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BIOGEOGRAPHY

The global distribution of plants used by humans

S. Pironon^{1,2,†,‡,*}, I. Ondo^{1,2,†}, M. Diazgranados^{1,3}, R. Allkin¹, A. C. Baquero², R. Cámara-Leret⁴, C. Canteiro¹, Z. Dennehy-Carr^{1,5}, R. Govaerts¹, S. Hargreaves¹, A. J. Hudson^{6,7}, R. Lemmens⁸, W. Milliken⁶, M. Nesbitt^{1,9,10}, K. Patmore¹, G. Schmelzer², R. M. Turner¹, T. R. van Andel^{8,11}, T. Ulian^{6,12}, A. Antonelli^{1,13,14}§, K. J. Willis^{1,14}§

Plants sustain human life. Understanding geographic patterns of the diversity of species used by people is thus essential for the sustainable management of plant resources. Here, we investigate the global distribution of 35,687 utilized plant species spanning 10 use categories (e.g., food, medicine, material). Our findings indicate general concordance between utilized and total plant diversity, supporting the potential for simultaneously conserving species diversity and its contributions to people. Although Indigenous lands across Mesoamerica, the Horn of Africa, and Southern Asia harbor a disproportionate diversity of utilized plants, the incidence of protected areas is negatively correlated with utilized species richness. Finding mechanisms to preserve areas containing concentrations of utilized plants and traditional knowledge must become a priority for the implementation of the Kunming-Montreal Global Biodiversity Framework.

Biodiversity provides essential goods and services that sustain human life and well-being (e.g., food, medicines, materials, fuel) (1, 2). The balance between humanity's needs and the protection of the natural environment is nevertheless fragile, as increased consumption of resources, global trade, land- and sea-use change, and socioeconomic inequalities are having a marked influence on biodiversity (3, 4). To minimize biodiversity loss, conservation biologists have focused on identifying and prioritizing regions of high species richness, endemism, and threat (5). The “biodiversity hotspot” concept (6) assumes that species diversity is spatially congruent with the contributions that it provides to people and therefore, protecting areas with the largest concentrations of threatened species will also protect humanity indirectly (5). Moreover, as biodiversity is most concentrated where human cultural diversity is highest, it is assumed that high biocultural diversity is associated with high concentrations of species used

by humans (7). Yet, these assumptions lack empirical support, leading to growing calls for better integration of human–nature interactions into conservation planning and implementation (3, 8–10), as highlighted by the recently adopted Kunming-Montreal Global Biodiversity Framework (GBF) and the 2022 assessment report on the sustainable use of wild species of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (2).

Plants are essential structuring components of ecosystems and human livelihoods (9, 11). Although the geography of terrestrial plant diversity has been extensively investigated globally (6, 12, 13), our understanding of the distribution of ecosystem services and societal benefits provided by plants is incipient, despite the importance of this information for decision-makers and local stakeholders in supporting the sustainable development agenda (14, 15). Recent modeling efforts have been dedicated to the global distribution of nature's contributions to people, including water quality, crop pollination, and carbon stocks (16, 17). However, the extent to which these contributions relate to species diversity remains largely unknown, hampering progress toward a more sustainable management of biodiversity. Assessing the global diversity and distribution of plant species used by people is thus critical to better understand, manage, and preserve both the intrinsic and instrumental values of biodiversity (18).

The global distribution of utilized plant species richness and endemism

Most plant species can potentially be useful to people, but only a fraction of plant diversity is currently known to be used. Here we consider utilized plants as vascular terrestrial species for which material and nonmaterial benefits to humans have been reported and made publicly accessible (19, 20). By extracting information from 12 databases containing plant uses

(table S1) (21), we identified 35,687 utilized species and assembled >11 million georeferenced occurrence records to map their global distribution (i.e., native and introduced ranges) (figs. S1 and S2) (19). We built species distribution models for each utilized species and stacked the resulting maps to assess the global distribution of their potential richness (figs. S3 to S6) (19). We find the highest concentrations of utilized plant species in the tropics (Fig. 1), but several temperate areas also contain high native (e.g., China, the Himalayas; fig. S7) and introduced richness (e.g., Western Europe, Eastern USA; Fig. 1). Despite large discrepancies in the sampling of species geographic records (fig. S1) (22), these results match our estimates using coarser but more complete independent distribution data from the World Checklist of Vascular Plants (WCVP) (23) (fig. S8), which provides additional support for our predictions.

