, prioritising botanical countries with more or less

income and/or environmental protection). Each scenario is described in more detail in the Results section below.

To calculate the benefit of collecting in each botanical country under each scenario, we rescaled between 0 and 1, and summed the darkspot score with the income and protection scores of each botanical country. We defined sets of global priorities for each scenario based on our darkspot definition. In addition, we defined continental priorities as the top five priority botanical countries by continent, as defined by the WGSRPD.

RESULTS

Global distribution of the Linnaean and Wallacean shortfalls

Overall, our PH models performed well with Brier scores very close to zero indicating a good fit across all botanical countries (mean iBS = 0.095, minimum=0.054, maximum=0.148 for species descriptions; mean iBS = 0.101, minimum=0.003, maximum=0.173 for species geolocations).

Our results indicate that taxonomic and geographic knowledge gaps expected by 2050 differ substantially in magnitude and vary widely across the globe (Table 1, SI Table S1-S2). The Linnaean shortfall is expected to be modest in most continental regions, with a vast majority of botanical countries predicted to contain less than 50 unknown species (Table 1). Yet, the Linnaean shortfall remains apparent in Asia-Tropical and South America (Fig. **1a** and SI Fig. **S2a**) with few botanical countries predicted to house hundreds of species still unknown to science (Table 1, Fig. **1a** and SI Fig. **S2a**), but also in Turkey, Cape Provinces, Madagascar and Southwest Mexico (Fig. **1a** and SI Fig. **S2a**). The Wallacean shortfall is expected to be large in many parts of the world and exhibits a very different global pattern, with thousands of known species still expected to be missing geographic records by 2050 in Asia-Tropical and Asia-Temperate, as well as North Africa, Angola, Albania, Trinidad-Tobago, and Haiti (Table 1, Fig. **1a** and SI Fig. **S2a**). Several botanical countries exhibit both taxonomic and geographic knowledge gaps, including the Philippines, Laos, Myanmar, India, West Himalaya, and Turkey (Fig. **1a**, SI Table S1 and Table S2).

Overall, Colombia, Myanmar and Assam have the greatest combined Linnaean and Wallacean shortfalls globally (SI Table S2), in decreasing order (Fig **1b**). By continent, New Caledonia and

Fiji have the greatest combined shortfall for the Pacific, Western Australia and Queensland for Australasia, Myanmar and Assam for Asia -Tropical, China South-Central and Turkey for Asia - Temperate, Sudan and Cape Provinces for Africa, Italy and Albania for Europe, Mexico Southwest and Mexico Southeast for North America, and Colombia and Peru for South America.

Table 1: Summary of the predictions for the Linnaean and Wallacean shortfalls expected by 2050 across all botanical countries of each continent**.**

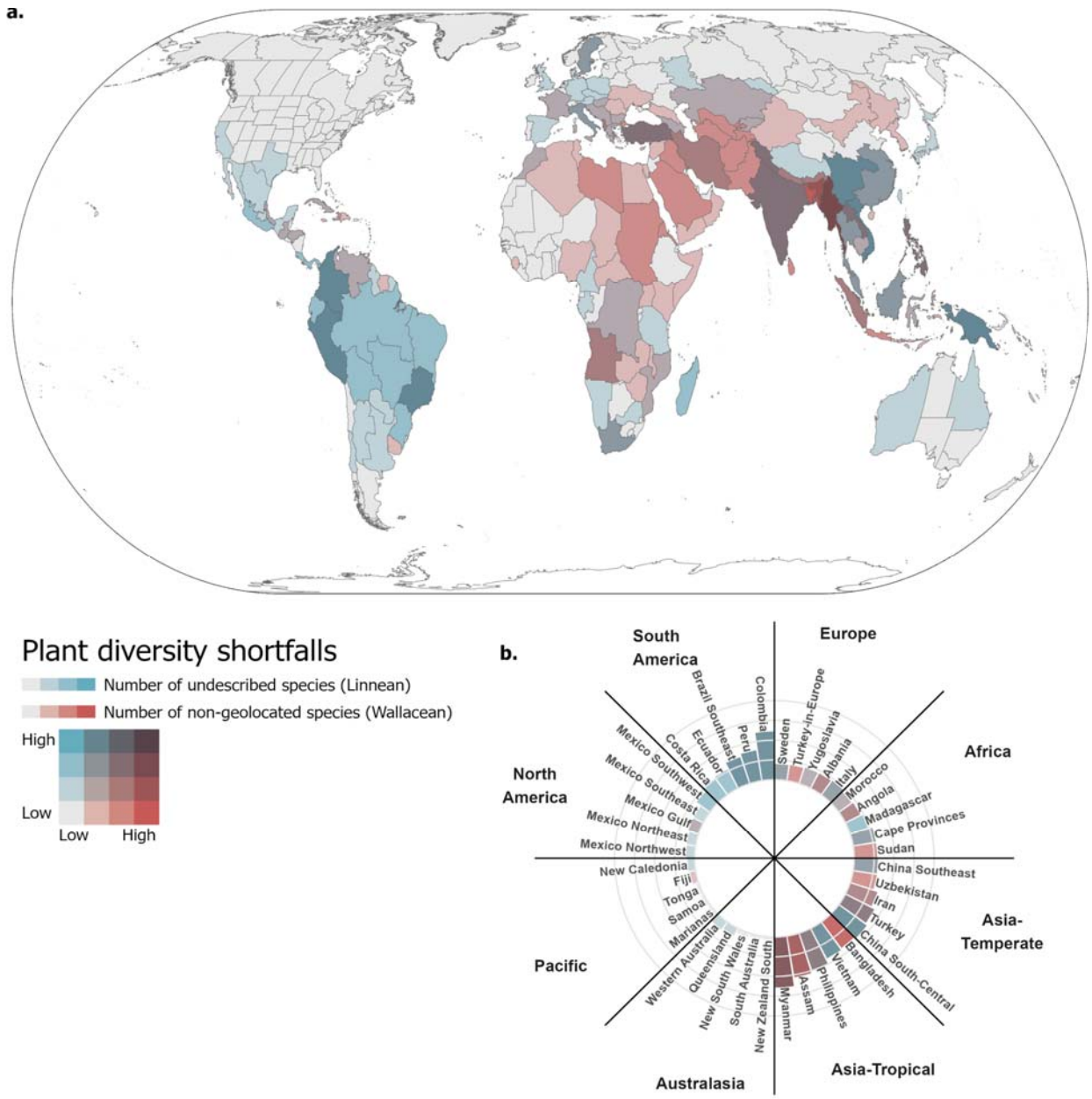

Figure 1: The Linnaean and Wallacean shortfalls for vascular plants expected by 2050. In panel **(a),** the Linnaean shortfall (blue gradient) is quantified as the predicted number of species yet to be described scientifically based on the estimated probability of species to remain undescribed by 2050. The Wallacean shortfall (red gradient) is quantified as the predicted number of species yet to be geolocated based on the estimated probability of species to have no geographic record available in GBIF in a given botanical country by 2050. Colours indicate the relative magnitude of each shortfall, with light grey and dark brown colours representing small and large values for both shortfalls, respectively. In panel **(b),** the top 5 botanical countries

with the largest combination of both Linnaean and Wallacean shortfalls are reported by continental region. Predictions were rescaled between 0 and 1 to allow for comparison.

