Lessons from 20 years of plant genome sequencing: an unprecedented resource in need of more diverse representation

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Abstract

The field of plant genomics has grown rapidly in the past 20 years, leading to dramatic increases in both the quantity and quality of publicly available genomic resources. With an ever-expanding wealth of genomic data from an increasingly diverse set of taxa, unprecedented potential exists to better understand the evolution and genome biology of plants. Here, we provide a contemporary view of plant genomics, including analyses on the quality of existing plant genome assemblies, the taxonomic distribution of sequenced species, and how national participation has influenced the field's development. We show that genome quality has increased dramatically in recent years, that substantial taxonomic gaps exist, and that the field has been dominated by affluent nations in the Global North, despite a wide geographic distribution of sequenced species. We identify multiple inconsistencies between the range of focal species and the national affiliation of the researchers studying the plants, which we argue are rooted in colonialism--both past and present. Falling sequencing costs paired with widening availability of analytical tools and an increasingly connected scientific community provide key opportunities to improve existing assemblies, fill sampling gaps, and, most importantly, empower a more global plant genomics community.

Introduction

The pace and quality of plant genome sequencing has increased dramatically over the past 20 years. Since the genome of *Arabidopsis thaliana*--the first for any plant--was published in 2000[1], over 1,000 plant genomes have been sequenced and made publicly available on GenBank, the leading repository for genomic data[2]. With large, complex genomes and varying levels of ploidy, plant genomes have been difficult to assemble historically, but technological advances, such as long-read sequencing, and new computational tools have had a major impact on the field[3–5]. As a result, the number and quality of plant genome assemblies is increasing, enabling the exploration of both evolutionary and applied questions in unprecedented breadth and detail.

Land plants (Embryophyta) are extremely diverse and publicly available genome assemblies span over ~500 million years of evolution and divergence[6]. However, only a small fraction (~0.16%) of the ~350,000 extant land plants have had their genome sequenced. Furthermore, sequencing effort has not been evenly distributed across clades[7]. For some plants (e.g., maize, arabidopsis, and rice[8–10]) multiple high-quality genome assemblies are available and thousands of accessions, cultivars, and ecotypes have been resequenced using high coverage Illumina data for other crop and model species[11]. Brassicaceae, a medium sized plant family, is the most heavily sequenced, with genome assemblies available for dozens of species including Arabidopsis and numerous cruciferous vegetables. These densely sampled clades are ideal systems for investigating intraspecific variation and pan-genome structure. In contrast, for most other groups, none or only a single species has a genome assembly. Ambitious efforts to fill taxonomic sampling gaps exist, including the Earth BioGenome, African BioGenome, and 10kp projects[12,13] among others, but individual researchers can also play a role in expanding taxonomic representation in plant genomics.

The field of plant genomics is expanding rapidly, and a new generation of genomic scientists is being trained. Consequently, this is an ideal time to assess scientific progress while also developing strategies to increase equity and expand participation in plant genomics. The history of colonialism has impacted all scientific disciplines, including genomics. Imperial colonialism provided scientists from the Global North access to a wealth of biodiversity, raw materials, and ideas that would have otherwise been inaccessible to them[14–16]. Over time, this led to a disproportionate accumulation of wealth and scientific resources in the Global North[17], which has contributed to the establishment and maintenance of global inequality[14,16,18]. Today, differences in funding, training opportunities, publication styles, and language requirements continue to drive similar patterns[16,19,20]. In plant genomics, the high costs of sequencing and provisioning computational resources are barriers to entry for less affluent institutions that perpetuate existing imbalances established due to scientific colonialism. Luckily, the diminishing cost and increasing accessibility of sequencing technologies provides an opportunity to broaden participation in plant genomics and increase equity. This will require affluent nations and individuals to recognize their disproportionate access to biological and genetic resources and seek to increase participation rather than capitalizing on their economic privilege.

