Legacy genetics of *Arachis cardenasii* in the peanut crop shows the profound benefits of international seed exchange

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The narrow genetics of most crops is a fundamental vulnerability to food security. This makes wild crop relatives a strategic resource of genetic diversity that can be used for crop improvement and adaptation to new agricultural challenges. Here, we uncover the contribution of one wild species accession, *Arachis cardenasii* GKP 10017, to the peanut crop (*Arachis hypogaea*) that was initiated by complex hybridizations in the 1960s and propagated by international seed exchange. However, until this study, the global scale of the dispersal of genetic contributions from this wild accession had been obscured by the multiple germplasm transfers, breeding cycles, and unrecorded genetic mixing between lineages that had occurred over the years. By genetic analysis and pedigree research, we identified *A. cardenasii*–enhanced, disease-resistant cultivars in Africa, Asia, Oceania, and the Americas. These cultivars provide widespread improved food security and environmental and economic benefits. This study emphasizes the importance of wild species and collaborative networks of international expertise for crop improvement. However, it also highlights the consequences of the implementation of a patchwork of restrictive national laws and sea changes in attitudes regarding germplasm that followed in the wake of the Convention on Biological Diversity. Today, the botanical collections and multiple seed exchanges which enable benefits such as those revealed by this study are drastically reduced. The research reported here underscores the vital importance of ready access to germplasm in ensuring long-term world food security.

peanut | wild species | disease resistance | food security | Convention on Biological Diversity

Globally, most of humanity's food is produced by only a few crop species, most of which have low genetic diversity (1–4). This presents a fundamental limitation to genetic improvement of crops and a key vulnerability for food security. Wild crop relatives have been used as a strategic source of diversity for plant breeders (4, 5). However, the agronomically unadapted phenotypes of wild species have hampered their use. For peanut (*Arachis hypogaea* L.), a crop with an exceptionally narrow genetic base (6, 7), the incorporation of wild relatives into breeding programs is further impeded

Significance

A great challenge for humanity is feeding its growing population while minimizing ecosystem damage and climate change. Here, we uncover the global benefits arising from the introduction of one wild species accession to peanut-breeding programs decades ago. This work emphasizes the importance of biodiversity to crop improvement: peanut cultivars with genetics from this wild accession provided improved food security and reduced use of fungicide sprays. However, this study also highlights the perilous consequences of changes in legal frameworks and attitudes concerning biodiversity. These changes have greatly reduced the botanical collections, seed exchanges, and international collaborations which are essential for the continued diversification of crop genetics and, consequently, the long-term resilience of crops against evolving pests and pathogens and changing climate.

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The authors declare no competing interest.

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by barriers in sexual compatibility between the tetraploid crop and its almost exclusively diploid wild relatives (8–10). This ploidy difference arose 5,000 to 10,000 y ago with the formation of the tetraploid species, via the hybridization and spontaneous polyploidization of the diploid "A" genome species, *Arachis duranensis* Krapov. & W.C. Greg. and the "B" genome species, *Arachis ipaënsis* Krapov. & W.C. Greg. The resultant tetraploid diversified into many peanut (*A. hypogaea*) landraces and varieties through artificial selection during cultivation. Peanut maintains almost-complete sets of chromosomes from the two ancestral diploid species thus having a genome almost entirely of "AABB" structure, a type of polyploid termed a segmental allotetraploid (2n = 4x = 40 chromosomes; genome size of ~2.7 Gb; 6, 11, 12).

Despite the difficulties presented by the ploidy barrier, considerable effort was invested during the 1960s in complex hybridizations between peanut and a diploid "A" genome wild species accession from Bolivia, *Arachis cardenasii* Krapov. & W.C. Greg. GKP 10017 [PI (Plant Introduction) 262141]. Interest in this accession had been stimulated by its identification as a source of very strong pest and disease resistance (13). Using two different hybridization schemes, two different research groups obtained fertile progeny which entered into breeding programs (see *Results* for more details). However, over time, the subsequent dispersal and development of the resultant germplasm, with multiple seed transfers, identification code reassignments, breeding cycles, and unrecorded mixing of lineages, left the actual genetic contribution of the wild species mostly forgotten, unrecorded, or undefined.

Here, we reveal the previously unknown scale of the genetic influence of *A. cardenasii* GKP 10017 as a donor of pest and disease resistances to the world's peanut crop. This study involved the sequencing and assembly of the genome of this wild species accession and genetic analysis and pedigree research of diverse peanut lines from around the world. Peanuts with genetic contributions from *A. cardenasii* were identified on every populated continent and in 30 countries. The cultivars provided improved food security for subsistence farmers and environmental and economic benefits.

