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Crop genetic erosion: understanding and responding to loss of crop diversity

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Summary

Crop diversity underpins the productivity, resilience and adaptive capacity of agriculture. Loss of this diversity, termed crop genetic erosion, is therefore concerning. While alarms regarding evident declines in crop diversity have been raised for over a century, the magnitude, trajectory, drivers and significance of these losses remain insufficiently understood. We outline the various definitions, measurements, scales and sources of information on crop genetic erosion. We then crop wild relatives, diachronic diversity, food security, plant genetic resources.

provide a synthesis of evidence regarding changes in the diversity of traditional crop landraces on farms, modern crop cultivars in agriculture, crop wild relatives in their natural habitats and crop genetic resources held in conservation repositories. This evidence indicates that marked losses, but also maintenance and increases in diversity, have occurred in all these contexts, the extent depending on species, taxonomic and geographic scale, and region, as well as analytical approach. We discuss steps needed to further advance knowledge around the agricultural and societal significance, as well as conservation implications, of crop genetic erosion. Finally, we propose actions to mitigate, stem and reverse further losses of crop diversity.

I. Introduction: evolving concerns over loss of crop diversity

Crop diversity – variation among crop species, their varieties and/or individual plants – underpins the productivity, resilience and adaptive capacity of agricultural systems (Gepts, 2006; Hajjar *et al.*, 2008; Renard & Tilman, 2019; Sirami *et al.*, 2019; Egli *et al.*, 2020). In traditional agroecosystems, for example, genetically heterogeneous 'crop landraces' (Table 1) are frequently cultivated in a mosaic of different varieties and of different crop species, spatial diversification providing a safeguard against catastrophic loss (Ayeh, 1988; Zeven, 2002; Jarvis *et al.*, 2008a). This diversity is managed through farmers' cultivation and selection practices, with local exchange and gene flow among landraces encouraging genetic variation, and continued cultivation leading to local adaptation (Bellon, 1996; Louette *et al.*, 1997; Mercer & Perales, 2010). Occasional introgression from progenitor 'crop wild relatives' (Table 1) occurring nearby can also introduce variation (Jarvis & Hodgkin, 2002).

The crop diversity profile differs in agroecosystems where production is based on varieties bred by plant scientists and distributed via private industry or government-sponsored extension programs (Duvick, 1984). As these 'modern crop cultivars' (Table 1) are genetically homogeneous and are typically cultivated over large geographic areas in monoculture, frequent turnover of cultivars (i.e. temporal diversification) is used to help keep pace with biotic and abiotic pressures (Zhu *et al.*, 2000).

The development of agroecosystems where modern crop cultivars are dominant was encouraged by the rediscovery of Mendel's laws of inheritance around the turn of the 20th century, which offered new explanations for plant breeders' practices and provided opportunities to promote novel breeding methods (Harwood, 2016). Landraces and their wild relatives had been recognized by scientists as valuable resources since the late 19th century (Baur, 1914; Zeven, 1998), with *ex situ* repositories (genebanks) established not long after to maintain collections in anticipation of their contributions to breeding for higher yield, greater pest and disease resistance, and other important traits (Vavilov, 1926; Lehmann, 1981; Saraiva, 2013).

In parallel, concerns began to be raised over losses of crop diversity from agricultural change and larger trends including economic development, globalization and demographic shifts (Baur, 1914; Harlan & Martini, 1936). As cultivars were derived from landraces and crop wild relatives, failure to conserve this diversity – particularly in the absence of widespread efforts to preserve it in genebanks – was later likened to building 'our roof with stones from the foundation' (Fowler & Mooney, 1991).