Here, we provide a high-level perspective on the first 20 years of plant genome sequencing. We describe the taxonomic distribution of sequencing efforts and build on previous estimates of genome availability and quality[21–23]. We show that an impressive and growing number of plant genome assemblies are now publicly available, that quality has greatly improved in concert with the rise of long-read sequencing, but that substantial taxonomic gaps exist. We also describe the geographic landscape of plant genomics, with an emphasis on representation. We highlight the need for the field, including its many northern researchers and institutions, to work towards broadening participation. In our view, the wealth of publicly available plant genome assemblies can be leveraged to better understand plant genome biology while also continuing to decolonize a major field of research.

Results

As of January 2021, 1,122 land plant genome assemblies were available on GenBank, representing 631 unique species. To compare resources within and across groups, we selected the highest quality genome (based on contiguity) as a representative for each species. Unless otherwise noted, all analyses were conducted on this curated dataset of 631 genome assemblies (Table S1).

The number of plant genome assemblies has increased dramatically in the past 20 years, with marked improvements in quality associated with the advent of long-read sequencing (Fig. 1). Overall, 59% of plant genome assemblies were produced in the last 3 years. Contig N50, the length of the shortest contig in the set of contigs containing at least 50% of the assembly length, also increased markedly in recent years, from 125 ± 57.6 Kb in 2010 to 3,186 ± 846 Kb in 2020. This increase appears to be driven primarily by advancements in sequencing technologies. Assemblies constructed with short-read technology (e.g., Illumina and Sanger) have significantly lower ($p<0.0001$) contig N50 (120.6 ± 94.9 Kb) compared to those that incorporate long reads (e.g., PacBio and Oxford Nanopore) which have a contig N50 of 3,929 ± 730 Kb. This difference translates to an impressive ~31x increase in mean contig N50 for long-read assemblies.

