

## Harnessing crop diversity

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Global food systems face unprecedented challenges from climate change, extreme weather events, land and water constraints, biodiversity loss, soil degradation, market volatility, and other environmental and socioeconomic crises. These challenges coincide with intensifying global demand for food, putting additional strain on our agri-food systems. Over the last 60 years, the modernization and globalization of agriculture have increased per capita food supplies overall, helping to expand global availability of a limited number of major crop plants. These efforts have resulted in increased homogeneity of diets worldwide and have narrowed the total diversity of crop species that contribute significantly to diets at the global level (Fig. 1) (1). Today, most of humanity depends on only a handful of crops for a majority of their calories, and the relative importance and availability of minor and geographically restricted food plants have decreased (see https:// alliancebioversityciat.org/changing-global-diet for more information). This narrowing of crop diversity introduces a degree of vulnerability into our agri-food systems that is increasingly problematic. In addition, the environments in which the major food staples have traditionally flourished are becoming progressively more erratic and unpredictable, further jeopardizing the future of food security.

Diversification, the process of becoming more diverse, is a strategy that is commonly used to reduce risk and minimize volatility in biological, physical, economic, and information systems (2, 3). In food systems, diversification typically refers to an increase in the richness, abundance, and composition of species and/or nutrients across scales, from the genetic/ species level to the ecosystem, landscape, regional, national, and global levels. Diversification strategies in the context of agri-food systems involve complex networks, often characterized by nonlinear relationships between crop genetic diversity, farming system diversity, diversity of market opportunities, and nutritional diversity (3–5). Thus, while diversification per se is often presented by the scientific and policy communities as socially and environmentally beneficial, more is not always better.

In this timely Special Feature, "Harnessing crop diversity," we explore the many benefits of incorporating greater diversity into agricultural systems and a variety of multifaceted approaches for doing so. We also point to potential obstacles, challenges, and considerations that must be addressed as we seek to augment the health, sustainability, and resilience of agri-food systems. We investigate questions at different scales and from different perspectives that collectively yield fascinating insights into what kinds of diversity need to be considered as we strive to enhance the four dimensions of food security: availability, access, stability, and utilization. What kinds of diversity matter? What is the "optimal" level of diversity in a given system? How do we manage crop diversity in our system of choice? How do components of diversity interact within or across systems and scales?

The papers in this Special Feature examine opportunities to augment crop diversity on many levels: by conserving crop diversity in situ and in gene banks, enhancing genetic diversity within existing crop species, expanding the repertoire of species planted and consumed, choosing crops and crop combinations to optimize nutrient availability under current and future climate scenarios, broadening participation in crop diversity management to address the needs of vulnerable populations, evolving cropping systems to improve soil health and ecosystem services, and strengthening institutional frameworks that maintain and promote diversity of both crops and actors across the world's heterogeneous food systems.

Plant genetic resources embody the fundamental components of genetic variation needed to augment crop diversity in agricultural systems. These resources, which include the genetic diversity within and among crop varieties, including crop wild relatives, must be available and accessible in order to be used. As discussed by Dempewolf et al. (6), plant genetic resources are at risk in natural habitats, and soundly managed and diversified gene banks are critical to ensure the availability of living collections of crop diversity at local, regional, and global levels. Managing these germplasm collections is costly and logistically challenging, and new strategies are needed to keep pace with evolving priorities, particularly related to the kinds of collections maintained and mechanisms for providing access to genotypic and phenotypic information about the holdings.

Wild and unadapted germplasm offers researchers and breeders a resource that can be used to broaden the genetic base of elite breeding populations and to search for novel traits of interest. However, injecting diversity into existing cultivars from wild, exotic, and nonadapted sources is challenging on many fronts. Often alleles or haplotypes do not perform as expected in a new genetic background, owing to the way they interact with existing quantitative or qualitative variation. The paper by Torgeman and Zamir (7) summarizes the development and utilization of a large collection of interspecific backcross introgression lines of tomato to explore the phenomenon of yield epistasis. The study highlights the challenges of predicting phenotypic outcomes when exotic

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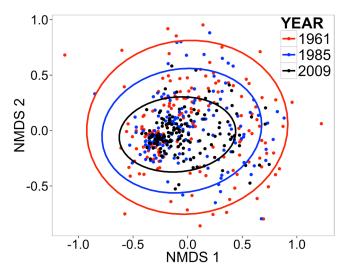
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**Fig. 1.** The changing global diet. Multivariate ordination of crop commodity composition in contribution to calories in national food supplies in 1961, 1985, and 2009. Red points represent the multivariate commodity composition of each country in 1961, blue points in 1985, and black points in 2009. Circles for each year represent 95% Cls around the mean; smaller circles indicate lower country-to-country variation in composition. Between 1961 and 2009, the area contained within these 95% Cls decreased by 68.8%, representing the decline in country-to-country variation of commodity composition (i.e., homogenization) over time. Reprinted with permission from ref. 1.