In the 1960s, the worldwide promotion of new high-yielding cultivars and associated agronomic practices as part of the 'Green Revolution' – argued by its proponents as necessary to address hunger, generate economic stability and secure political alliances – was thought to be accelerating the replacement of crop landraces and the destruction of the habitats of their wild relatives (Frankel, 1974; Pistorius, 1997; Fenzi & Bonneuil, 2016). Alarm was voiced at the Food and Agriculture Organization of the United Nations (FAO), where the term 'genetic erosion' was coined to describe this dramatic loss of 'genetic resources'. These were understood to be critical to addressing present as well as unforeseen future plant breeding needs (Bennett, 1964, 1968; Frankel & Bennett, 1970) (Table 1; Fig. 1). Simultaneously, awareness of the susceptibility of modern cultivars to pests and diseases as a consequence of their genetic uniformity was increasing (Table 1), particularly after the Southern Corn Leaf Blight epidemic of 1970–71 in the USA (Tatum, 1971; US Senate, 1980). Recommendations were made to widen the genetic variation among cultivars of major staples (National Research Council, 1972).

An outcome of these concerns was the expansion of national and international programs to collect and maintain the genetic diversity of crops in genebanks (Plucknett *et al.*, 1987). The International Board for Plant Genetic Resources (IBPGR) was established in 1974 to coordinate a global program to conserve threatened diversity before it disappeared. IBPGR supported the collecting of over 200 000 samples of landraces, crop wild relatives and other genetic resources in 136 countries between 1975 and 1995, and helped establish international genebank collections to maintain these samples (Thormann *et al.*, 2019).

By the 1980–1990s, FAO had announced that three-quarters of previously cultivated crop diversity had disappeared from fields since the beginning of the century (FAO, 1993), a narrative based on estimates and broad generalizations, but so evocative that it continues to be widely cited (Box 1). Moreover, alongside landraces and crop wild relatives in the field, scientists were worried about the vulnerability of the hundreds of thousands of samples conserved *ex situ*, due mainly to unstable funding and deficient infrastructure. Genebanks were encouraged to duplicate their holdings to mitigate these challenges as well as to protect the resources from natural disasters, war and civil strife (Holden, 1984; Lyman, 1984; Peeters & Williams, 1984).

Concerns around the loss of agricultural diversity also began to expand, coming to include livestock, pollinators, agrarian landscapes and wild species providing ecosystem services to farming (Allen-Wardell *et al.*, 1998; Tisdell, 2003; Garibaldi *et al.*, 2013). These worries were no longer solely focused on the contribution of

Table 1 Definitions related to crop genetic erosion.