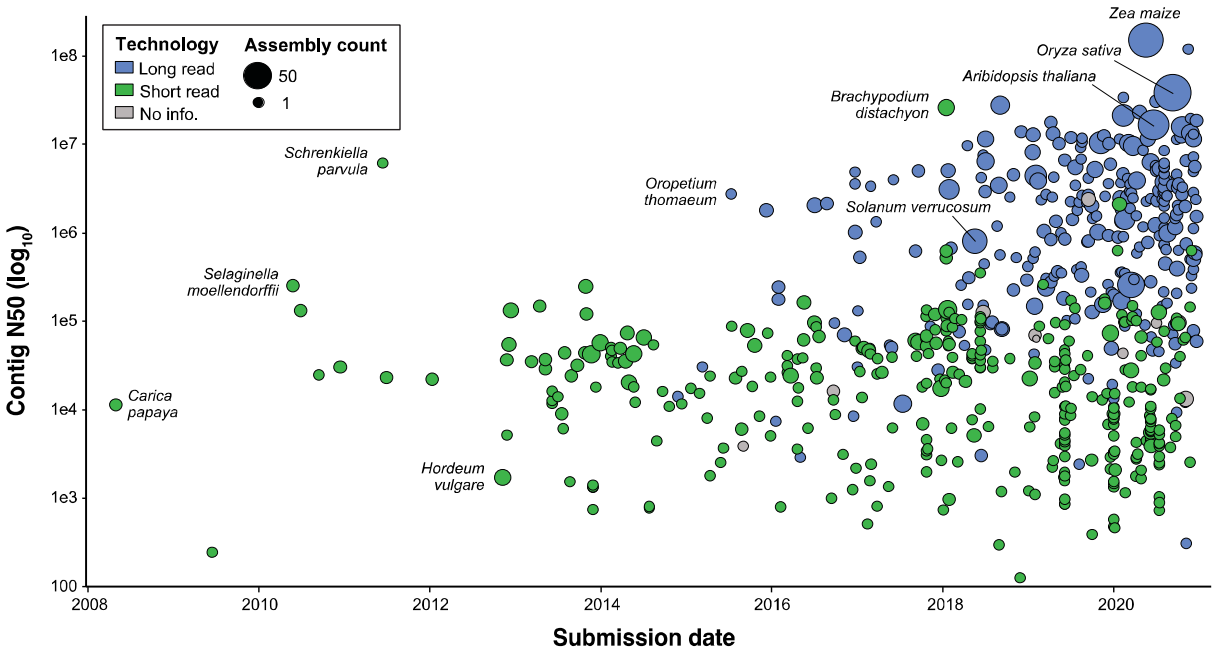

Figure 1. Changes in plant genome assembly quality and availability over time. Assembly contiguity by submission date for 631 plant species with publicly available genome assemblies. Points are colored by the type of sequencing technology used and scaled by the number of assemblies available for that species. There is an improvement in contiguity associated with the advent of long-read sequencing technology, and a noticeable increase in the number of genome assemblies generated annually. Assemblies generated prior to 2008 have since been updated and are therefore not included.

The first plants to have their genomes sequenced were model or crop species with simple genomes, but it is now feasible to assemble a genome for virtually any taxon. Still, sampling gaps persist. Of the 138 land plant orders that have been described[24], more than half (86) lack a representative genome assembly on GenBank. For the 52 orders with at least one genome assembly, a wide range of sampling depth is evident. For example, there are 73

species with sequenced genomes in Brassicales, 63 in Poales, and 54 in Lamiales, yet there are 36 orders with just 10 or fewer sequenced species. Genome assemblies are statistically over-represented in seven vascular plant orders based on species richness. These include the agriculturally and economically important clades of Brassicales, Cucurbitales, Dioscoreales, Fagales, Malvales, Myrtales, and Solanales. Four orders of vascular plants had significantly fewer genome assemblies than expected based on their species richness (Fig. 2). Not surprisingly, these were speciose orders with significant ecological but comparatively less economic importance--Asparagales, Asterales, and Gentianales--and the primarily polyploid order of Polypodiales (Fig. 2a). Bryophytes are poorly represented with assemblies for only three mosses, three liverworts, and a single hornwort (Fig. 2a and Fig. S1). However, recent work describes another two moss (*Sphagnum spp.* and *Syntrichia spp.*) and two hornwort (both *Anthoceros spp.*) genome assemblies that are not yet available on GenBank[23]. Diploid species are also statistically overrepresented in terms of genome availability (Fig. 2b and Fig. S1) despite the widespread occurrence of polyploid plants[25]. Until recently, technological limitations have made it difficult to assemble high-quality polyploid genomes[4]. To illustrate this point, the most polyploid species represented in our dataset (*Trifolium medium*, n=10) also has a very low contig N50 of 292 bp. However, with the improvements that long-read sequencing technology offers, it is becoming more feasible to sequence and assemble complex polyploid genomes, and there are some highly contiguous tetraploid and reasonably contiguous hexaploid genome assemblies with mean contig N50's of 1,855.7 ± 474.3 Kb and 251.9 ± 99.8 Kb respectively (Fig. S1).

To further assess differences in assembly quality and completeness, we quantified the percentage of Benchmarking Universal Single-Copy Orthologs (BUSCO; v.4.1.421) from the Embryophyta gene set in OrthoDB v.10[26] that were present in each genome assembly. There was a high degree of variability in BUSCO completeness; percentages of complete BUSCOs (single and duplicated genes) ranged from 0 to 99% (Fig. 2d). More contiguous genome assemblies (higher contig N50) had more complete BUSCOs ($p<0.0001$), driven largely by the use of long reads in the assembly process ($p<0.001$; Fig. 2c-d and Fig. S3). Despite the wide range of assembly quality and completeness, no significant associations with taxonomy were identified ($p=0.99$).