Results

The investigative work reported in this manuscript started some years ago when we began to suspect that a breeding line in Brazil, previously thought to be of pure cultivated peanut pedigree, may owe its exceptional resistance against foliar pathogens to ancestry of the wild species accession *A. cardenasii* GKP 10017. Over several years, the scope of our investigation grew, involving genetic and genome analyses, personal communications, and the searching of records, reports, and published papers. To refine these analyses and to provide a genetic resource for future research, we developed a reference quality genome of *A. cardenasii* GKP 10017 [PI 262141; GenBank JADQCP000000000 (14); PeanutBase] using ~43X coverage PacBio sequences. The assembled DNA sequences were composed of 24 scaffolds and formed the expected 10 chromosomes, with total size of 1.13 Gb. There is a one-to-one correspondence between the chromosomes of *A. cardenasii* GKP 10017 and the A subgenome of *A. hypogaea*. Modal identity between the two genomes is 96 to 97% (*SI Appendix*).

We identified genetic contributions of *A. cardenasii* GKP 10017 in cultivated peanuts using characteristic single-nucleotide polymorphisms (SNPs) assayed using the Axiom Arachis Genotyping Array (15) and Illumina whole-genome sequencing. Using comprehensive Axiom Array genotyping panels of 256 wild *Arachis* accessions representing almost all botanical collections of the 31 described diploid species in the botanical section *Arachis* (including all 19 accessions of *A. cardenasii*) and 383 *A. hypogaea* of pure pedigree from the US Core collection (16), we identified 707 SNPs characteristic of *A. cardenasii* GKP 10017. All these SNPs distinguished *A. cardenasii* GKP 10017 from the 383 *A. hypogaea* of pure pedigree. Furthermore, contiguous stretches of these SNPs uniquely identified *A. cardenasii* GKP 10017 among the 256 wild accessions; the wild accession most closely related to *A. cardenasii* GKP 10017, a different accession of the same species, had less than one-half (352) of these characteristic SNPs (*SI Appendix*, Fig. S1 and Dataset S1) (17). For fine-scale analysis, we used whole-genome sequencing of 19 of the most phylogenetically diverged representatives of the tetraploid species to identify 2.3 million SNPs characteristic of *A. cardenasii* GKP 10017 (Dataset S2). This comparison set of 19 diverged tetraploids included both subspecies and all six botanical varieties of *A. hypogaea* and the wild tetraploid species of common origin, *Arachis monticola* Krapov. & Rigoni (*SI Appendix*, Table S1).

Using these characteristic SNPs, *A. cardenasii* GKP 10017 chromosome segments were detected in 82 registered peanut lines and cultivars (Fig. 1 and Dataset S3). This information, together with pedigrees, allowed the inference of about 169 more. These 251 peanut lines and cultivars were distributed in 30 countries on every populated continent (Dataset S4). The greatest genome coverage and diversity of introgression patterns was uncovered in the United States, where we detected *A. cardenasii* GKP 10017 genetic contributions from eight chromosomes (all except A04 and A06) in 32 registered peanut germplasm lines and cultivars (Fig. 1 and Dataset S3). The introgressions from chromosome A09 have been previously well defined and derive from an introgression scheme known as the "tetraploid route," which was developed at Texas A&M University (9). This route involved crossing A and B genome diploids to produce a sterile AB diploid hybrid. Fertility was regained by treatment with colchicine to produce an AABB tetraploid, which in turn was hybridized with *A. hypogaea* to give fertile progeny. Introgressions via the tetraploid route gave rise to the only source of nematode resistance currently deployed in the peanut crop and are mostly confined to the United States, where this pest is of greatest importance (18, 19). However, the great majority of the introgressions found worldwide could be traced back to a different hybridization scheme known as the "hexaploid route" which also used *A. cardenasii* GKP 10017. This work was initiated in the 1960s at North Carolina State University. The wild diploid species *A. cardenasii* GKP 10017 (from Bolivia) was crossed with a purple-seeded peanut, *Arachis hypogaea* subsp. *fastigiata* (accession PI 261942, from Paraguay), to produce a sterile triploid with an AAB genome (20). This was colchicine treated to induce chromosome doubling, resulting in a hexaploid with an AAAABB genome and partially restored fertility. After five generations of selfing, progenies spontaneously returned to the fully fertile AABB tetraploid state (13). Two very large introgressions from the hexaploid route were found from chromosomes A02 and A08 in the US peanut cultivar 'Bailey,' a pattern found in some legacy North Carolina breeding lines with the nomenclature prefix "WS" (Dataset S3). With good resistance to fungal leaf spots, Bailey is the most widely grown cultivar in North Carolina and has simultaneously allowed the reduction of fungicide sprays and increase in yields (21). A different characteristic pattern of introgression was found in some North Carolina breeding lines denominated with the prefix "CS" (cercospora spot): two introgressed chromosome segments from A02 and one from A03. This pattern is the most widely distributed globally (Fig. 1 and Dataset S3), and its dispersal could be traced back to shipments of seeds in 1978/1979 and 1984/1985 from North Carolina to International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India, from where it was subsequently distributed around the world for use in breeding (Fig. 2 and *SI Appendix* and Dataset S4). Genetic analysis shows that almost all of the globally dispersed lines with a genetic contribution from *A. cardenasii* share this common origin, with shared introgression break points and fine-scale fingerprints of genetic exchange between subgenomes at the ends of chromosomes being the same (Fig. 1 and Datasets S3 and S5). More than one-half a century of propagations, selections, breeding cycles, and germplasm transfers