Term	Definition as applied in this review	Notes	Key references
Crop diversity	Variation among crop species, their varieties, and/or individual plant genotypes and phenotypes	Crop diversity is commonly conceptualized at three main scales: species, variety (within species) and genetic (within varieties)	van de Wouw *et al*. (2009); van Heerwaarden *et al*. (2010); Hufford *et al*. (2019)
Crop diversity conservation	The safeguarding of crop diversity	Crop diversity conservation is commonly accomplished either in genebanks and other repositories (*ex situ*) or on-farm/in natural habitats (*in situ*). The integration of both approaches is considered the most robust form of conservation. Various alternative terms are also common, including 'genetic resource conservation' and 'genetic conservation' (typically emphasizing conservation for use in plant breeding and other research) and 'agrobiodiversity conservation' (potentially referring to a wider array of relevant diversity, with crops being one component)	Bennett (1964, 1968); Frankel (1970; 1974); Berthaud (1997); Gepts (2006)
Crop genetic erosion	The loss of crop diversity in a given area over a given amount of time, typically measured by decline of species, variety and/or within-variety (genetic/genomic) variation	A very wide variety of interpretations of the meaning of crop genetic erosion have been published, including specifying or limiting the definition to taxonomy level (species, variety, genetic), genetic resource type (landrace, modern cultivar, crop wild relative), system (traditional, modern/industrial, conservation repositories) and whether changes are permanent and/or pertain to functional diversity; as well as identifying specific drivers of loss (Supporting Information Table S1). Supplementary terms have been proposed to fit different interpretations, including 'genomic erosion' in the case of substitution of one crop type for another or the elimination of the crop entirely, and 'varietal erosion' or 'native/landrace cultivar loss' for decline at the varietal level. Alternatives such as 'dediversification' and antonyms such as 'genetic sedimentation' have also been coined, although they are not widely used. In this review we embrace the full array of meanings of the term, noting that decline at the species and variety/population level generally also equates to loss of genetic diversity	Bennett (1964, 1968); Frankel & Bennett (1970); Harlan (1972); Szabó (1981); Hawkes (1983); Wilkes (1989); Zimmerer (1991); Qualset *et al*. (1997); FAO (1998; 2010); Brush (1999); Sperling (2001); Gepts (2006), van de Wouw *et al*. (2009); Brown & Hodgkin (2015)
Crop genetic resources	Reproductive and genetic materials in crops and their wild relatives	This term is widely defined, and can include associated genetic or phenotypic information. 'Plant genetic resources' is a common alternative term	Frankel & Bennett (1970); Hawkes (1971); Harlan (1972); FAO (1998); Gepts (2006)
Crop genetic uniformity	A high degree of genetic similarity at relevant loci among individual genotypes within a crop variety and/or among varieties in a given area (i.e. a narrow genetic base)	While the term is commonly applied in the context of modern/industrial agriculture, genetic uniformity has been recognized in longer term contexts as a result of drift and genetic bottlenecks. Among the requirements for the establishment of intellectual property over crop varieties, such as under UPOV or patent law, is genetic uniformity	National Research Council (1972); FAO (1998)
Crop genetic vulnerability	The susceptibility of a crop or crop variety to biotic or abiotic stresses as a result of genetic uniformity, creating the potential for widespread crop failure	Although susceptibility of crops was recognized previously, the term may have been coined in the 1970s to explain losses in the USA during the Southern Corn Leaf Blight epidemic of 1970–1971	Meadows *et al*. (1972); National Research Council (1972); Harlan (1975); US Senate (1980); Brown (1983); Duvick (1984); FAO (1998); Brown & Hodgkin (2015)
Crop landrace	A crop variety or population managed by farmers through cultivation, selection and diffusion, which is typically adapted to a local area and to traditional farming systems, has a recognizable identity and geographic origin, and is often genetically heterogeneous	Different definitions have been proposed since the early 20th century. Some specify autochthonous (native) vs allochthonous (relatively recently introduced) landrace types, or primary (locally evolved) vs secondary (originating as a modern cultivar but now maintained through farmer selection) types. Some definitions assert that landraces are typically resilient to abiotic and biotic stress and therefore display yield stability under low input systems; others have emphasized that these farmer varieties have strong cultural associations including unique local uses. Some have differentiated between landraces as populations with limited intentional selection by farmers, and folk varieties as populations with intentional selection. Landraces constantly change over time through local practices of cultivation, selection, breeding and diffusion	Hawkes (1983); Harlan (1992); Brush (1995); Zeven (1998); Negri (2003); Camacho Villa *et al*. (2005); Berg (2009)

Table 1 (Continued)

Term	Definition as applied in this review	Notes	Key references
Crop wild relative	A wild plant taxon with a relatively close phylogenetic relationship to a crop	Crop wild relatives are typically assigned to gene pools in relation to the crop, based on the degree of crossability, evolutionary lineage and other factors. For most crops, wild relatives are typically considered to include the congeneric taxa, although some crops have wild relatives from multiple genera (e.g. wheat). Others exist in such large genera that only a subset of taxa within the genus (i.e. a section or clade) are considered to be wild relatives (e.g. crops in the genus *Solanum*)	Harlan & de Wet (1971); Maxted *et al*. (2006); Castañeda-Álvarez *et al*. (2016); Miller & Khoury (2018)
Modern crop cultivar	A crop variety bred by plant scientists, which is typically genetically homogeneous and which displays high yield potential under optimal conditions	This term is synonymous with 'improved cultivars/varieties', 'high-yielding varieties', 'scientifically bred varieties', 'elite varieties' and 'advanced cultivars', and is typically associated with Green Revolution technologies, although techniques pre-date the spread of fertilizer-responsive dwarf cereal varieties	Zeven (1998); van de Wouw *et al*. (2009, 2010)