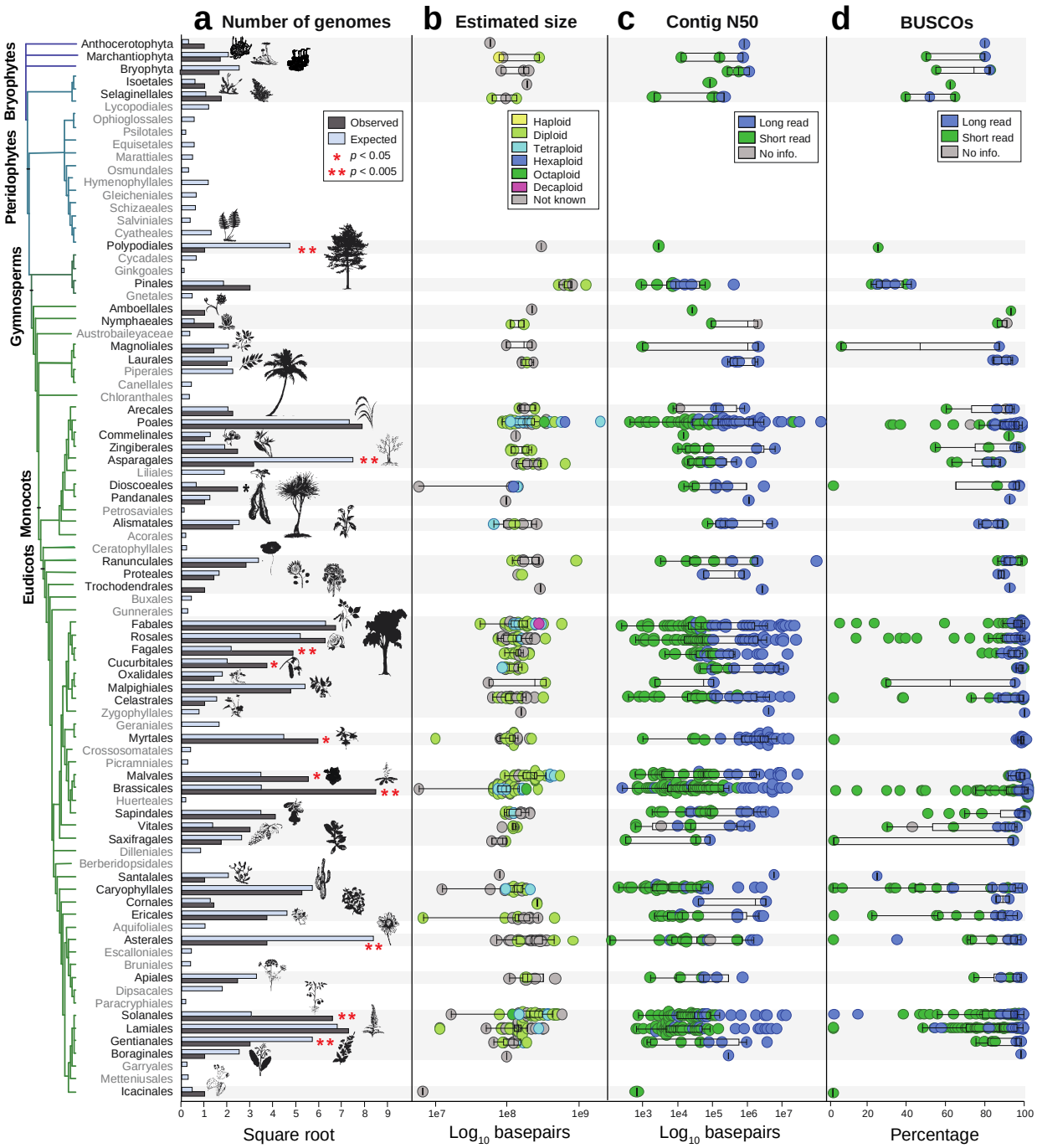

Figure 2. Comparison of genome availability and quality metrics for each land plant order. a) The number of species with publicly available genome assemblies on GenBank as of January 2021 (n = 631) versus the number expected for each order. Orders with no genome assemblies are shown in grey. Bryophytes are plotted at the phylum level but see Fig. S2 for bryophyte orders. Orders that showed a significant over- or under-representation are marked with asterisks. **b)** Estimated genome size for each assembly from k-mer or flow cytometry-based estimations as reported with each submission. Points are colored by ploidy. **c)** Contig N50 for each genome assembly. **d)** Percentage of complete BUSCOs for each genome assembly. For (c) and (d), points are colored by sequencing technology.