Distribution patterns in species richness do not systematically match those of other biodiversity indices considered important for conservation such as rarity or threat (5, 6). Therefore, we also estimated the distribution of utilized plant species richness weighted by each species' range size (i.e., weighted endemism) to identify areas with high concentrations of rare and potentially irreplaceable species. We find that many areas with high richness of utilized plant species also exhibit high endemism (e.g., Mesoamerica, Gulf of Guinea, Southern Africa, the Himalayas, Southeast Asia; Fig. 1 and fig. S8). Other areas also to emerge as exceptional centers of endemic utilized plant species include California, Macaronesia, Madagascar, the Eastern Mediterranean, the Western Ghats, Sri Lanka, Eastern Australia, and the Pacific islands. Conversely, concentrations of endemic utilized species are relatively low across temperate areas. This confirms that the high species richness observed in some temperate regions is due to a high concentration of well-surveyed, widely distributed, and often-introduced plant species of economic importance (22, 24). Overall, the distribution of utilized plant endemism mirrors patterns observed across all vascular plants, with higher endemism in areas with insularity and high topographic and environmental heterogeneity (25, 26).

The latitudinal distribution of utilized plant species and their different uses

To refine our understanding of the geographic patterns underpinning the diversity of utilized plant species, we disaggregated plant-use reports into 10 use categories, adapted from the Economic Botany Data Collection Standards: human food (including beverages and additives), vertebrate food (forage and fodder), invertebrate food (e.g., plants feeding honey bees or silkworms), materials (e.g., wood, fiber), fuels (e.g.,

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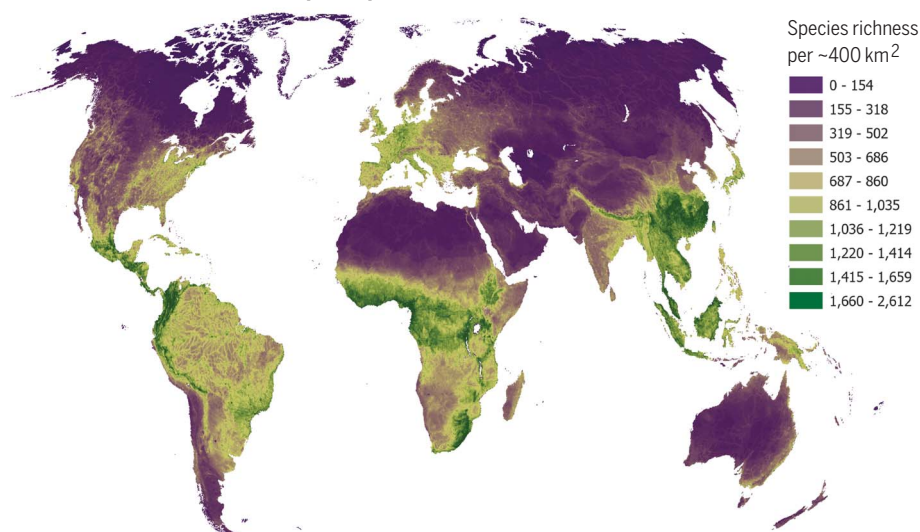
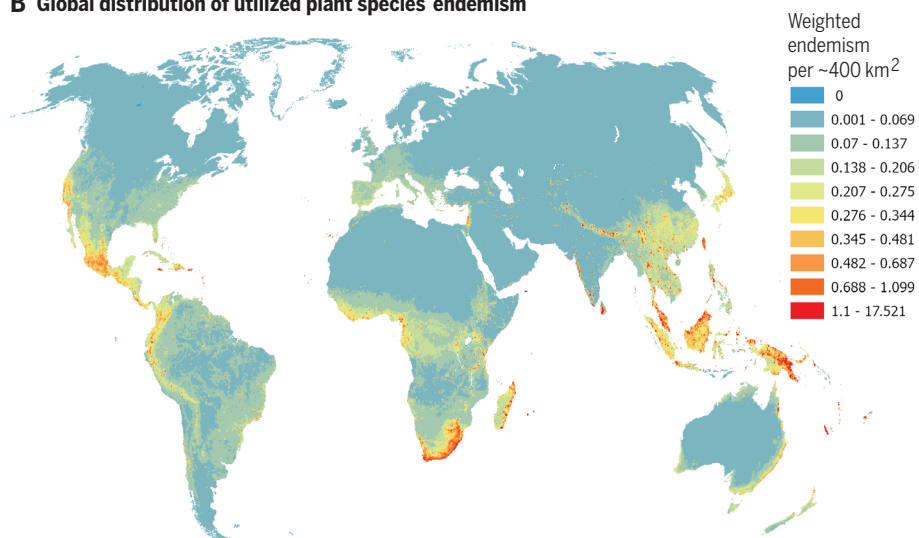
A Global distribution of utilized plant species richness**B Global distribution of utilized plant species endemism**