Species attributes associated with early description and geolocation

Assessing the importance of different species attributes on their early description and geolocation, we find that range size is the most important driver of the Wallacean shortfall: the larger the range of a species, the longer it takes before recording its first geographic location in all applicable botanical countries (Fig. 2). Conversely, range size has an opposite effect on the Linnaean shortfall, with widely distributed species being slightly but consistently more likely to be described before small-range species. This also means that recently described species tend to be characterised by smaller ranges.

We find that early-described species, and to a lesser extent rapidly geolocated species, are mostly characterised by a higher number of uses by humans (Fig. 2). Early descriptions are also associated positively with high taxonomic activity at a given time, while taxonomic activity shows no effect on species geolocation. The magnitude and direction of the effects of elevation, temperature seasonality and annual precipitation strongly vary across botanical countries such that none of these environmental variables seem to consistently influence species description or geolocation in one direction or another. However, precipitation seasonality seems to slighly decrease the chance of species geolocation: i.e., it takes longer to geolocate a species inhabiting arid or semi-arid environments.

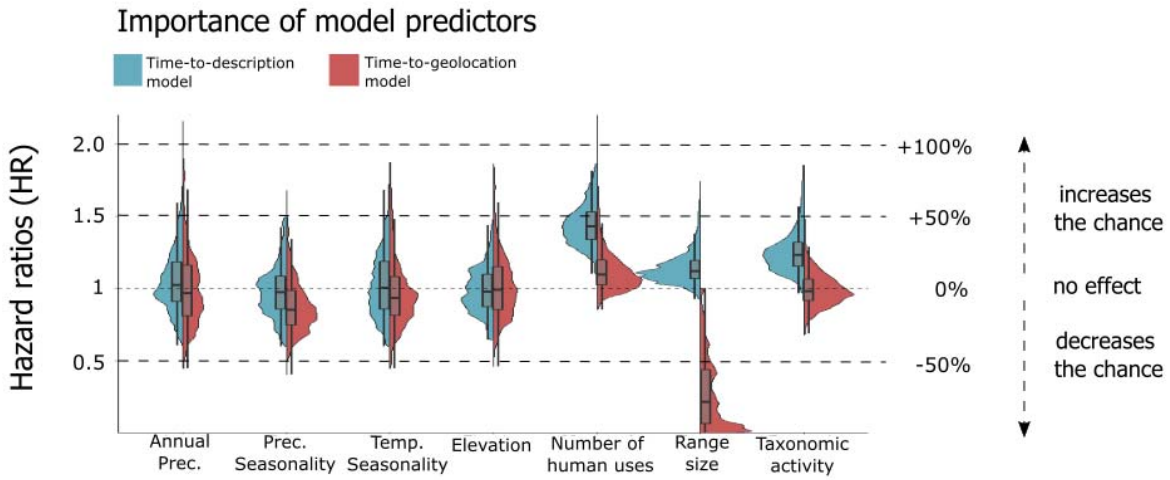

Figure 2: Importance of variables for the description and geolocation of vascular plant species. The violin and box plots show the 95% posterior distribution of the hazard ratio (HR) (exponential of our time-to-event model coefficients). HR measures the change in the chance of describing or geolocating a new species in a given botanical country following an increase in the considered variable. For example, if a time-to-description model has one variable, such as range size, with a HR of 1.5, it means that a species with a range size of 3 (botanical countries) has |1 - 1.5| x 100 = 50% more chance to be described than a species with a range size of 2. In other words, the time to describe a species with a range size of 3 is reduced by 50% compared to a species with a range size of 2, meaning that it would take twice as long to describe a species with a range size (one-unit) smaller.

Past collection dynamics and plant diversity shortfalls

Species descriptions first peaked in Europe and large parts of North America and Australasia in the 1850s, before peaking in most of Africa, Asia-Temperate and the Pacific in the last century (SI Fig. **S6a** and **S6b**). Species geolocations peaked in eastern Russia and North Africa in the 1850s, and more recently in Europe, South East Asia and Sub-Saharan Africa (SI Fig. **S6c** and **S6d**).

We find a mismatch between the geographic distribution of collection rates over the 2010-2019 period (SI Fig. **S6b**) and the distribution of gaps expected by 2050 (Fig. **1a**). Kendall's

correlations tests highlighted weakly positive but significant correlation between description rates in 2010-2019 and the predicted number of species remaining to be described by 2050 (Fig. **3a**). We also find a stronger and significant correlation between geolocation rates (2010-2019) and where most species are predicted to remain to be geolocated in the future (Fig. **3b**).