To better understand national participation in plant genomics, we identified the submitting institution for each genome assembly in our data set. If the submitting institution was not listed, we identified the corresponding author for the associated publication and assigned the genome to the location of that institution. While this approach does not account for secondary affiliations in other nations, it does reveal where most of the scientific credit for a genome assembly is likely placed. We find that plant genome sequencing is dominated by the USA, China, and central Europe, with 76% of genome assemblies attributed to one of those three regions (Fig. 3). Far fewer plant genome assemblies have been attributed to the Global South; only 40 assemblies from Oceania, 12 from Central and South America, and a single genome with a primary affiliation in Africa. These patterns likely reflect well-documented differences in training incentives, facilities, and funding opportunities between nations[20,27–29], many of which have been established and perpetuated through colonial practices[16].

Figure 3. The geographic distribution of submitting institutions for plant genome assemblies. Circles are scaled by the number of genome assemblies produced in each nation and colored by the relative proportion of domesticated, cultivated, feral, natural commodity, wild, and wild relative species sequenced.

It is noteworthy that many of the sequenced plant genomes are of species that are native to or have economic importance in the Global South but have been sequenced elsewhere. We compared the center of diversity for 110 major domesticated crops[30] with the location of the institution that sequenced and assembled their genome. Although we did not account for geographical patterns of contemporary cultivation, the findings shed light on a disconnect between the origin of many crop species and the institutions leading genomic research on these species. While there has been some reciprocal exchange between continents, the Global North has sequenced far more non-native species than native species, and nearly all the species native to the Global South have been sequenced elsewhere. This represents a substantial global imbalance in genomics, with the Global South functioning as an exporter (possibly non-consensually) of plant genomic materials. There are dozens of major crops native to Africa and South America represented in GenBank, yet only two (*Persea americana* and *Phaseolus lunatus*) have primary affiliations in South America and none in Africa

(Fig. 4). International collaborations can be mutually beneficial, but it is likely that in some instances of off-content genomics, sequenced material is chosen with minimal input from local stakeholders. Thus, the resulting genome assemblies may not represent the germplasm grown in production regions, making the science less relevant where it matters most. That being said, there are a growing number of inclusive and collaborative plant genomics projects such as the Orphan Crop Genome Consortium (http://africanorphancrops.org) and Africa BioGenome project that are broadening participation in plant genomics by including diverse stakeholders at multiple levels[20].