Fig. 1. Global species richness and endemism of plants with known uses by humans. (A) Utilized plant species richness corresponds to the sum of species occurrence probabilities predicted in each 10 arc min (~20 km) pixel found across their native and introduced ranges. (B) Utilized plant species endemism corresponds to the sum of species occurrence probabilities predicted in each pixel weighted by the inverse of their range size, calculated as the sum of the predicted probabilities within their study region (i.e., weighted endemism). High values are thus associated with areas containing high concentrations of species with small geographic ranges.

charcoal, alcohol), social uses (e.g., narcotics, ritual, religious uses), poisons (for both vertebrates and invertebrates), medicines (for both human and veterinary use), environmental uses (e.g., intercrops, windbreaks, ornamentals), and gene sources (e.g., crop wild relatives) (19, 21). We find that latitudinal variation of utilized plant species richness is broadly consistent for all 10 use categories, with higher values in the tropics gradually declining toward high latitudes (Fig. 2 and figs. S9 and S10). Therefore, areas with high concentrations of uti-

lized plant species also contain large numbers of species for each use type. Despite the overall similarity in latitudinal patterns among use categories, there are notable differences among temperate regions that are proportionally richer in plant species associated with vertebrate food, social uses, and poisons, compared to species-rich tropical environments that contain proportionally more species associated with the most essential uses for human subsistence (i.e., human food, material, and medicine). Concentrations of species used as gene

sources are exceptionally high around the equator and thus diverge from domestication centers originally proposed by Vavilov (27). This is due to our consideration of a larger set of both domesticated species and wild relatives of potential interest for contemporary breeding programs (15). Utilized plant weighted endemism also follows a latitudinal gradient with larger relative concentrations of species at higher latitudes and consistent latitudinal variation among uses (figs. S11 to S13).

Spatial concordance between utilized plant species, total plant species, and human cultures

Although quantitative evidence is scarce, areas of high plant diversity are expected to contain more species that are beneficial to human populations (5). Our global analyses at (sub)country resolution indicate that utilized plant species richness is strongly positively associated with total plant species richness (t value = 20.703, $P < 0.001$; figs. S14 and S15 and table S2), and that this relationship holds for all categories of uses and for endemism (fig. S15 and table S3). It also highlights that large proportions of the flora of relatively low-diversity regions have documented uses (e.g., Scandinavia, Canada, Sahel), whereas smaller proportions of utilized species are reported across megadiverse regions (e.g., Madagascar, Brazil, tropical Andes; fig. S14). Future investigation will be required to identify whether this pattern is due to sampling gaps in our database or in the wider literature for these regions, or because the areas have reached a maximum capacity of utilized plant species richness. Overall, our findings substantiate the combined importance of preserving hotspots of plant diversity, which contain not only many distinctive species but also a considerable diversity of potential services for humanity (1). Nevertheless, although the spatial concordance between total plant diversity and utilized plant diversity is evident at a global scale, it is now crucial to assess whether this pattern holds at smaller scale, where political decisions are taken and management strategies implemented (28, 29).