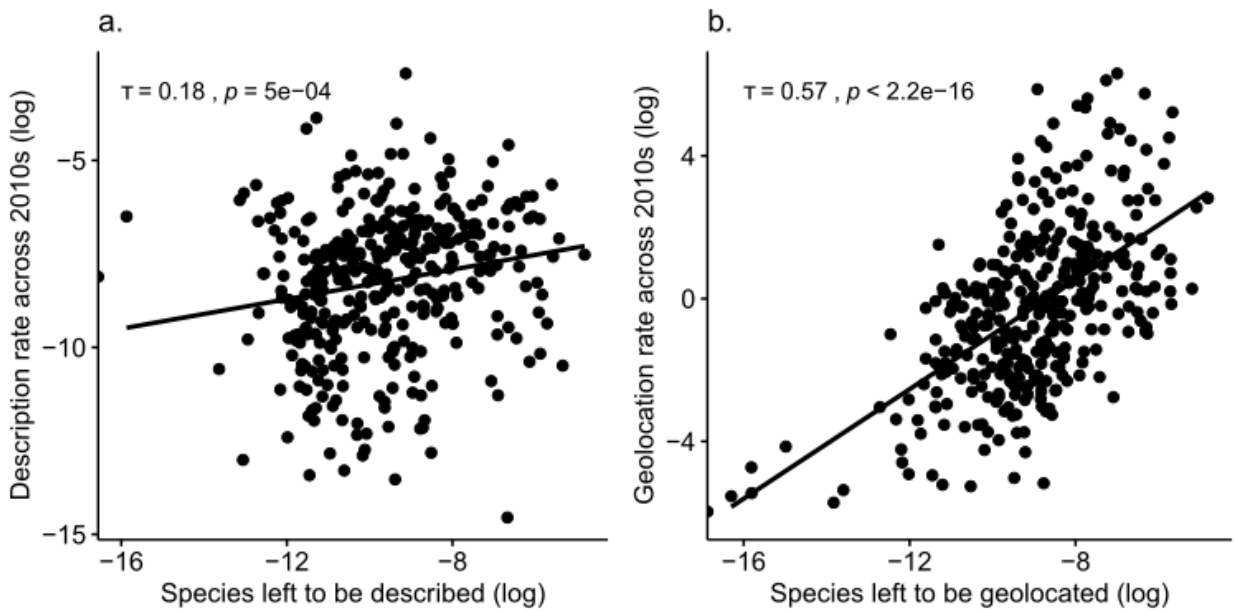

Fig. 3: Kendall's correlations between past collections and future needs. Dots represent botanical countries. In panel **(a),** the x-axis represents the log-transformed number of species predicted to be described by 2050 and the y-axis represents the log-transformed average species description rate estimated across 2010s. The weak positive relationship means there is a slight trend of higher description rates in areas that are predicted to have more species remaining to be described. In panel **(b),** the x-axis represents the log-transformed predicted number of species to be geolocated by 2050 and the y-axis represents the log-transformed average species geolocation rate estimated across 2010s. The positive relationship means sampling has recently occurred in areas that are predicted to have more species remaining to be geolocated. We are therefore more effective in bridging the Wallacean than the Linnaean gap.

Plant diversity darkspots and biodiversity hotspots

Vascular plant diversity darkspots are represented by botanical countries exhibiting the highest darkspot scores globally (i.e., sum of the estimates of the rescaled Linnaean and Wallacean shortfalls), and a cumulative area equal to that of biodiversity hotspots to allow for comparison. We identified 29 darkspots: 15 across large parts of Asia - Tropical (Myanmar, Assam, Philippines, Vietnam, Bangladesh, New Guinea, India, East and West Himalaya, Thailand, Sumatera, Laos, Malaya, Pakistan and the Andaman Islands), 7 in Asia - Temperate (China South-Central, Turkey, Iran, Uzbekistan, China Southeast, Afghanistan and Iraq), 5 in South America (Colombia, Peru, Brazil Southeast, Ecuador, Costa Rica) and 2 in Africa (Sudan and Cape Provinces). Brazil North was ranked 30th and was the first botanical country to reach and exceed the cumulative area of biodiversity hotspots; therefore it was not considered a darkspot.

We find that the 29 darkspots overlap to a very large degree with the 36 biodiversity hotspots, with the notable exception of New Guinea (Fig. 4). In contrast, there is a large number of hotspots that are not identified as darkspots in our analysis, particularly in the Pacific, Australasia, North America and Europe. When re-scaling the darkspot score to a fixed area, 27 new botanical countries (e.g. Taiwan, Madagascar, Cuba and Nepal) become darkspots (SI Fig. S3). Their area is equal to that of Brazil North that was previously found under the area threshold.

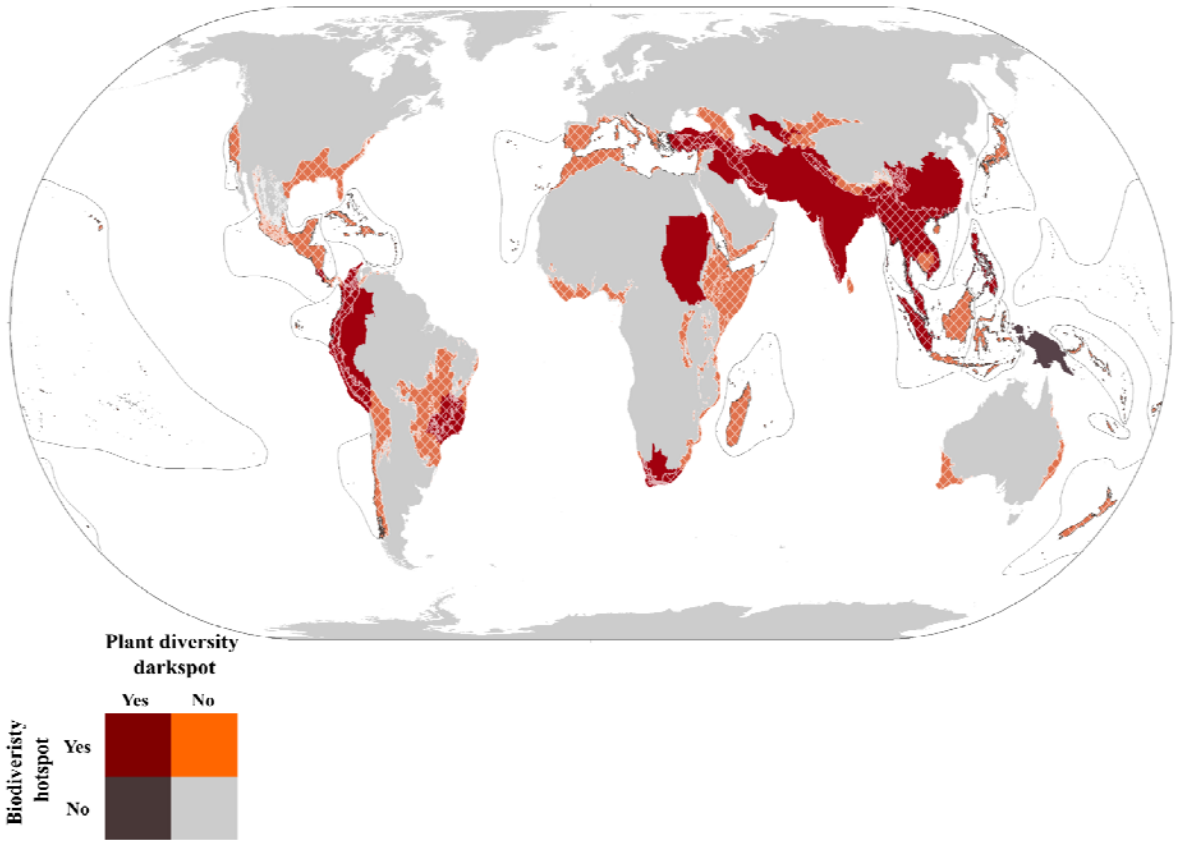

Figure 4: Global darkspots of vascular plant diversity and biodiversity hotspots. Dark red indicates botanical countries that are identified as darkspots and that contain hotspots. Black indicates botanical countries uniquely defined as darkspots (i.e. New Guinea). Orange indicates areas containing hotspots but not overlapping with any darkspot, and grey indicates areas containing neither darkspots nor hotspots. The cross-hatched areas and black lines indicate the terrestrial and marine delimitation of biodiversity hotspots, respectively. All darkspots overlap with hotspots, except New Guinea.