variation is introduced into an elite breeding population. The paper by Sanchez et al. (8) presents a strategy to efficiently incorporate exotic diversity into an established breeding pipeline in a time and cost-effective matter. Using modeling and simulation, the authors demonstrate how genomic selection can be used to maintain or augment diversity in a breeding population while simultaneously driving selection to improve genetic gain. The models focus on mechanisms for identifying and utilizing gene bank material in a sustained, productive, elite variety improvement effort.

Introgressing novel variation from wild or unadapted sources in any species has the potential to significantly diminish the performance of an elite line or a population owing to linkage drag (i.e., the unintentional coselection of undesirable gene variants linked to selected loci). Huang et al. (9) explore recent insights into the genomic architecture of wild species introgressions in modern sunflowers, where wild species have been used as donors of traits designed to facilitate the production of commercial hybrids. They document extensive structural variation in the introgressed regions, including >3,000 new genes that had been introduced into the cultivated sunflower gene pool, and pervasive linkage drag affecting yield and quality. Possible solutions are discussed, including efforts to remodel the recombination landscape.

Our inability to regulate recombination is a major limitation for breeding, particularly in eliminating deleterious alleles or maintaining favorable linkage relationships. One approach to this problem is to globally increase recombination rates, but this has a limited effect on heterochromatic regions of chromosomes, which often show little to no recombination. Other methods, still under development, permit targeting of cross-over events to particular chromosomal regions (e.g., heterochromatin) or specific chromosomal sites. Epstein et al. (10) use simulations to ask whether these different approaches to enhancing recombination can enhance the efficiency of breeding programs and found that all produce some benefits. The targeting of cross-over events to specific chromosomal sites was especially effective for reducing linkage drag.

As reviewed by Krug et al. (11), global nutritional resilience will not be achieved through the improvement of current staple crops alone but rather through the development of a diverse tapestry of crops and agricultural systems that reconfigure the dynamic, interdependent relationships among plants, humans, and ecosystems—the "crop domestication triangle." Resilience-building strategies proposed by von Zonneveld et al. (12) are targeted at enhancing nutritional security in sub-Saharan Africa. The authors promote a process of crop replacement with the strategic addition of "forgotten food crops" that are already adapted to the culture and the region, as well as the integration of underutilized species with the potential to fill critical nutrition gaps. Climate niche modeling is used to predict current and future climate suitability for crops from specific food groups and to identify best-bet options for nutrient-sensitive as well as climateresilient cropping systems. Respective drawbacks and challenges are also discussed.

Van Etten et al. (13) argue that we can build flexibility and resilience into future food systems using data-driven, decentralized approaches to crop diversity management. These approaches incorporate new domains of gender and socioeconomic data and use dynamic modeling processes to predict how decisions about crop diversity will impact the lives of some of the world's most vulnerable people. An example of such an approach is presented by Gesesse et al. (14) whose work focuses on the implementation of a breeding strategy that combines genomics, citizen science that mobilizes traditional Ethiopian farmers' knowledge, and environmental analysis to enhance local adaptation and rapid adoption of new wheat varieties in challenging production environments.

Looking to the future, we recognize that multicropping systems represent an underutilized avenue for boosting crop diversity, soil health, ecosystem services, and the potential for carbon sequestration. Moore et al. (15) delve into the complexities involved in breeding for these unconventional systems and the many ways in which multicropping systems can be designed and configured over space and time.

Finally, Marden et al. (16) offer a practical guide to understanding and navigating international agreements governing fair and equitable access to plant genetic resources. They provide a brief history and overview of three key international agreements, highlight the coverage and key considerations of each agreement, and discuss access and benefit sharing obligations. The goal is to help those who use plant genetic resources in plant genetics research and breeding to better understand when and how international agreements apply, and—where rules are unclear—to suggest best practices for compliance with these agreements.

The broad arc of topics and perspectives represented in this Special Feature offer readers an intriguing view of many different dimensions of research focused on harnessing crop diversity. Collectively and individually, the papers propose thought-provoking ideas and strategies about how to improve the resilience and sustainability of our agri-food systems and promote food security around the world.

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