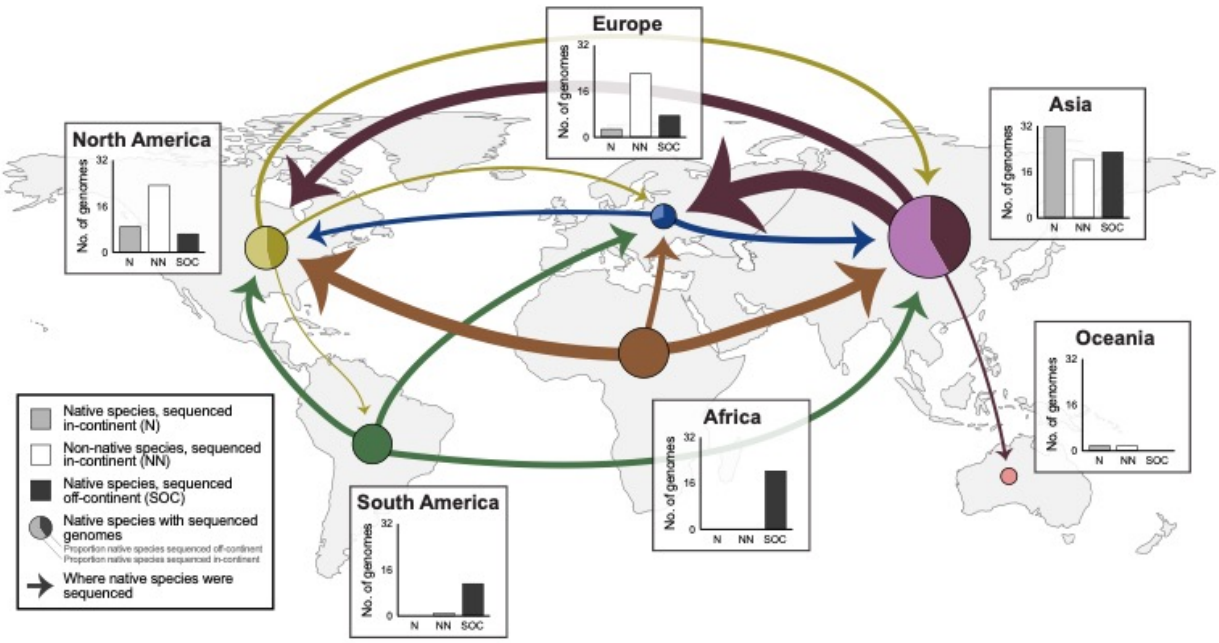

Figure 4. A geographic perspective on where domesticated species (N=110) are native to versus where their genome assemblies were produced. The continents where arrows terminate represent where species were sequenced. Circle size and arrow weights are scaled by the number of genome assemblies being represented.

We suspected that there has been a preference for sequencing economically important plants compared to wild or ecologically important species. To explore this, we classified the domestication status of each species with a genome assembly into six categories: (1) *domesticated* plants that have undergone extensive artificial selection, (2) *cultivated* plants that are used by humans but have not been subjected to substantial artificial selection, (3) *natural commodity* plants that are harvested with little cultivation, (4) *feral* plants that are not economically important but have still been influenced by human selection, (5) *wild* plants that occur in the wild and have not been directly impacted by humans, and (6) *wild relatives* plants that are closely related to domesticated or cultivated crops. Based on these categories, genome assemblies are available for 125 domesticated, 85 cultivated, 85 natural commodity, and 10 feral species. The remaining 328 genome assemblies are from wild species. Of these, 65 are wild relatives of crops (Fig. 3 and S4). While the number of human-linked (domesticated, cultivated, natural commodity, and feral) species with genome assemblies is largely equivalent to wild species and their relatives, this equivalence reflects an extreme bias. There are far more wild (~350,000[31]) than domesticated (~1,200-2,000 species[32,33]). Thus, wild plants clearly represent an untapped reservoir of genomic information.

Discussion

The field of plant genomics has grown rapidly in the last 20 years, giving rise to an array of new tools, datasets, and insights into plant biology. The quality of genome assemblies being produced today is much improved compared to even a few years ago, and this trend shows no signs of slowing. As has been observed for insects[34], the improvement in plant genome quality appears to be driven largely by increased use of long-read sequences in assemblies. These technologies have enabled assembly of increasingly complex and polyploid genomes, opening up new arenas of research for plant genomocists. Despite these advances, major biases exist in both taxonomic sampling and participation. As the field continues to grow, there is an opportunity to fill key taxonomic gaps and build a broader, more representative discipline.