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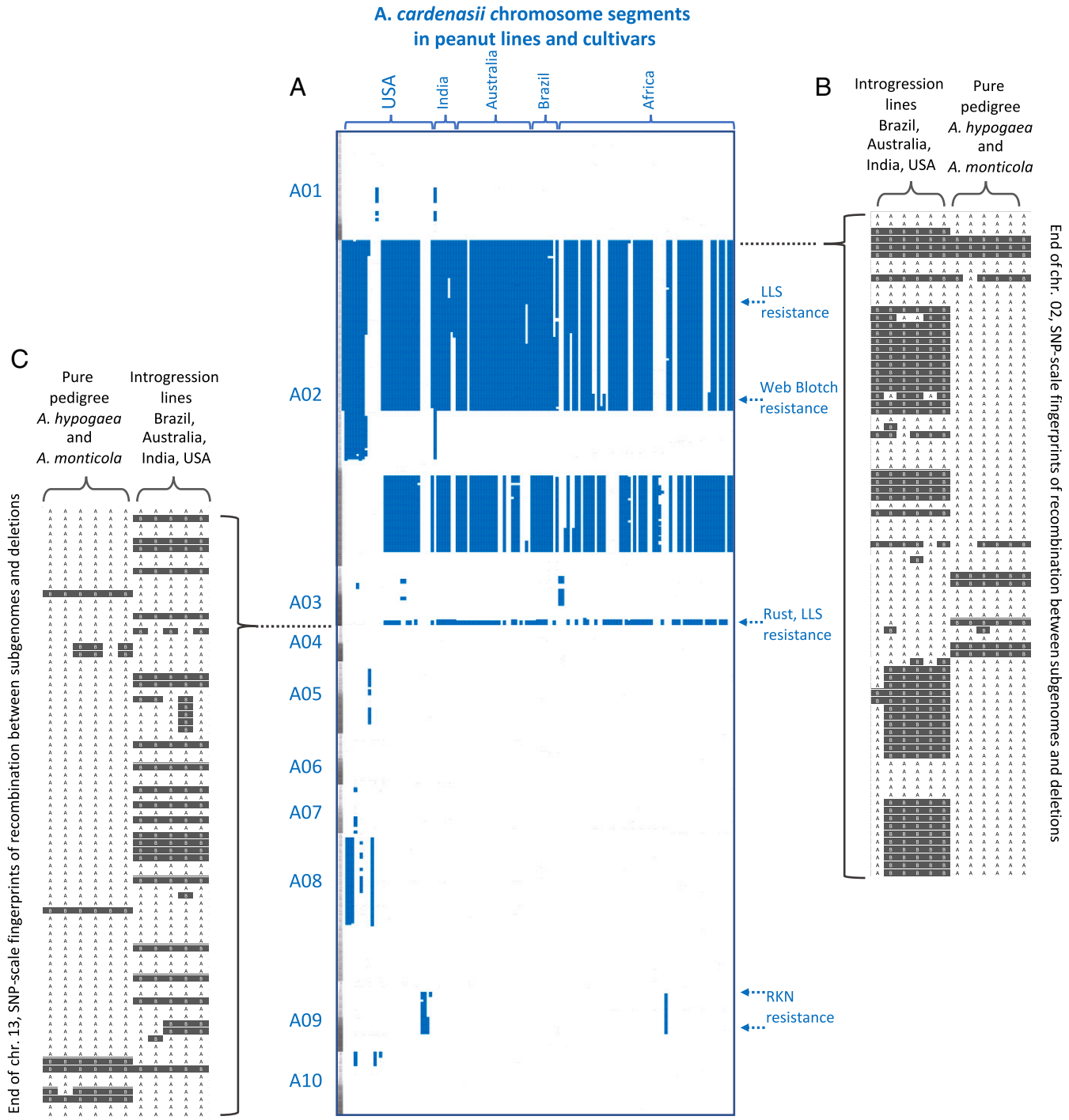

Fig. 1. Visualization of introgressed chromosome segments from the wild species *A. cardenasii* in 142 samples comprising 82 registered peanut lines and cultivars from around the world. (*A*) Overview of chromosomes from A01 to A10. Each peanut genotype is represented as a vertical column, with introgressed wild species chromosome segments in blue. The common origin of the vast majority of peanut introgressions is indicated by the extreme similarity of introgression patterns, which have dispersed from the US, to India, to the rest of the world. Chromosome size is proportional to number of polymorphic markers and is not to scale. QTL regions for disease and pest resistance are indicated to the *Right* of the panel (LLS, late leaf spot; RKN, root-knot nematode). (*B* and *C*) Representations of fine-scale recombination between A and B subgenomes at chromosome terminals which have the most common introgressions: the uppermost region of *A. hypogaea* chromosome 02 and the lower end of 13, respectively. B genome alleles being represented with black background and A genome alleles with white background. Lines with introgressions have patterns that are very similar to each other, and distinct from all peanuts of pure pedigree and its wild counterpart *A. monticola*.