Plant collection priorities

We defined nine scenarios based on different trade-offs between the darkspot score, the income group, and level of environmental protection (SI Fig. S6). Scenario 1 is considered our baseline scenario and is represented by the darkspot score with no consideration for the botanical countries' level of income or environmental protection (Fig. 1 and SI Fig. S1).

Scenarios 2-9 highlight regional and global collection priorities deviating from the baseline and varying greatly across space according to different income-protection combinations (Fig. 5, SI Fig. S4, and Fig. S9-S16). However, consistent global priorities arise across all scenarios: Assam, Bangladesh, Colombia, East Himalaya, Iran, Myanmar, Peru, the Philippines and Turkey (Fig 5). When re-scaling the darkspot score to area, Iran is no longer a global priority across all scenarios, while Albania, the Andaman islands, Costa Rica, Cape Provinces, Ecuador, Laos, Nicobar islands, Panama, Selvagens, Uzbekistan, Thailand, Vietnam and West Himalaya become consistent global collection priorities (SI Fig. S4).

When prioritising botanical countries with low income levels (i.e., Scenarios 2, 6 and 7), Madagascar and Angola become global priorities consistently, while Ecuador and Costa Rica are not considered global priorities anymore (Fig. 5, SI Fig. S9 , Fig. S12 and Fig. S15). Conversely, when prioritising high-income botanical countries (i.e., Scenarios 3, 8 and 9), North Brazil and Italy become global priorities consistently, while Sudan, Afghanistan and Pakistan are consistently removed from the global priority list (Fig. 5, SI Fig. S10, Fig. S13 and Fig. S16). When prioritising botanical countries with low levels of environmental protection (i.e., Scenarios 4, 6 and 8), Borneo and Trinidad-Tobago become global priorities consistently, while no botanical country is consistently removed from the global priority list (Fig. 5 and SI Fig. S11-S13). Finally, when prioritising botanical countries with high levels of environmental protection (i.e., Scenarios 5, 7 and 9), no botanical country becomes a global priority consistently, while the Andaman islands, China Southeast, Laos, Malaya and Sumatera are no longer considered global priorities (Fig. 5 and SI Fig. S14-S16).