Biodiversity and cultural diversity have been shown to be highly intertwined spatially, giving rise to the notion of biocultural diversity (7, 30). Our data suggest that cultural diversity not only correlates with total plant richness, but also covaries with utilized plant species richness (t value = 5.743, $P < 0.001$; figs. S14 and S15 and table S2) and inconsistently with endemism indices (fig. S15 and table S3). This finding supports previous hypotheses that geographic similarities between biodiversity and cultural diversity could be due to increased competition or reduced necessity for collaboration among human populations when biological resources (including plants) are widely available, ultimately causing social separation and

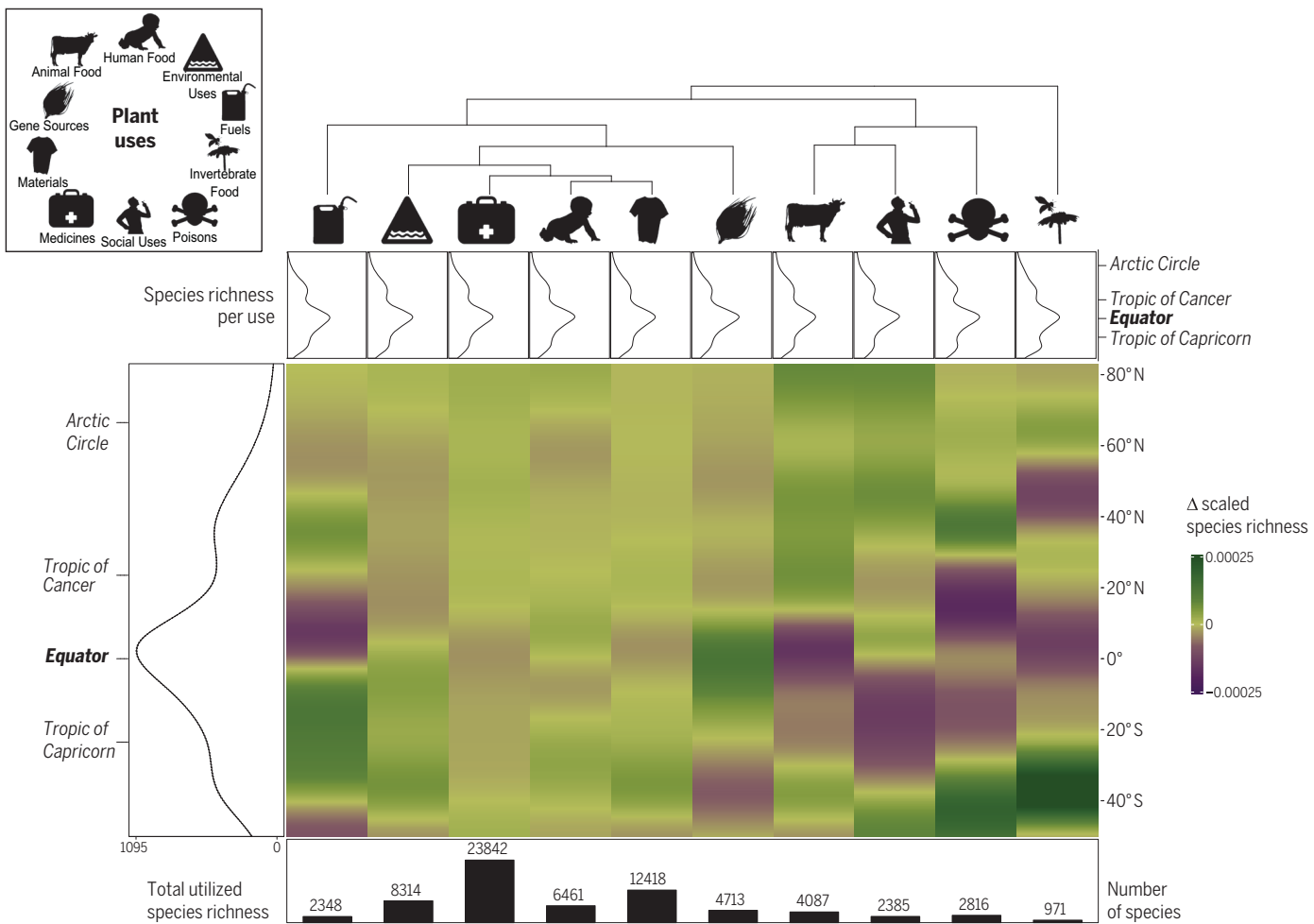


Fig. 2. Latitudinal distribution of utilized plant species richness across 10 categories of plant uses. The black curve on the left represents the latitudinal distribution of all utilized plant species richness. The dendrogram on the top orders the 10 use categories according to the (dis-)similarity of their species richness latitudinal profiles. Black curves underneath the dendrogram correspond to the species richness latitudinal profile for each use category. The heatmap

describes the latitudinal variation in the deviation of utilized plant species richness for the 10 plant-use categories from total utilized plant species richness. Colors indicate higher (green) or lower (purple) proportions in utilized plant species richness of a given use relative to the total utilized plant species richness pattern. The bar chart underneath the heatmap shows the number of species considered in each use category.