have elapsed since the initial crosses of the hexaploid route. We identified a significant number of pedigree inconsistencies where peanut lines and cultivars with *A. cardenasii* introgressions did not have a wild species recorded in the pedigree, and/or the introgressed wild chromosome segments were inconsistent with parental genotypes. In several cases, phenotypic inconsistencies, breeder observations, and genetic profiling indicated that these were the results of unrecorded cross pollinations or seed contamination; the strong

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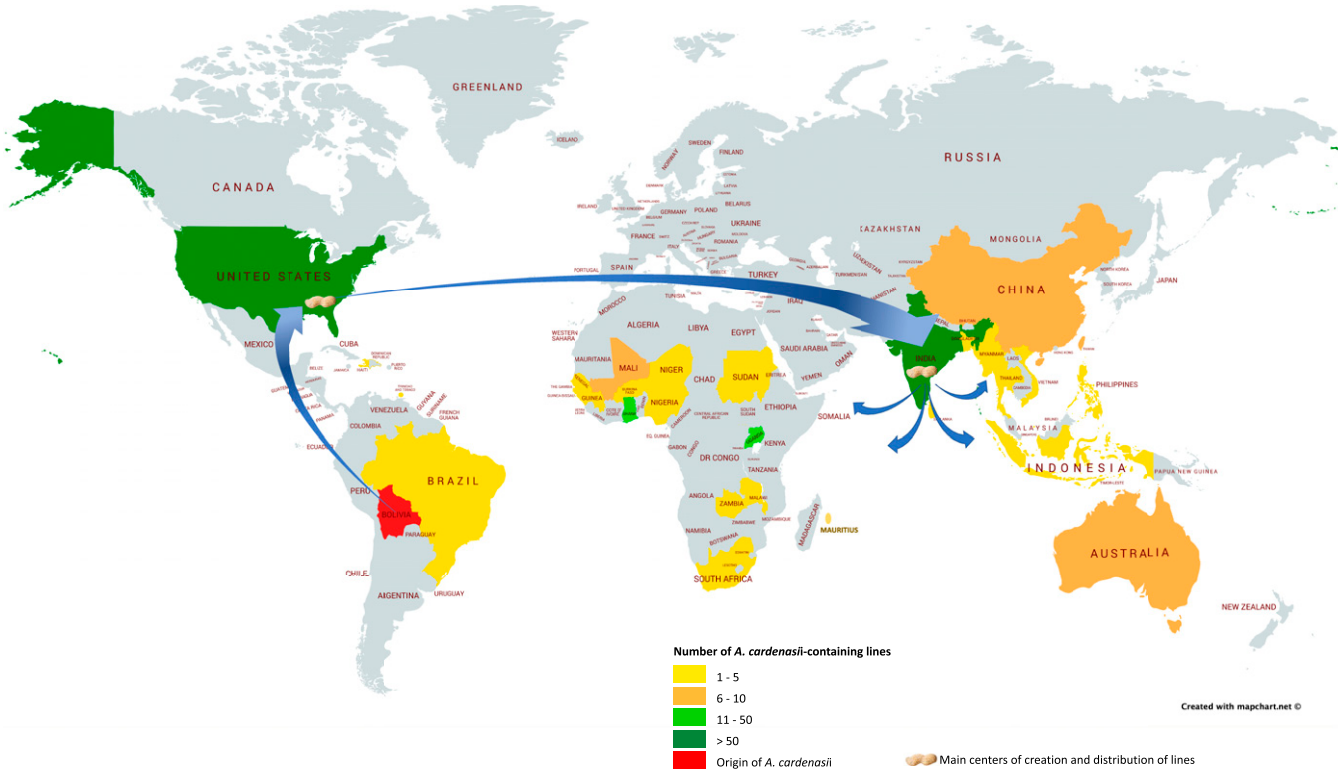

Fig. 2. Global dispersal of *A. cardenasii* GKP 10017 and its genetic contribution to the peanut crop. Note: counts are of cultivars and lines, which are registered and/or publicly available and do not include lineages that are confined to a single breeding program or lineages from segregating populations.

beneficial phenotypes conferred by the wild chromosome segments presumably being favored during selection (*SI Appendix*).

The breeding line in Brazil, IAC 69007, the study of which initiated the research reported here, has exceptional resistance to foliar fungal diseases. It was previously thought to be of pure cultivated peanut pedigree. However, our analyses confirmed genetic contributions of *A. cardenasii* GKP 10017 thus confirming that an old "CS 16" pedigree annotation that accompanied the germplasm receipt from ICRISAT in 1992 (from where it had been received as ICGV 86687 CS 16-B2-B2-B1-B1) was indeed indicative that it originated from the North Carolina hexaploid route CS lines. IAC 69007 harbors three chromosome segments from *A. cardenasii* from chromosomes A02 and A03 (Dataset S3). To investigate how these segments had introgressed into peanut's