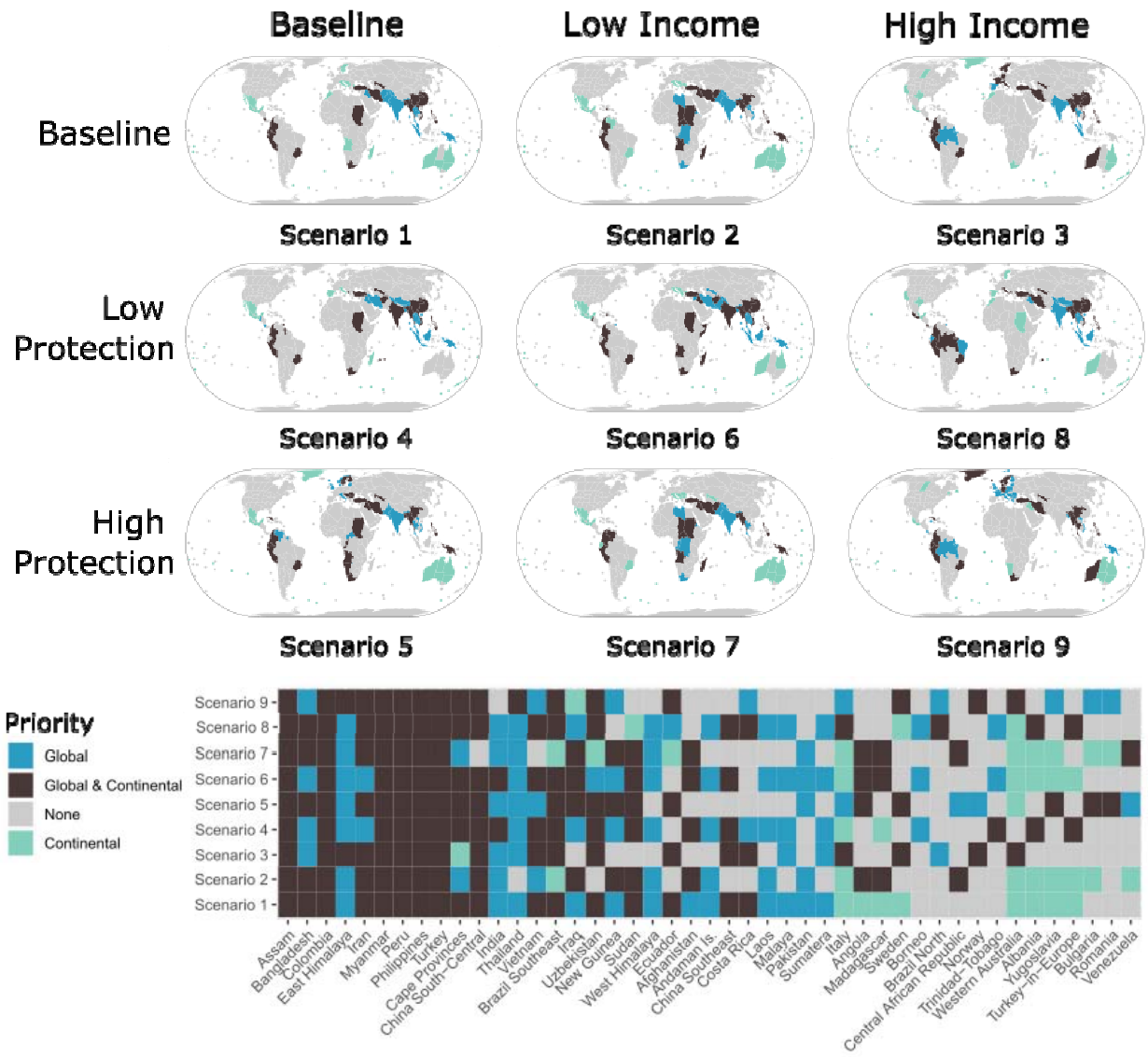

Figure 5: Collection priorities under nine income and environmental protection scenarios. Different scenarios investigate different tradeoffs between the darkspot score (i.e., sum of scaled taxonomic and geographic shortfalls), income group (i.e., first axis of the Principal Component Analysis (PCA) summarising the variation of the Sustainable Development Goals' indicators across botanical countries) and environmental protection level (i.e., second axis of the PCA). Top global (blue) and continental (green) collection priorities are provided across scenarios, as well as their overlap (black) and absence (grey). The bottom matrix provides more detail on top priority countries across the nine scenarios. Assam, Bangladesh, Colombia, East Himalaya, Iran, Myanmar, Peru, the Philippines and Turkey appear consistently as global priorities across all scenarios, providing very little risk and high potential for new species

descriptions and geolocations. Collections in other botanical countries will depend on tradeoffs between income and environmental protection.

DISCUSSION

Global distribution of the Linnaean and Wallacean shortfalls

Using the most extensive dataset to date on standardised plant distributions at the botanical country level, our research provides a joint assessment of the global taxonomic and geographic data shortfalls. Our predictions indicate that a complete documentation of the geographic distribution of all vascular plants will not be achieved by 2050 if botanical collections continue to follow past trends of species description and geolocation (Fig. 1). An incomplete understanding of plant diversity and occurrences could jeopardise actions towards implementation of some of the goals of the GBF, including protecting and restoring plant diversity.

Predicting numbers of species remaining to be documented comes with high uncertainty (Bebber *et al.*, 2007; Moura & Jetz, 2021). Although the models developed here performed well, confidence intervals around our predicted absolute numbers are inevitably large (SI Table S1). Even so, relative comparisons across botanical countries of the world reveal well-supported insights. Many species are predicted to remain undescribed by 2050 in areas of the world already known for their exceptional levels of plant endemism (Kier *et al.*, 2009), generally suggesting that there may be more species to describe where there are more narrowly distributed species currently known to science. Expected gaps in geographic records follow very different distribution patterns, with larger numbers of species remaining to be geolocated in both species-rich and species-poor regions, mainly in eastern regions from North Africa to the Indo-Burma region, Central Asia and the Middle East.

Our results suggest that the Wallacean shortfall may be driven by other factors than the intrinsic characteristics of plant diversity; in particular, they may be more related to political, economic, or socio-cultural conditions, as highlighted in previous publications (Fig. 2, SI Fig. S5 and Fig. S6; Meyer *et al.*, 2015, 2016; Zizka *et al.*, 2021). Filling both knowledge gaps will therefore imply actions at global to local scales, from policy, finance and science, to ultimately influence where future botanical surveys should be conducted.

Species-level drivers of plant description and geolocation

Our results corroborate studies conducted on other biodiversity data shortfalls (Rudbeck *et al.*, 2022; Maitner *et al.*, 2022), by showing that species range size is a major driver of knowledge gaps (Hortal *et al.*, 2015). Similarly to vertebrates (Essl *et al.*, 2013; Moura & Jetz, 2021) – plant species with large geographic ranges are described earlier than small-ranged species (Fig 2). Since they are also more likely to be rare locally (Brown, 1984), narrowly-distributed species may be harder to detect and thus remain scientifically unknown.

Conversely, the geolocation of widespread species takes considerably longer, which may be explained by the fact that more ground needs to be covered to record their geographic position, and that their commonness makes them less sought-after by botanists (Fig. 2; Daru *et al.*, 2018). Additionally, the higher the socio-eco-cultural value of a species (as measured by the number of uses by humans), the sooner it is likely to be studied (Adamo *et al.*, 2021), described, and to a lesser extent geolocated. Species described longer ago may also have had more time to be used in a variety of ways across the world. Species' appeal to botanists accelerates their description, while it does not relate to their geolocation. This follows the documented pattern of botanists being unwilling to collect the same species across different regions (Steege *et al.*, 2011). Aligning both taxonomic and geographic sampling efforts will be key to filling plant diversity shortfalls. Taken together, our results suggest that most currently unknown plant species may be from groups of taxa neglected for taxonomic and societal reasons, occupying restricted ranges across diverse environmental conditions.

(Mis-)matches between past trends and future needs

Our findings align with previous studies highlighting spatial and temporal biases in species collections shaped by the history of botanical sciences, the advent of technologies (e.g., Global Positioning Systems), geographic patterns of species richness and other socio-economic factors (SI Fig S5; Meyer *et al.*, 2015, 2016; Farooq *et al.,* 2021; Hughes *et al.*, 2021).

Our analyses also feature a positive overall correlation between where collections have happened in the recent past and where the largest data gaps are estimated to remain in the future, which indicates a good general progress towards bridging the Linnaean and Wallacean shortfalls (Fig. 3 and SI Fig. S2). However, while the correlation is relatively strong for geolocations, it is weaker for species descriptions. We interpret this difference with caution given that predicting future description needs may come with higher uncertainties than for geolocations. In fact, predictions of potentially missing geolocations are based on expected

targets defined by the known species richness of each botanical country, whereas predictions of future gaps in descriptions cannot be informed in such a way. In addition, predictions of gaps in geolocation do not account for currently undescribed species. Beyond uncertainty, large recent description rates across many islands (e.g., Kriti, Mozambique Channel islands, Comoros, Corse) may indicate preferences for areas with high endemicity levels and constrained spaces to search for new species (Fig. **S5b;** Kier *et al.*, 2009). Botanical countries such as New Zealand, British Columbia and Ireland have attracted extensive description efforts recently, but have limited predicted numbers of species remaining to be described in the future. Conversely, several areas containing potentially large numbers of undescribed species (e.g. Peru, Colombia and New Guinea) have had relatively little attention and require immediate strategic investments to expand botanical science capacity.

Knowledge gaps and conservation priorities

By identifying darkspots of vascular plant diversity and comparing their distribution to that of the biodiversity hotspots, we intended to assess whether some regions could represent neglected conservation priorities globally. Our results follow previous assessments based on estimates of the Linnaean shortfall, indicating a general overlap between collection and conservation priorities (Joppa *et al.*, 2011).