generating greater linguistic diversity (7, 30, 31). However, other historical, evolutionary, and environmental factors may also be involved, and the identity and directionality of causal links for these correlations remain elusive and deserve future investigation (7, 30).

Indigenous Peoples and protected areas: Preserving plant diversity and its contributions to people

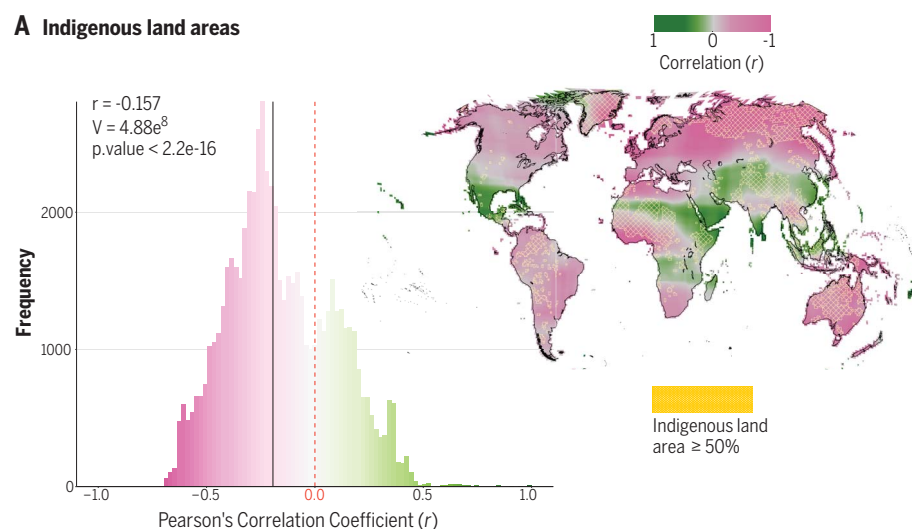
Indigenous Peoples are particularly dependent on wild species for subsistence and well-being, in addition to being critical custodians of both plant diversity and traditional knowledge (32). Unexpectedly, at a large spatial scale, we find that the lands over which the estimated >370 million Indigenous Peoples of the world exert traditional rights do not contain higher concentrations of plant species with globally documented uses compared to neighboring

non-Indigenous regions (Fig. 3 and fig. S17). This finding may reflect the fact that many Indigenous Peoples have been dispossessed of their lands throughout history (33), including biologically diverse areas, and that the largest remaining Indigenous territories are located in remote areas of low primary productivity (e.g., Greenland, Siberia, the Tibetan plateau, the Sahara, Sahel, Central Australia) (34). Exceptions include Indigenous lands located in multiple biocultural hotspots that harbor higher utilized plant species richness and endemism than do surrounding non-Indigenous regions: Central America, the Horn of Africa, South and Southeast Asia. Although Indigenous areas containing exceptionally high utilized plant diversity should be considered priorities for the joint conservation of nature and traditional knowledge (34, 35), Indigenous lands containing fewer species should not be overlooked given

that local populations may be particularly vulnerable to changing environmental conditions and species losses (36). Fostering the engagement of Indigenous, local, and scientific knowledge systems will be essential for enhancing ethics and actions toward protection at multiple scales (37).