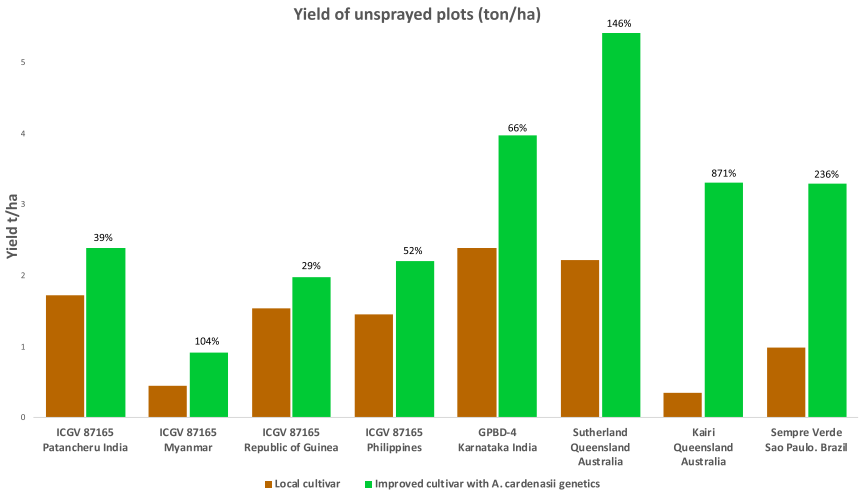

Fig. 3. Yields from improved cultivars with disease and pest resistances conferred by *A. cardenasii* GKP 10017 (in green) compared to the locally adapted, farmer-preferred cultivars of pure *A. hypogaea* pedigree (in brown). Percentage increases in yields are indicated above the green columns. All field trials were unsprayed with fungicides. Comparative yield data for, ICGV 87165, GPBD-4, and Sutherland were previously published (33, 36, 38), and Kairi and Sempre Verde are from this study. Breeder observations consistently highlighted the exceptional disease resistances of the improved cultivars as the reason for improved yields. Where tested (for Kairi and Sempre Verde in this study) under sprayed conditions, the difference in the yields between the improved and farmer preferred cultivars substantially disappears, thus enabling yield differences to be substantially assigned to the disease resistances conferred by *A. cardenasii* introgressions (*SI Appendix* and Dataset S4).

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genome, we identified polymorphisms characteristic of the A and B subgenomes of *A. hypogaea* using the Axiom Array genotyping of species closely related to peanut's ancestors and *A. cardenasii* GKP 10017. Using these polymorphisms, we showed that following the pattern of recombination most probable in a segmental allotetraploid (11, 22, 23), the *A. cardenasii* segments have replaced their homologous A-subgenome alleles (Dataset S3). These segments are found on chromosomes 02 and 13 of *A. hypogaea*, respectively (refer to *SI Appendix* for an expanded explanation of why chr. 13 and not the more expected chr. 03). Using the much higher–density polymorphisms assayed with whole-genome sequencing, we show that introgressed *A. cardenasii* genetic material, which is more distally positioned on the chromosomes, has generally been more eroded by invasion of cultivated alleles (*SI Appendix*, Figs. S2 and S3 and Dataset S2). This apparently mirrors the genetic erosion of the ancestral A genome of cultivated peanut following polyploidy by invasion of B genome alleles into the A subgenome (6, 12, 16, 24) (*SI Appendix*, Fig. S3).

Regarding the disease resistance of IAC 69007 conferred by the wild species genetics, notably, the introgression from the top of A02 covers the largest NB-LRR (Nucleotide Binding-Leucine Rich Repeat) resistance gene cluster in the genome of *A. cardenasii* GKP 10017. In comparison with the corresponding region in *A. duranensis* Krapov. & W.C. Greg. V 14167 (a representative of the A-genome ancestral donor species of cultivated *A. hypogaea*), this 5.4-Mb region from A02 of *A. cardenasii* has a greatly expanded component of NB-LRR genes, with 107 in comparison to 72 in the syntenic region of *A. duranensis*. Similarly, in the 2.6-Mb introgression region of A03, the NB-LRR gene count is 13 in *A. cardenasii* versus 1 in *A. duranensis* (*SI Appendix*, Table S2). Selected progeny lines in the Brazilian breeding program with this upper A02 segment and the A03 segment had 60 to 75% lower severity of late leaf spot (*Nothopassalora personata* syn. *Cercosporidium personatum* (Berk. & Curt.) Deighton) than lines without the segments. Lines with these segments were also resistant to rust fungus (*Puccinia arachidis* Speg.), whereas lines without were susceptible (*SI Appendix*, Table S3). The first cultivar derived from this line ('IAC Sempre Verde') has all three introgressions. In unsprayed field tests, its yield was more than three times the peanut variety currently most widely grown in Brazil [Figs. 3 and 4*A* and *SI Appendix*, Fig. S4 and Dataset S4 (25)]. Where standard spraying schemes for peanut cultivation in São Paulo incorporate nine applications of fungicides, cultivation of Sempre Verde is recommended to be grown without fungicide sprays (25). This variety is now being used as a donor of foliar disease resistance for peanut breeding in Georgia, United States (26) (Fig. 4*D*).