To date, plant genome scientists have focused mainly on sequencing economically important and model species with relatively simple genomes. This has led to major agricultural breakthroughs and fundamental scientific insights. However, this approach has overlooked the wealth of information contained within the genomes of wild plants, which are extremely diverse, and largely untapped. Wild plants exhibit numerous diverse properties and produce a wide range of secondary compounds, many of which have important traditional and emerging pharmaceutical and industrial applications[35]. Many medical therapeutics and commercial materials are derived from or made to mimic plant-based compounds[36], yet we have only begun to explore the rich chemical diversity of wild plants. Given the rapid loss of global biodiversity, it is critical that we take the opportunity to learn what we can from wild species before they disappear. Over the past ~100 years, we have witnessed a 60% increase in plant extinction[37], and despite conservation efforts, this loss of biodiversity is projected to continue even under the most optimistic scenarios[38]. Improving genomic technologies provide an opportunity to explore, catalogue, and mine the immense diversity of information contained within wild species.

In addition to taxonomic gaps, participation gaps are also prevalent in plant genomics. The field is dominated by just a handful of affluent nations. We argue that these dynamics are rooted in historical colonialism, economic barriers to entry, and perpetuated by contemporary "parachute science". Historically, science was intimately linked to the rise of imperial colonialism[14–16]. Innovations in navigation and cartography enabled conquest of new territories by nations in the Global North and scientific curiosity actually motivated many early colonial expeditions[14]. Once colonies were established, they became the first sites for parachute science. Imperial scientists would drop in, make collections, and take credit for any "discoveries" made, frequently discounting the substantial knowledge held by local indigenous communities. Over time, this led to a disproportionate accumulation of wealth in the Global North that continues to drive economic disparities and participation imbalances in science today[16–18]. Despite outward criticism of colonialism and legal provisions aimed at preventing international transport of biological and genetic resources (e.g., the Nagoya Protocol), affluent nations continue to lead bio and genomic prospecting efforts and parachute science remains prevalent[40,41].

Our analyses reveal a discrepancy between where species originate and where their genomes are sequenced and assembled. Much of the evolutionary innovation observed in landraces, locally adapted cultivars, and wild plants is exclusively maintained in the Global South, but only a handful of genome assemblies have been led by teams in those regions. In our view, the rich local knowledge associated with the global reservoir of plant diversity[39,42] should form the backbone of future genomics projects. Currently there are over a dozen plant genomics projects with African institutions as partners[20], collaborative projects integrating indigenous knowledge[42], and large-scale consortia with multinational participants are being established, all of which could help broaden participation in plant genomics. As American scientists, the authors acknowledge our own implicit and sometimes explicit participation in the

sequencing and analysis of non-native plants, but we are committed to including and uplifting local participants in future work. We encourage all plant scientists to strive to support local stakeholders, to incorporate indigenous knowledge into their work, and to invest in building systems and expertise for working with genomic resources in the location where they occur naturally. We believe that local institutions should be encouraged to lead and be the first to publish genomic data for native species.

The field of plant genomics has arrived at an exciting moment with a rapidly expanding pool of genomic resources being generated by an increasingly diverse group of scientists. However, to take full advantage of the opportunities that a modern discipline affords and to ensure that the field continues striving for equity, we offer three recommendations. (1) Plant genome scientists should embrace long-read sequencing technologies and leverage them whenever possible to generate new assemblies. This is already occurring but given the massive disparity in quality between assemblies generated with short-read versus long-read data, the need for continued adoption cannot be overstated. (2) Despite considerable progress, the taxonomic scope and domestication status of plants with available genome assemblies should continue to be expanded. In our view, attention should be focused on generating assemblies for clades that have none (e.g., Hymenophyllales, Cyatheales, Geraniales, Dipsacales; see Fig. 2a), adding more complex plant genome assemblies (e.g., repetitive and/or polyploid), and sequencing wild species. (3) While the progress driven by large-scale consortia is undeniable, it is important that researchers in the discipline are mindful of the signatures of colonialism--past and present--in plant genome science. To this end, we should collectively monitor consortia, collaborations, and projects to ensure that ethical approaches are being taken, in-country peoples are given a voice, and that participation and access to resources is broadened at every level. Ultimately, a diverse, thriving discipline with empowered researchers across continents regardless of socioeconomic status will yield the greatest potential to meet the economic, social, and evolutionary challenges facing 21st century plant science.