Overview of key terms relevant to this review of crop genetic erosion. Definitions provided are our own, adapted from and supplementary to pertinent literature.

this diversity to agricultural modernization. Rather, crop and other forms of agricultural diversity were increasingly understood to be important for ecological processes, including adaptive capacity and evolutionary potential, as well as for agroecosystem resilience, ultimately affecting farmers' livelihoods and self-determination (Mijatović *et al.*, 2013; Fenzi & Bonneuil, 2016; Sirami *et al.*, 2019). Losses of associated cultural diversity were also recognized, including indigenous languages and traditional agricultural knowledge (Benz *et al.*, 2000). Support for *in situ*/on-farm conservation began to be explored (Brush, 1991; Wood & Lenne, 1997; Bellon, 2004), though some doubted its efficacy (Frankel & Soule, 1981; Zeven, 1996; Peres, 2016).

In the 1990s, concern about biodiversity in all its forms became a global priority through the Convention on Biological Diversity (CBD), which mandated conservation, sustainable use, and fair and equitable sharing of the benefits arising from use (CBD, 1992). National sovereignty over biodiversity and benefit sharing were a response to disparities in genetic resource distribution and use, as well as concern over the increasing potential for privatization of these resources, for example via the International Union for the Protection of New Varieties of Plants (UPOV), patent law and trade agreements (Jefferson *et al.*, 2015; Smith *et al.*, 2016). After the CBD came into force, earlier international agreements on the conservation of crop diversity (e.g. FAO, 1983) were updated to fit within this larger biodiversity framework, providing new avenues for international collaboration through the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) (FAO, 2002) and the Global Crop Diversity Trust (Esquinas-Alcázar, 2005).

In recent decades, the CBD, ITPGRFA and even the United Nations Sustainable Development Goals have set specific targets for the conservation of crop diversity (CBD, 2002, 2010; FAO, 2002; United Nations, 2015). After over a century of alarm regarding its loss, and more than 50 yr of concerted efforts toward its conservation, safeguarding crop diversity has become well integrated in the major international agreements on biodiversity and human development, which highlight the importance of both *ex situ* and *in situ* conservation. Current negotiations are projected to renew these conservation targets, which were not met by the previous 2020 deadline (Díaz *et al.*, 2020).

There are now *c.* 1750 genebanks worldwide, maintaining over seven million samples, with botanic gardens, universities, non-profits, community seedbanks and local conservation networks further contributing to safeguarding crop diversity *ex situ* (FAO, 2010; Miller *et al.*, 2015; Vernooy *et al.*, 2017). Safety duplication of some of this diversity is accomplished among genebanks and at global backup repositories (Westengen *et al.*, 2013). Protected areas offer habitat conservation for some crop wild relatives (Khoury *et al.*, 2019a) and, to a much more limited degree, landraces, although both are very rarely prioritized in management plans (Khoury *et al.*, 2020). Various initiatives promote *in situ*/on-farm crop diversity conservation (e.g. Stenner *et al.*, 2016; AGUAPAN, 2021; Global Environmental Facility, 2021).

Despite these remarkable efforts to prioritize and conserve crop diversity, the magnitude, trajectory, drivers and especially the significance of its loss remain insufficiently understood. This may in part be an inadvertent consequence of the perceived urgency of the threat, which was posited – before the global focus on climate change – as 'perhaps the biggest single environmental catastrophe in human history' (Fowler & Mooney, 1991). This urgency understandably led to an emphasis on action rather than detailed documentation and theoretical analysis (Brush, 1999; Sackville Hamilton, 1999) and continues to provide impetus for interventions. Global climate change has only increased this urgency (Dyer *et al.*, 2015), as crop diversity is both threatened by it and also a critical resource for mitigation, resilience and adaptation (Burke *et al.*, 2009; Dempewolf *et al.*, 2014; Pilling *et al.*, 2020).