New Guinea, the island with the largest number of plant species (Cámara-Leret *et al.*, 2020), is the only identified darkspot that is not considered a hotspot (Fig. 4; Joppa *et al.*, 2011). Brazil North, which contains large parts of the Amazonian rainforest, was nearly considered a darkspot and is not a hotspot either. Under the most recent hotspot assessment, both New Guinea and Brazil North were recognized as species-rich regions but were not considered threatened enough to be included (Mittermeier *et al.*, 2011). Given land-use changes primarily associated with agriculture are increasingly threatening those regions (Brun *et al.*, 2015; Lapola *et al.,* 2022), the hotspot status of those regions may need re-evaluation before many of their known and yet-to-be-known species become threatened, or possibly extinct. When controlling for the effect of area (SI Fig. S3), we also identify islands at the edge of current hotspots whose status could potentially be reconsidered (i.e., Trinidad-Tobago and Taiwan).

Beyond the hotspot classification (which has a range of limitations; Mace *et al.*, 2000), considering plant diversity darkspots could have wider implications for the identification of priority areas and species for conservation (e.g., Jung *et al.*, 2021), including for the

International Union for Conservation of Nature's Red List of Threatened Species (Rodrigues *et al.*, 2006), and the designation of Key Biodiversity Areas (KBAs) and (Tropical) Important Plant Areas ((T)IPAs; Darbyshire *et al.*, 2017).

Future collection priorities

There are many nuances involved in how, where, when and why specimens are collected (Meyer *et al.*, 2015). Yet despite considering a wide range of prioritisation scenarios accounting for different socioeconomic and environmental trade-offs (Fig. 5 and SI Fig. S4), some botanical countries are consistently identified as global priorities: the Philippines, Myanmar, Assam, Bangladesh, East Himalaya, Iran, Turkey, Colombia, and Peru. Amongst these botanical countries, some are predicted to contain many species remaining to be described (e.g., Colombia, Peru), geolocated (e.g., Bangladesh), or both (e.g. Myanmar), and all overlap with biodiversity hotspots.

Our results add to a body of literature showing that decision-making can be robust to uncertainty (McCarthy *et al.*, 2003; McDonald-Madden *et al.*, 2011), with clear win-win sampling strategies across scenarios. However, decision uncertainty increases as darkspots become less strong and tradeoffs between socioeconomic and environmental values come into play to drive the prioritisation. Our results (especially Fig. 5, and the shiny app released with this study) provides an evidence-based and flexible framework to prioritise future collection efforts, which highlights the importance of a coordinated and inclusive effort towards tackling plant diversity shortfalls.

Data portals have changed the face of biodiversity science in recent decades and are still expected to play a major role in the future (Nelson & Ellis, 2019). Despite being one of the most complete data portals for species observation, GBIF does not include information from several existing (sub-)national databases. This has likely impacted our findings by suggesting some spots are "darker" than they truly are. It will therefore be key to integrate and share species information coming from these existing databases, as well as other collections (Heberling *et al.*, 2021). In fact, the digitization of some of the largest herbarium collections in the world has contributed to filling major knowledge gaps, but this effort is largely incomplete and remains a priority (Nelson & Ellis, 2019). Moreover, many smaller-scale (and often under-resourced) herbaria containing exceptionally unique information remain inaccessible and vulnerable globally (Paton *et al.*, 2020).

Citizen science can also greatly improve our botanical knowledge, as it requires less resources, relies greatly on individual decisions, and allows for the upscaling of science outreach and botanical education (Pocock *et al.*, 2018; Callaghan, 2022). Many identified darkspots contain large human populations and thus many potential contributors to citizen science projects (Cincotta *et al.*, 2000). On the other hand, vouchered botanical specimens remain essential to a large number of scientific projects, and can seldom be replaced by photographs or undocumented observations (Troudet *et al.,* 2018).

Implementation of the actions described above has several fundamental requirements (that are also potential barriers). These include supporting botanical sciences and institutions financially, and enhancing the education and development of a new and diverse generation of plant taxonomists – both of which will be key to fill knowledge gaps with high-quality information (Paton *et al.*, 2020). It is fundamental to incentivize data collection, integration, and sharing, not only in global policy frameworks but also at (sub-)national scale. In this context, our analyses may have limited reach given their coarse resolution, and much effort will be required in the future to provide assessments of data collection (and subsequently conservation) priorities at higher spatial resolution within countries. General levels of development and botanical sampling are also intertwined: access to food, water, medicine, and education, and the presence and quality of general infrastructure to travel, work and live safely are essential factors required to support the successful conduct of botanical activities (Meyer *et al.*, 2015; Paton *et al.*, 2020).

While using botanical information is necessary to develop efficient strategies to conserve plant diversity, delaying the protection of species and areas may lead to the extinction of species before they are even named scientifically and geolocated. The collection and preservation of global plant diversity is urgent, for their intrinsic value, to safeguard ecosystems, and to enhance people's awareness and well-being (Antonelli *et al.*, 2020; Pironon *et al.*, 2020).

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AUTHOR CONTRIBUTIONS

Alexandre Antonelli (AA) initiated the project, devised the paper with Samuel Pironon (SP), and both supervised the development of the analyses. Ian Ondo (IO) compiled and processed spatial datasets, with support from Nicky Nicolson (NN) and Barnaby Walker (BW). Kiran Dhanjal-Adams (KDA) compiled the SDG datasets. IO, KDA, SP, and DS contributed to the analyses with support from AA. IO performed the time-to-event analyses, KDA and SP performed analyses regarding future collection trends, and DS performed the skyline modelling. IO and KDA generated the figures, with support from SP. KDA proposed and implemented the shiny web application to visualise the modelling outputs. SP and AA led the writing together with IO and KDA. BW, DS, Alexandre K. Monro (AM), Victor Deklerck (VD), NN and Olwen Grace (OG) provided feedback. All authors revised and approved the final version.

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SUPPORTING INFORMATION

All analysis was performed in R (version 4.1.3), except retrieving data from MPC and modelling past collection patterns, which were performed in python (version 3.10). We used the python package *pystac* to search the MPC catalogue and downloaded the resulting data using the *planetary-computer* package.

DATA AND CODE AVAILABILITY

The data and code that support the reproduction of the findings and figures of this study will be made openly available at [repository name] and https://github.com/DarkSpots respectively, upon publication acceptance.