In Australia, although the breeders were unaware of the genetic contribution of the wild species, CS peanut breeding lines of the same origin and harboring the same three characteristic chromosome segments were used in the breeding program of The Peanut Company of Australia in Kingaroy, Queensland, Australia. Derived cultivars ('Sutherland,' 'Taabinga,' and 'Kairi') have strong resistances to foliar fungi (Fig. 4*B*). They contain *A. cardenasii* segments from the upper A02 and lower A03 (Dataset S3). Quantitative trait locus (QTL) analysis using a segregating population indicates that the introgressions confer an estimated 33 and 10% late leaf spot reduction for the A02 and A03 introgressions, respectively (*SI Appendix*, Table S4 and Dataset S6). In unsprayed trials, Kairi (27) yielded about 10 times more than the previously most popular variety, 'Holt' (Fig. 3 and Dataset S4). To obtain maximum yield, Kairi needs approximately one-half the number of sprays of fungicides than varieties without the *A. cardenasii* GKP 10017 segments (*SI Appendix*, Dataset S4).

Subsequently, we investigated peanut breeding lines and cultivars selected by African breeders as the most important in their programs in Ghana, Mali, Malawi, Mozambique, Nigeria, Togo, Senegal, Uganda, and Zambia. About 7% of the nominated lines (64 in total), from all countries except for Togo, had *A. cardenasii* chromosome segments (Fig. 1 and Dataset S3 and *SI Appendix*). Almost all segments were the characteristic CS introgressions or could be derived from them by simple genetic crossover. Distinct introgressions from the middle of A03, of unassignable origin, were also identified in two of the lines from Ghana, and one line with the tetraploid route introgression from A09 was identified from Mozambique (Fig. 1 and Dataset S3). The breeders were unaware of the genetic contributions of *A. cardenasii*. Interestingly, one of the highly resistant cultivars with characteristic CS introgressions, 'Waliyar Tiga' (28), was shown to three of the authors during a visit to Mali in 2009 [S.C.M.L.-B., D.J.B., and H.T.S. (Fig. 4*C* and *SI Appendix*)]. It was highlighted as one of the greatest achievements in peanut breeding of ICRISAT, Mali at that time, having greatly benefitted the lives of subsistence farmers of the region. It has exceptional resistance to foliar fungi and increased yields of both grain and the foliage used as animal feed. Notably, Waliyar Tiga is recorded as having its origin in a North Carolina line (NC Ac 10811A), created around the same time as the CS lines, but without wild species in its pedigree. The introgressions in Waliyar Tiga are presumably the result of unrecorded insect cross pollination or mixing of lineages (*SI Appendix*).

We detected introgressed *A. cardenasii* segments of the same common pattern (from A02 and lower A03; Fig. 1 and Dataset S3) in ICGV 86699, which has been an important donor of exceptional leaf spot and rust resistance in Asia and Africa. This line derives from CS 29, also from North Carolina (Dataset S4). However, the presence of these *A. cardenasii* introgressions must again be due to an error of some sort because the recorded pedigree of CS 29 does not contain *A. cardenasii* but two other wild species, *Arachis batizocoi* Krapov. & W.C. Greg. and *A. duranensis*—introgressions from which we could not detect (*SI Appendix*). ICGV 86699 has been used extensively as a donor of disease resistance and other desirable traits in China, India, Myanmar, Niger, Sri Lanka, and South Africa (29–31).

The best previously documented example of a resistant peanut cultivar derived from the *A. cardenasii* hexaploid route line was 'GPBD-4' and its derivatives. Although previously published research did not confirm the role of wild alleles with complete confidence (32), the results of the genetic analyses here confirm that the exceptional resistance of GPBD-4 is indeed derived from *A. cardenasii* GKP 10017. We detected two chromosome segments from *A. cardenasii* in this cultivar; one from the bottom of A03, in common with the majority of CS introgressions found worldwide, and a much shorter introgression from the top of A02. These introgressions were inherited from ICGV 86855, a selection from CS 16 (33, 34) (Dataset S4). Fine-scale fingerprints of genetic recombination at the ends of chromosomes harboring introgressions indicate the same North Carolina origin as the introgressions from Brazil, Australia, and a different line from India (Fig. 1 and Dataset S5). The introgression in GPBD-4 is from chromosome A03 and corresponds to a very strong QTL that confers resistance to rust and late leaf spot (32, 35) (Fig. 1 and Dataset S3 and *SI Appendix*). GPBD-4 grown in unsprayed field trials in Karnataka, India yielded 66% more than a popular variety that lacks the wild chromosome segments (33, 34) (Fig. 3 and Dataset S4 and *SI Appendix*).

Building on the genetic profiles and using published articles, documents, and pedigrees, we also identified lines and cultivars from 17 other countries whose exceptional resistance indicates they also have *A. cardenasii* introgression: Bangladesh, Burkina Faso, East Timor, Indonesia, Mauritius, Myanmar, Niger, Philippines, Republic of Guinea, South Africa, Sri Lanka, Sudan, Taiwan, Thailand, Trinidad, Vietnam, and Haiti (Dataset S4). Results from eight different field trials in six countries gives an idea of the scale of the benefit. When unsprayed, cultivars with genetic contribution from *A. cardenasii* yielded on average 193% more than the farmer-preferred pure *A. hypogaea* cultivars (30, 33, 36–38) (Fig. 3; and this study, Dataset S4).