However, lack of information on genetic erosion detracts from the effectiveness of conservation efforts, including the ability to take full stock of what is presently safeguarded, to identify what remains to be protected and to use this information to halt further loss.

Fig. 1 The urgency of crop genetic erosion. This five-part series from 1971 on 'Genetic Conservation', depicted in the University of Sydney project 'Frontiers of Science', originally ran as a weekly pull in newspapers, with one strip for each weekday. The strips were initially published in the *Sydney Morning Herald* and syndicated to other Australian newspapers; they were also available throughout the USA and Canada, and internationally through over 600 newspapers. From the perspective of the present day, some language used and nuances of the science may be problematic, but the urgent need to conserve diversity is timeless. From the Rare Books and Special Collections, the University of Sydney Library (Butler *et al*., 1971).

In this review, we outline the varied definitions, measurements, scales and sources of information on crop genetic erosion. We provide a synthesis of published evidence regarding changes in diversity of crop landraces on farms, modern crop cultivars in agriculture, crop wild relatives in their natural habitats and crop genetic resources held in *ex situ* conservation repositories. We then discuss steps needed to further advance knowledge around the agricultural and societal significance, as well as conservation implications, of crop genetic erosion. Finally, we propose actions to mitigate, stem and reverse further losses of crop diversity.

Box 1 Just how much crop diversity has disappeared worldwide? The mysterious origins of the 75% narrative

Among the most common genetic erosion narratives, often repeated since the 1990s, is that three-quarters of crop diversity disappeared in the 20th century. The estimate is attributed to the FAO, invariably without original citation. The statement also commonly specifies that the 75% loss stems from the replacement of crop landraces with modern varieties (e.g. FAO, 2004).

This ubiquitous statistic may have its roots in efforts by the FAO's Commission on Genetic Resources for Food and Agriculture, associated international organizations such as the IBPGR, and nongovernmental organizations such as the Rural Advancement Foundation International (RAFI) to synthesize disparate evidence and anecdotes of loss from around the world, possibly in contribution to early CBD negotiations and processes (J. Esquinas-Alcázar, pers. comm.; P. Mooney, pers. comm.). The earliest published appearance of this quote that we have found is from an FAO document prepared for Earth Day 1993, written by Hope Shand of RAFI, twice stating that 'Since the beginning of this century about 75% of the genetic diversity among agricultural crops has been lost' (FAO, 1993).

It is also possible that the statistic has a more singular origin. In two sections of Fowler and Mooney's (also of RAFI) book *Shattering: Food, Politics, and the Loss of Genetic Diversity* (1991), while discussing the ongoing replacement of landraces with modern cultivars, the authors communicated an FAO expert's concerns about the narrowing list of vegetable crop varieties permitted to be grown in Europe and the consequences for the region's landrace diversity: 'As the mid-1970s were reached, three-quarters of Europe's traditional vegetable seed stood on the verge of extinction' (p. xii), and 'Many varieties – indeed up to three-quarters of all those presently grown in Europe, according to Erna Bennett – will become extinct within ten years!' (pp. 85–86).

Erna Bennett was a pioneer in crop diversity conservation who coined the terms 'plant genetic resources', 'genetic conservation' and 'genetic erosion' (Pistorius, 1997; Hanelt et al., 2012). She worked at the FAO from 1967 until 1982. During a phone interview with Fowler and Mooney in 1978, she voiced her concerns regarding reductions in European varieties (M. C. Fowler, pers. comm.). She later served on the Board of RAFI, and eventually resigned from the FAO over her opposition to the increasing influence of corporate agriculture in the organization.