The shiny app used to explore the relationship between plant diversity knowledge, knowledge gaps, and socio-economic variables is available at https://kiranlda.shinyapps.io/darkspots_shiny/

The LiteRate program is available here: https://github.com/dsilvestro/LiteRate and the version used in this manuscript is included in the [repository name].

COMPETING INTERESTS

None declared.

REFERENCES

Adamo M, Chialva M, Calevo J, Bertoni F, Dixon K, Mammola S. 2021. Plant scientists' research attention is skewed towards colourful, conspicuous and broadly distributed flowers. *Nature Plants* 7: 574–578.

Antonelli A, Smith RJ, Fry C, Simmonds MSJ, Kersey PJ, Pritchard HW, Abbo MS, Acedo C, Adams J, A. M. A, *et al.* 2020. *State of the World's Plants and Fungi*. Royal Botanic Gardens (Kew) ; Sfumato Foundation.

Bebber DP, Marriott FHC, Gaston KJ, Harris SA, Scotland RW. 2007. Predicting unknown species numbers using discovery curves. *Proceedings of the Royal Society B: Biological Sciences* 274: 1651–1658.

Brown JH. **1984**. On the relationship between abundance and distribution of species. *The American Naturalist* **124**: 255–279.

Brummitt RK. **2001**. *World geographical scheme for recording plant distributions* (HI for Botanical Documentation, Ed.). Pittsburgh, Pa.: Published for the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) by the Hunt Institute for Botanical Documentation, Carnegie Mellon University.

Brummitt N, Lughadha EN. **2003**. Biodiversity: Where's hot and where's not. *Conservation Biology* **17**: 1442–1448.

Brun C, Cook AR, Lee JSH, Wich SA, Koh LP, Carrasco LR. **2015**. Analysis of deforestation and protected area effectiveness in indonesia: A comparison of bayesian spatial models. *Global Environmental Change* **31**: 285–295.

Cai L, Kreft H, Taylor A, Denelle P, Schrader J, Essl F, Kleunen M van, Pergl J, Pyšek P, Stein A, *et al.* 2023. Global models and predictions of plant diversity based on advanced machine learning techniques. *New Phytologist* **237**: 1432–1445.

Callaghan TAA Corey T. AND Mesaglio. **2022**. The benefits of contributing to the citizen science platform iNaturalist as an identifier. *PLOS Biology* **20**: 1–6.

Cámara-Leret R, Frodin DG, Adema F, Anderson C, Appelhans MS, Argent G, Arias Guerrero S, Ashton P, Baker WJ, Barfod AS, et al. 2020. New guinea has the world's richest island flora. Nature 584: 579–583.

Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A. **2017**. Stan: A probabilistic programming language. *Journal of Statistical Software* **76**: 1–32.

Cincotta RP, Wisnewski J, Engelman R. **2000**. Human population in the biodiversity hotspots. *Nature* **404**: 990–992.

Danielson JJ, Gesch DB. **2011**. *Global multi-resolution terrain elevation data 2010 (GMTED2010)*. U.S. Geological Survey.

Darbyshire I, Anderson S, Asatryan A, Byfield A, Cheek M, Clubbe C, Ghrabi Z, Harris T, Heatubun CD, Kalema J, *et al.* 2017. Important plant areas: Revised selection criteria for a global approach to plant conservation. *Biodiversity and Conservation* **26**: 1767–1800.

Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJS, Seidler TG, Sweeney PW, Foster DR, Ellison AM, *et al.* 2018. Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytologist* **217**: 939–955.

Díaz S, Settele J, Brondízio ES, Ngo HT, Agard J, Arneth A, Balvanera P, Brauman KA, Butchart SHM, Chan KMA, *et al.* 2019. Pervasive human-driven decline of life on earth points to the need for transformative change. *Science* **366**: eaax3100.

DuBay S, Palmer Droguett DH, Piland NC. **2022**. Global inequity in scientific names and who they honor. *bioRxiv*.

Essl F, Rabitsch W, Dullinger S, Moser D, Milasowszky N. **2013**. How well do we know species richness in a well-known continent? Temporal patterns of endemic and widespread species descriptions in the european fauna. *Global Ecology and Biogeography* **22**: 29–39.

Farooq H, Azevedo JAR, Soares A, Antonelli A, Faurby S. **2021**. Mapping africa's biodiversity: More of the same is just not good enough. *Syst Biol* **70**: 623–633.

Gardner EM, Ahmad Puad AS, Pereira JT, Tagi J anak, Nyegang S anak, Miun P, Jumian J, Pokorny L, Zerega NJC. **2022**. Engagement with indigenous people preserves local knowledge and biodiversity alike. *Current Biology* **32**: R511–R512.

Geldmann J, Heilmann-Clausen J, Holm TE, Levinsky I, Markussen B, Olsen K, Rahbek C, Tøttrup AP. **2016**. What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions* **22**: 1139–1149.

Gelman A, Rubin DB. **1992**. Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science* **7**: 457–472.

Gjesfjeld DAC Erik AND Silvestro. **2020**. A quantitative workflow for modeling diversification in material culture. *PLOS ONE* **15**: 1–16.

Goodrich B, Gabry J, Ali I, Brilleman S. **2020**. Rstanarm: Bayesian applied regression modeling via Stan.

Govaerts R, Nic Lughadha E, Black N, Turner R, Paton A. **2021**. The world checklist of vascular plants, a continuously updated resource for exploring global plant diversity. *Sci Data* **8**: 215.

Heberling JM, Miller JT, Noesgaard D, Weingart SB, Schigel D. **2021**. Data integration enables global biodiversity synthesis. *Proceedings of the National Academy of Sciences* **118**: e2018093118.

Hoffman MD, Gelman A. **2014**. The no-u-turn sampler: Adaptively setting path lengths in hamiltonian monte carlo. *Journal of Machine Learning Research* **15**: 1593–1623.

Hoffman M, Koenig K, Bunting G, Costanza J, Williams KJ. **2016**. Biodiversity hotspots (version 2016.1).

Hortal J, Bello F de, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle Richard. **2015**. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **46**: 523–549.

Hosmer L D. W., Lemeshow S, May S. **2008**. Applied survival analysis: Regression modeling of time-to-event data, second edition. In: Applied survival analysis. John Wiley & Sons, Ltd.

Hughes AC, Orr MC, Ma K, Costello MJ, Waller J, Provoost P, Yang Q, Zhu C, Qiao H. **2021**. Sampling biases shape our view of the natural world. *Ecography* **44**: 1259–1269.

Joppa LN, Roberts DL, Myers N, Pimm SL. **2011**. Biodiversity hotspots house most undiscovered plant species. *Proceedings of the National Academy of Sciences* **108**: 13171–13176.