Protected areas are at the forefront of global actions to preserve biodiversity and drive sustainable development (38). However, despite currently covering ~17% of Earth's terrestrial surface, the protected area network contributes to the conservation of a small fraction of plant diversity and ecosystem services (16). Spatial correlations between the proportion of land that is protected, and utilized plant species richness and endemism, indicate that regions with large protected area networks do not contain higher numbers or more distinctive utilized plant species than their nonprotected

A Indigenous land areas



B Terrestrial protected areas

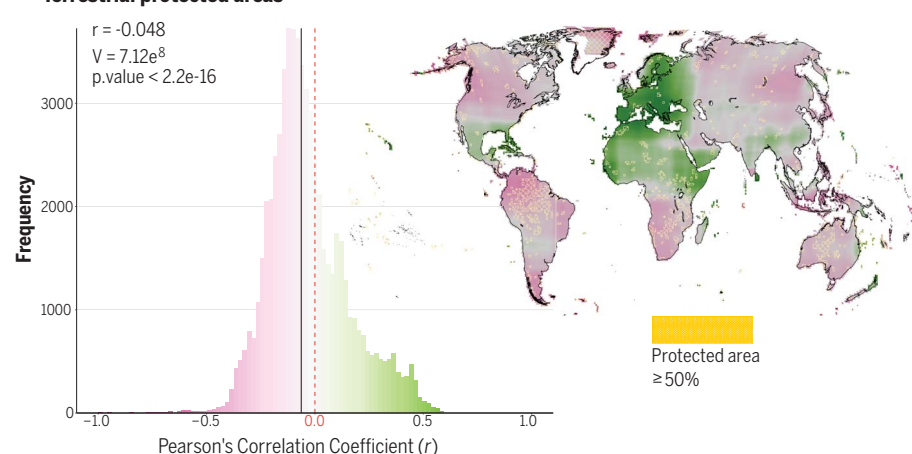


Fig. 3. Spatial correlations between utilized plant species richness and proportions of both Indigenous lands and terrestrial protected areas. (A and B) Pearson's correlation coefficients were computed across all values contained in 71 cells (~3550 km)² wide windows built around each pixel. Pixel color indicates regions where utilized plant species richness is positively (green) or negatively (pink) correlated with the proportion of Indigenous lands and terrestrial protected areas. Regions crossed in beige indicate pixels containing more than 50% of Indigenous lands and protected areas. All Indigenous lands and protected areas are thus not represented on the maps, although they are all accounted for in the analyses. Frequencies of Pearson's correlation coefficients found across the world are given in histograms. The median correlation across the world is indicated by the black vertical line, and zero correlation is indicated by the red dashed line. One-sample Wilcoxon signed rank tests were performed to assess whether median correlations are significantly different from zero.

counterparts (Fig. 3 and fig. S17). Indeed, although protected areas in Europe, the Mediterranean, West Africa, and the Horn of Africa contain more and more distinctive utilized plant species than nonprotected neighboring regions, several regions exhibit higher relative richness and endemism of utilized plant species outside of protected areas (e.g., Americas, Southern Africa, Southeast Asia, Australia). Our results point to the urgent need of considering plant diversity and its contributions to people in future area-based conservation planning (10, 29, 39), especially under the ambitious Target 4 of the

GBF, which aims to conserve biodiversity across 30% of global land areas by 2030 (40). The latter also acknowledges the importance of “recognizing and respecting the rights of Indigenous Peoples and local communities” and “ensuring that any sustainable use...is fully consistent with conservation outcomes.” In this context, it is essential to strike an appropriate balance between strictly protected areas that limit access to humans, and protected areas that accommodate the sustainable use of natural resources by local populations while preserving their well-being and cultural heritage (41, 42).

Halting the overexploitation of species and ensuring their sustainable use have also been highlighted as a key priority by the GBF, notably in Target 5. The sustainable management of a few animal and plant species has proved to be an efficient tool for conservation (43, 44). However, the sustainability of species use remains unknown across most plant diversity. Out of 2800 utilized plant species previously assessed by the International Union for Conservation of Nature (IUCN), more than 1 in 3 is considered to be at risk of global extinction (43). More than 1 in 10 plant species with a documented human food use in our study is also considered globally threatened (45). Although our findings show that utilized plant diversity remains largely underprotected in the wild, most species (and their genetic diversity) additionally lack representation in ex situ collections such as seed banks and botanical gardens (46). Documenting and understanding the diversity and distribution of plant species used by humans are thus crucial to implement conservation strategies and develop plant-based solutions to address global societal challenges such as hunger, diseases, and climate change (47–49). Our study aims to pave the way for efforts toward reconciling human needs and biodiversity protection for a more sustainable future.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S17
Tables S1 to S3
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