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Fig. 4. Examples of peanut lineages improved by *A. cardenasii* GKP 10017 introgressions derived from North Carolina State University's "hexaploid route" hybridization program. (*A*) Brazil: segregating lineages under late leaf spot and rust disease pressure. (*B*) Australia: experimental field with, in foreground, Middleton, a previously popular variety lacking wild species segments and, in background, segregating lineages with resistance to late leaf spot, web bloch, and rust (with Shona Wood). (*C*) Mali: Farid Waliyar and Emmanuel Monyo pose next to the peanut variety with *A. cardenasii* genetics, Waliyar Tiga in 2009. (*D*) United States: segregating lineages in Georgia, under disease pressure from leaf spots. The *Right* plant harbors *A. cardenasii* introgressions, and the *Left* plant, derived from the same cross, does not (with Samuele Lamon).

Discussion

The improvement of many of the crop species on which humanity depends is limited by narrow genetic diversity. To overcome these limitations, breeding programs can strategically hybridize crops with their wild relatives, this increases genetic diversity and expands the range of adaptations obtained (4, 5). As a general trend, crop species have become most important in regions far removed from their origins and the centers of diversity of their wild relatives (39). This makes international collaboration and seed exchange essential elements for crop improvement in the modern world.

In this study, we uncover the global scale of genetic influence on the peanut crop of the wild species accession *A. cardenasii* GKP 10017, which was collected in 1959 in Bolivia, close to the origins of the genus and of the domesticated species *A. hypogaea* (8). Via international collaboration, seeds were sent to germplasm banks. Subsequently, research groups in Texas and North Carolina (United States) hybridized this wild accession with *A. hypogaea*, using different methods to overcome the ploidy barrier between wild and cultivated species (9, 13, 20, 40, 41). Progeny from both hybridizations brought new pest and disease resistances to the peanut crop. Lineages from North Carolina became particularly influential after being transferred to ICRISAT (India) from where they were distributed worldwide (Figs. 1–4). The introgression and global spread of these wild alleles required multiple factors: genetic resources, diverse expertise, great effort, and networks of exchange—a combination of natural and human resources only available within an international context. Over time, with multiple transfers, further breeding cycles, and mixing of lineages, the networks of genetic influence of *A. cardenasii* GKP 10017 became complex and obscured. Even though the wild genetics became mostly forgotten or unrecorded, the usefulness of the improved lineages ensured their uptake by breeding programs. The free exchange of seeds allowed the valuable resistances to spread to many countries and made their benefits widely available, including to many of the world's poorest and most food-insecure people who rely on this crop in Asia and Africa. The improved peanut cultivars especially benefit low-income and small-scale farmers who are less able to use fungicides to control leaf diseases. In larger-scale farms, these cultivars delivered environmental benefits from reduced applications of fungicide and the accompanying reduction in use of fuel and carbon dioxide emissions, while at the same time

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providing economic benefits of increased yields and decreased production costs. In total, we identified the genetic influence of *A. cardenasii* GKP 10017 in 251 peanut lines and cultivars in 30 countries. The further spread of these wild genetics is facilitated by key *A. cardenasii*–introgressed germplasm lines being freely available worldwide through the US Department of Agriculture (USDA) National Plant Germplasm System (https://npgsweb.ars-grin.gov/gringlobal/search). These introgressed lineages broaden the genetic base of peanut. In pure pedigree peanut, alleles are derived from the two ancestral species, *A. duranensis* and *A. ipaënsis*. The introgressed lineages contribute alleles from a third species, *A. cardenasii*. Selection pressures and the highly anthropic dynamics of crop genetics will determine allelic frequencies. We anticipate that the CS chromosome segments will become more frequent over time because they confer resistance to late leaf spot and rust, two of the most damaging peanut diseases worldwide. In the long term, overreliance on this source of resistance will leave it vulnerable to being broken by the pathogens. Maximum benefit is only likely to be achieved with the introduction of further new allelic diversity from other wild species or accessions.