Jung M, Arnell A, Lamo X de, García-Rangel S, Lewis M, Mark J, Merow C, Miles L, Ondo I, Pironon S, *et al.* 2021. Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nature Ecology & Evolution* **5**: 1499–1509.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M. **2016**. CHELSA climatologies at high resolution for the earth's land surface areas (version 1.2).

Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. **2009**. A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* **106**: 9322–9327.

Koch B, Silvestro D, Foster JG. **2020**. The evolutionary dynamics of cultural change (as told through the birth and brutal, blackened death of metal music).

Lapola DM, Pinho P, Barlow J, Aragão L, Berenguer E, Carmenta R, Liddy HM, Seixas H, Silva CVJ, Silva-Junior CHL, *et al.* 2023. The drivers and impacts of amazon forest degradation. *Science* **379**: eabp8622.

Mace GM, Balmford A, Boitani L, Cowlishaw G, Dobson AP, Faith DP, Gaston KJ, Humphries CJ, Vane-Wright RI, Williams PH, *et al.* 2000. It's time to work together and stop duplicating conservation efforts …. *Nature* **405**: 393–393.

Mair A Louise AND Ruete. **2016**. Explaining spatial variation in the recording effort of citizen science data across multiple taxa. *PLOS ONE* **11**: 1–13.

Maitner B, Gallagher R, Svenning J-C, Tietje M, Wenk EH, Eiserhardt WL. **2022**. Socioeconomics and biogeography jointly drive geographic biases in our knowledge of plant traits: A global assessment of the raunkiærian shortfall in plants. *bioRxiv*.

McCarthy MA, Andelman SJ, Possingham HP. **2003**. Reliability of relative predictions in population viability analysis. *Conservation Biology* **17**: 982–989.

McDonald-Madden E, Chadès I, McCarthy MA, Linkie M, Possingham HP. **2011**. Allocating conservation resources between areas where persistence of a species is uncertain. *Ecological Applications* **21**: 844–858.

Meyer C, Kreft H, Guralnick R, Jetz W. **2015**. Global priorities for an effective information basis of biodiversity distributions. *Nature Communications* **6**: 8221.

Meyer C, Weigelt P, Kreft H. **2016**. Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters* **19**: 992–1006.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C. **2011**. Global biodiversity conservation: The critical role of hotspots. In: Zachos FE, Habel JC, eds. Biodiversity hotspots: Distribution and protection of conservation priority areas. Berlin, Heidelberg: Springer Berlin Heidelberg, 3–22.

Morais AR, Siqueira MN, Lemes P, Maciel NM, De Marco P, Brito D. **2013**. Unraveling the conservation status of data deficient species. *Biological Conservation* **166**: 98–102.

Moura MR, Jetz W. **2021**. Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nature ecology & evolution* **5**: 631—639.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB da, Kent J. **2000**. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Nelson G, Ellis S. **2019**. The history and impact of digitization and digital data mobilization on biodiversity research. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**: 20170391.

Nic Lughadha E, Bachman SP, Leão TCC, Forest F, Halley JM, Moat J, Acedo C, Bacon KL, Brewer RFA, Gâteblé G, *et al.* 2020. Extinction risk and threats to plants and fungi. *PLANTS, PEOPLE, PLANET* **2**: 389–408.

Page RDM. **2016**. DNA barcoding and taxonomy: Dark taxa and dark texts. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**: 20150334.

Pascual U, Adams WM, Díaz S, Lele S, Mace GM, Turnhout E. **2021**. Biodiversity and the challenge of pluralism. *Nature Sustainability* **4**: 567–572.

Paton A, Antonelli A, Carine M, Forzza RC, Davies N, Demissew S, Dröge G, Fulcher T, Grall A, Holstein N, *et al.* 2020. Plant and fungal collections: Current status, future perspectives. *PLANTS, PEOPLE, PLANET* **2**: 499–514.

Pimm SL, Joppa LN. **2015**. How Many Plant Species are There, Where are They, and at What Rate are They Going Extinct? *Annals of the Missouri Botanical Garden* **100**: 170–176.

Pironon S, Borrell JS, Ondo I, Douglas R, Phillips C, Khoury CK, Kantar MB, Fumia N, Soto Gomez M, Viruel J, *et al.* 2020. Toward unifying global hotspots of wild and domesticated biodiversity. *Plants* **9**.

Pocock MJO, Chandler M, Bonney R, Thornhill I, Albin A, August T, Bachman S, Brown PMJ, Cunha DGF, Grez A, *et al.* 2018. Chapter six - a vision for global biodiversity monitoring with citizen science. In: Bohan DA, Dumbrell AJ, Woodward G, Jackson M, eds. Advances in ecological research. Next generation biomonitoring: Part 2. Academic Press, 169–223.

Roberts DL, Taylor L, Joppa LN. **2016**. Threatened or data deficient: Assessing the conservation status of poorly known species. *Diversity and Distributions* **22**: 558–565.

Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M, Brooks TM. **2006**. The value of the IUCN red list for conservation. *Trends in Ecology & Evolution* **21**: 71–76.

Rudbeck AV, Sun M, Tietje M, Gallagher RV, Govaerts R, Smith SA, Svenning J-C, Eiserhardt WL. **2022**. The darwinian shortfall in plants: Phylogenetic knowledge is driven by range size. *Ecography* **2022**: e06142.

Silvestro D, Salamin N, Antonelli A, Meyer X. **2019**. Improved estimation of macroevolutionary rates from fossil data using a Bayesian framework. *Paleobiology* **45**: 546–570.

Steege H ter, Haripersaud PP, Bánki OS, Schieving F. **2011**. A model of botanical collectors' behavior in the field: Never the same species twice. *American Journal of Botany* **98**: 31–37

Troudet J, Vignes-Lebbe R, Grandcolas P, Legendre F. **2018**. The Increasing Disconnection of Primary Biodiversity Data from Specimens: How Does It Happen and How to Handle It? *Systematic Biology* **67**: 1110–1119.

Zizka A, Rydén O, Edler D, Klein J, Perrigo A, Silvestro D, Jagers SC, Lindberg SI, Antonelli A. **2021**. Bio-dem, a tool to explore the relationship between biodiversity data availability and socio-political conditions in time and space. *Journal of Biogeography* **48**: 2715–2726.

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, *et al.* 2019. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*: –7.

Zuur AF, Ieno EN, Elphick CS. **2010**. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**: 3–14.