Whether the 75% estimate is an extrapolation of many sources of information or stems from this single source, the questions of which other lines of evidence potentially contributed, which stakeholders were involved and how the jump from specific findings to a global estimation was made remain a mystery. The result – a simple, single number for the loss of crop diversity at the global scale, attributed to an authoritative international organization – has clearly had a big impact on the field.

A second message very often accompanying statements about the decline of infraspecific crop diversity is that very few crops presently feed the world. This is also attributed to FAO, and is equally conceptually challenging due to its reliance on relatively limited data regarding human diets and nutrition worldwide (Prescott-Allen and Prescott-Allen, 1990), as well as a lack of perspective on how crop species diversity has changed over time (Khoury *et al*., 2014). While this message is conveyed with a variety of numbers, among the most common is that a very limited number of crops (i.e. around nine to 12) provide *three quarters* of the world's food (e.g. FAO, 1998; 2004). Given the ubiquity of these 75% narratives in the literature and in the news, it is clear that they have proven to be powerful communication tools to raise awareness about crop diversity and the potential vulnerability of food systems, even if their accuracy in quantifying change in crop diversity over time is questionable.

II. Defining and measuring crop genetic erosion

1. Expanding definitions and conceptualizations of crop genetic erosion

The term 'genetic erosion' (Table 1) is commonly attributed to crop diversity conservation pioneers Erna Bennett and Otto Frankel (Bennett, 1964, 1968; Frankel & Bennett, 1970), who chose it as a metaphorical parallel to soil erosion, a widely recognized environmental challenge (Fenzi & Bonneuil, 2016). Early conceptualizations of genetic erosion focused on the disappearance of landraces from the geographic regions of crop origins, often specifying that the losses were due to replacement of these locally adapted materials with modern cultivars (Frankel, 1970; Harlan, 1972; Wilkes, 1977). The rates and scales of the loss of landraces during this period led some experts to use more dire phrases, referring to 'genetic wipeout' (Harlan, 1972, 1975) and the need to 'freeze' the genetic landscape (Iltis, 1974).

These early assertions were grounded in direct and anecdotal field observations, as well as information on the diffusion of modern cultivars in particular regions, not on systematic efforts to analyze the structure and dynamics of landrace populations across varied ecogeographic and socioeconomic conditions (Brush, 2004; Fenzi & Bonneuil, 2016). They appear to have been based on a view of crop landraces as fairly stable if not unchanging, drawn from perceptions of traditional farmers as similarly unchanging or timeless, in contrast to European cultures (Fig. 1) (Frankel, 1970; Frankel & Bennett, 1970; Harlan, 1975). These perspectives parallel equilibrial concepts in ecology (e.g. the 'climax' state in ecological succession and the Gaussian framework of competitive exclusion), although these parallels were not explicitly drawn at the time.

As more systematic approaches to researching genetic erosion in traditional agricultural landscapes have been developed, complex patterns of loss, maintenance and increase of diversity have been revealed. In response, attempts have been made to better understand this dynamism (Brush, 1991; van Heerwaarden *et al*., 2010). Priority has been placed on differentiating permanent or marked loss vs normal variation over time (Brush, 1999; Guarino, 1999; Brown, 2008) and on documenting functionally relevant change, such as fitness, long-term viability and capacity to adapt to dynamic environmental conditions (Eticha *et al*., 2010). Proximate anthropogenic and environmental drivers of change have been aligned with concepts from evolution and ecology, including mutation, drift, gene flow, migration and selection (Fig. 2). Theoretical frameworks, including island biogeography, isolation by distance, niche theory and metapopulation models, have provided further ecological insights, recognizing that agroecosystems undergo