This investigation adds to many other known examples where wild species have conferred new important traits to crops. The case of wheat may be the most important in benefitting world food security. While wheat's origin is the Fertile Crescent, over history, its cultivation has dispersed widely over the globe, becoming most important in China, India, Europe, and North America. Germplasm transfers of wild relatives from the Middle East to the International Research Center, CYMMIT (Centro Internacional de Mejoramiento de Maíz y Trigo) in Mexico formed the basis of a program to create wheat synthetic hexaploid lines, which have been made available through their germplasm bank (42). Over the years, these synthetic hexaploids have been a key resource to breeders around the world and have been shown to be exceptional sources of variation for biotic and abiotic stress tolerance, agronomic, and novel grain quality traits (42). A remarkable impact, especially for poorer farmers who have less access to fungicide sprays, has been from the introduction of wild species–derived resistance to stem rust (*Puccinia graminis* Pers. f. sp. *tritici*). Virulent strains of rust periodically arise, requiring continued deployment of new resistance loci to maintain yields (43). Although the contribution of wild species to the wheat crop is well documented, the complex pedigrees and networks of exchange make it difficult to track wild genetics and make precise estimates of importance (44). In other less-studied crops, unknowns are greater still. For instance, a recent broad survey of cassava (*Manihot esculenta*), a key crop in Africa, revealed that introgressions from the wild cassava relative, the Ceará rubber tree (*Manihot glaziovii*), were widespread in landraces and elite varieties. These introgressions, a legacy of breeding in the 1930s, confer resistance to important diseases such as brown streak and agronomic traits such as the number of storage roots and percent dry matter. Notably, suppressed recombination within the introgressions is leading to the accumulation of deleterious mutations (45). The purging of deleterious alleles and new introgressions will be required to safeguard these traits in the longer term. Without DNA and genetic analyses, the source of these important traits, which have increased food security and reduced the pressure to expand agriculture into wild areas, would be unknown. Other examples of crops improved using wild relatives include rice, maize, and potato (5). Indeed, in a world of global movement of pests and pathogens (46) and changing climate, it is difficult to overstate the long-term importance of wild crop relatives to crop improvement.

Notably however, the botanical collections and seed exchanges that have made these crop improvements possible have very greatly reduced since 1993, the date of implementation of the Convention on Biological Diversity. The Convention itself was, at least in part, a reaction to legal rulings in the 1980 allowing the patenting of living organisms and their components. These rulings were greatly asymmetrical with prior treatments of biodiversity as a "common heritage of humankind" and created the situation where products developed from germplasm which had been supplied for free, could be patented and sold back to the supplier. This in turn politicized issues surrounding germplasm and generated a sea change in attitudes. The response of the Convention was to assign sovereignty over biodiversity to national governments, while at the same time establishing principles aimed to promote conservation, sustainable use, and equitable sharing of benefits from the utilization of genetic resources (47, 48). However, that the practical outcomes of the Convention and the national laws that have followed in its wake have been fraught with unintended consequences, is widely recognized (49). Bureaucratic burdens, politicization, and the reframing of researchers as potential "biopirates" have created an atmosphere of fear around collection and research in biodiverse countries (50). While the destruction of wild areas continues, researchers are hindered and inhibited from making new biological collections by confusing bureaucracy and the threat of personal consequences if they get the paperwork wrong (49). Of the smaller number of collections that are made, a far smaller proportion are transferred across, or even within national boundaries. As a result, the diminished number of new germplasm collections are no longer safeguarded by being held in multiple germplasm banks (51). Internationally, a chilling atmosphere has descended on germplasm exchange, impacting the ability of plant breeders to incorporate improved traits into local cultivars and hindering their ability to respond to new crop pests and diseases (52–57).

In revealing the benefits of past germplasm exchange and international collaboration, this study highlights the costs of current restrictive laws and attitudes concerning biodiversity. Today, the wild species collection, hybridizations, and multistage widespread exchange of seed that enabled the worldwide benefits to humanity and the environment described here would be practically impossible. The net result of the current collection of national laws, attitudes, and practices is a "hyperownership" of germplasm, which effectively imposes a gridlock on biological collection and exchange (47, 58, 59). This is resulting in irretrievable lost opportunities to collect germplasm and loss in capacity and agility to improve and adapt crops [indeed, it has even impacted the ability to respond to pandemics (60)]. This study highlights the need for parties involved to focus on the common goals of preservation of biodiversity and its use for the benefit of humanity and the environment.

Materials and Methods

We built a reference genome sequence for *A. cardenasii* Krapov. & W.C. Greg. Accession No. GKP 10017 (PI 262141) using whole-genome shotgun sequencing and assembly with PacBio and Illumina reads. Scaffolding into chromosome-scale sequences was done using reference genomes of *A. duranensis* and Hi-C. To characterize introgressed chromosome segments in diverse genotypes of peanut (*A. hypogaea* L.) from around the world, we identified SNPs which differentiate *A. cardenasii* GKP 10017 from comprehensive panels of genotypes of *A. hypogaea* of pure pedigree (16) and wild species accessions from the botanical section *Arachis*. SNPs were assayed using the Axiom Arachis Genotyping Array (15) and Illumina whole-genome sequencing. Fine-scale fingerprints of genetic exchange between subgenomes were visualized using methods essentially as previously described (6). Characterization of NB-LRR–resistance genes was done using sequence similarity ("homology") searches. QTL were identified using a peanut recombinant inbred line population genotyped using the Axiom Array and phenotyped for disease severity using visual scores, together with standard methods. Field trials under different spray regimes were done using standard methods.

Detailed Materials and Methods and expanded explanations are available in *SI Appendix*.

Data Availability. Genome sequence, genotyping, pedigree information, and yield trial data have been deposited in National Center for Biotechnology Information (NCBI), PeanutBase, and USDA Data Repository (NCBI: JADQCP000000000) (14). Datasets S1–S6 are available at USDA Ag Data Commons:

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https://data.nal.usda.gov/dataset/data-legacy-genetics-arachis-cardenasii-peanut-crop-v2 (17). All other study data are included in the article and/or supporting information.

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