Methods

Data associated with this project are provided in Table S1. We compiled all land plant genome assemblies that were publicly available on GenBank, in January 2021. From this set, we retained the single most contiguous genome for each species. Genome assemblies were downloaded using the *download-genome* function of NCBI's datasets tool (v.10.9.0). Genome meta-data were extracted using the *assembly-descriptors* function of NCBI's datasets tool. Higher level taxonomy for each species was integrated with taxonkit[43]. Data on sequencing technology, coverage, and assembler were retrieved using the python script *scrape_assembly_info.py* available at: https://github.com/pbfrandsen/insect_genome_assemblies. For genome assemblies with no reported sequencing technology on GenBank, we went to the publication associated with the assembly (if available), and identified the sequencing technology from the reported methods.

To place species in a phylogenetic context, we identified the most up-to-date phylogenies for each major group of land plants and grafted them together. For angiosperms we used the APG IV tree[44], for gymnosperms and pteridophytes we used the APGweb tree (http://www.mobot.org/MOBOT/research/APweb), and for bryophytes we used iTol[45]. Many of the relationships among these groups are still poorly resolved or under ongoing revision, but for the purposes of this work, they are sufficient to visualize general relationships among clades.

We tested for an over- or under-representation of genome assemblies in each land plant order using Fisher's Exact Tests to identify cases where the observed number of genome assemblies differed significantly from the expected number based on species richness. To do

so, we compiled a list of the total numbers of species in each land plant order. For vascular plants we used the Leipzig Catalogue of Vascular Plants (LCVP; v 1.0.3)[24] in combination with the summaries provided in[46]. For bryophytes, we compiled data from the Plant List (http://www.theplantlist.org; accepted names only) and cross referenced these against the Missouri Botanical Gardens *Index of Bryophytes* (http://www.mobot.org/mobot/tropicos/most/bryolist.shtml).

We pulled data on chromosome number and ploidy from the Kew Botanical Garden's plant C-values database[47], from which we calculated the total number of species reported to have a given ploidy level. We used these data to calculate the expected values for Fisher's Exact Tests to test for over- or under- representation of genome assemblies with each ploidy level.

We investigated the completeness of genome assemblies by quantifying the percentage of complete, fragmented, and missing Benchmarking Universal Single-Copy Orthologs (BUSCO; v.4.1.421) from the Embryophyta gene set in OrthoDB v.10[26]. We ran BUSCO (v.4.1.4) in *--genome mode* on each assembly with the *--long* option. We tested for an association between the contiguity of genome assemblies (contig N50) and the percentage of complete BUSCOs (single and duplicated) using a mixed effects linear model. The estimated genome size was included in the model as a random effect. Similarly, we tested for an effect of sequencing technology on the percentage of complete BUSCOs, with the estimated genome size included as a random effect.

To estimate the geographic distribution of plant genome projects, we identified the submitting institution for each genome assembly in our data set. If the submitting institution was not listed, we identified the corresponding author for the publication and assigned the genome to the location of that institution. Next, we compiled data on the center of diversity for 110 of the world's major crops using the data provided in[30]. We used these data to compare the location of the sequencing institution to the center of origin for all crops.

We classified the domestication status of each species using a six-category scale. Each species was designated as either (1) *domesticated* plants that have undergone extensive artificial selection, (2) *cultivated* plants that are used by humans but have not been subjected to substantial artificial selection, (3) *natural commodity* plants that are naturally harvested with little cultivation, (4) *feral* plants that are not economically important but have still been influenced by human selection, (5) *wild* plants that occur in the wild and have not been directly impacted by humans, and (6) *wild relatives* plants that are closely related to domesticated or cultivated crops.

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