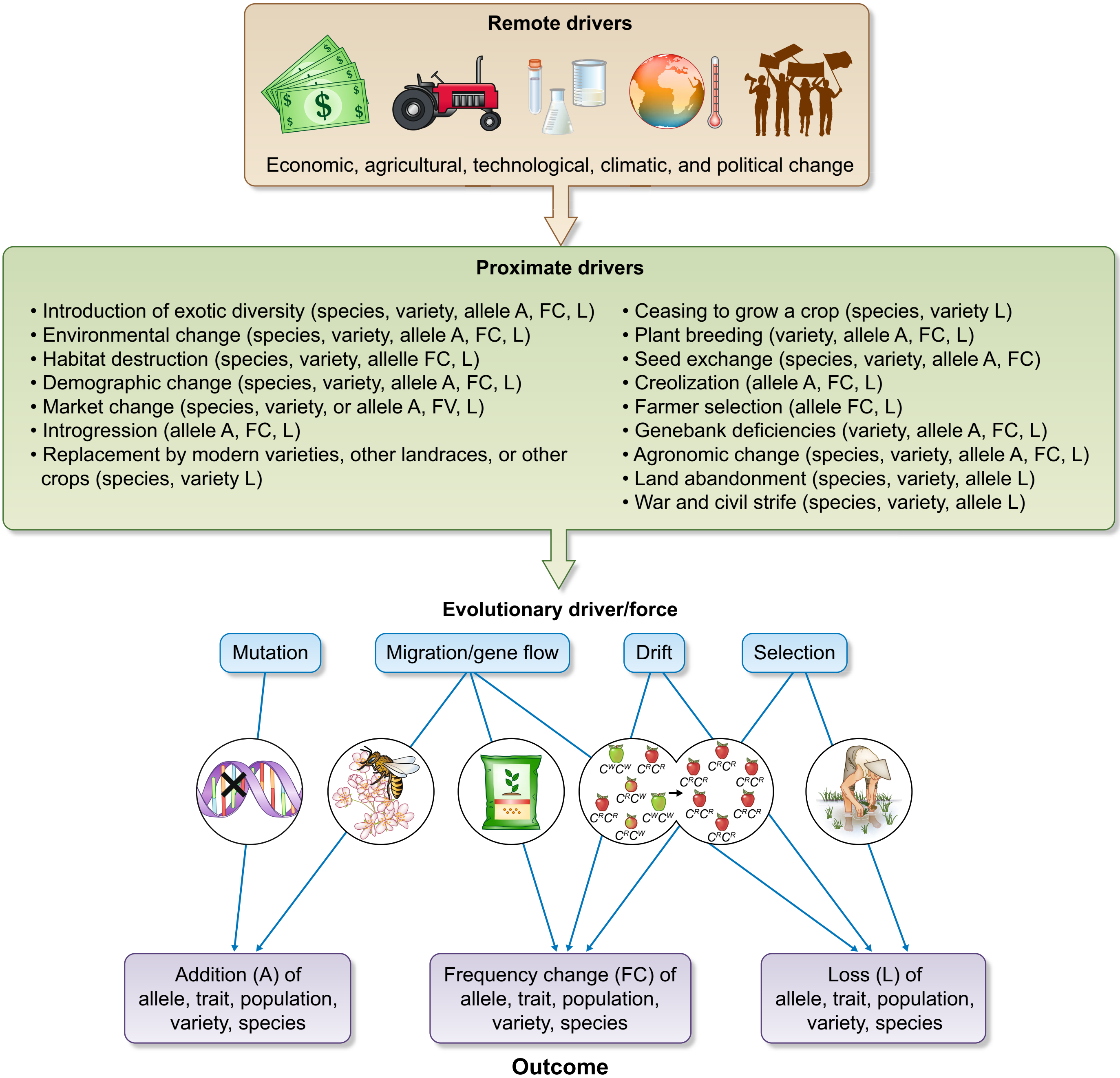

Fig. 2 Evolutionary drivers of change in crop diversity. Conceptual diagram with examples of how crop diversity outcomes, including genetic erosion, are mediated via evolutionary forces, driven by proximate forces, originating in larger changes in society and nature. Note that examples are not comprehensive and provide typical outcomes. A, addition; FC, frequency change; L, loss.

similar ecoevolutionary processes (Brush, 1999; Schoen & Brown, 2001; van Heerwaarden *et al.*, 2010; Tomich *et al.*, 2011). These innovations have made it possible to entertain more effective pathways for on-farm conservation, emphasizing conditions and processes that foster diversity (Brush, 2004; Bellon *et al.*, 2017).

Genetic erosion studies have expanded: from their original geographic focus on regions of crop origins to locations all over the world (e.g. Portis *et al.*, 2004; Priolli *et al.*, 2004; Reif *et al.*, 2005a); from landraces to also include crop wild relatives and modern cultivars (e.g. Kiambi *et al.*, 2005; Reif *et al.*, 2005a; van de Wouw *et al.*, 2010); and from farms to also include wild spaces, seed systems and conservation repositories (e.g. Stehno *et al.*, 1999; Parzies *et al.*, 2000; Negri & Tiranti, 2010). Associated research has further widened to cover farming landscapes, traditional knowledge and culture, and supporting ecosystem services (Sackville Hamilton, 1999; Gepts, 2006). Many other anthropogenic and environmental drivers of crop diversity loss, beyond replacement of landraces with modern cultivars, have been investigated (Fig. 2). Genetic erosion as a term and as a concern has also expanded beyond agriculture to include a wide range of studies on wild plants and animals (e.g. Van Treuren *et al.*, 1991; Rogers, 2004; Rubidge *et al.*, 2012; Díez-del-Molino *et al.*, 2018; Leigh *et al.*, 2019).

The concept of genetic erosion is now widely known in biodiversity conservation – almost 400 articles have been published with the term in the title and over 23 000 with the phrase in the text (Google Scholar, 2020). This has been enabled by the expanding scope and accompanying variety of interpretations: we found *c.* 50 different definitions/descriptions just in the crop diversity literature (Table S1). These mainly vary by improvement type (landraces only, or also modern cultivars and/or wild relatives), geographic scope (within regions of crop domestication only, or also elsewhere), setting (*in situ* only, or also including *ex situ*) and degree to which drivers of loss are specified.

2. Diverse measures, scales and sources of information about crop genetic erosion

As genetic erosion research has evolved, three main measurement targets have emerged: absolute losses (e.g. Colunga-GarcíaMarín *et al.*, 1996; Laghetti *et al.*, 2009; Megersa, 2014), changes in richness (e.g. Hammer & Laghetti, 2005; Nabhan, 2007; Dyer *et al.*, 2014), and changes in abundances, frequencies or evenness (e.g. Khlestkina *et al.*, 2004). These interrelated measurements may also be combined, reflecting metrics commonly used in ecology and population genetics such as Shannon and Simpson indices (Bonneuil *et al.*, 2012; Brown & Hodgkin, 2015). Quantification may be direct, or through proxies such as numbers of farmers or villages (e.g. Teklu & Hammer, 2006; McLean-Rodríguez *et al.*, 2019; Olodo *et al.*, 2020).

While researchers have identified multiple scales at which crop diversity and its loss may be understood (van de Wouw *et al.*, 2009; van Heerwaarden *et al.*, 2010), studies have generally focused either on broader levels, namely change among named varieties, races and species (e.g. Hammer *et al.*, 1996; Tsegaye & Berg, 2007; Perales & Golicher, 2014; Box 2) or on genetic variation, that is in alleles, genes, gene complexes or traits (e.g. Reif *et al.*, 2005b; Malysheva-Otto *et al.*, 2007; Thormann *et al.*, 2017a,b).

Genetic research has employed a suite of molecular marker techniques and population genetic analyses, including estimates for diversity, differentiation, demographic history and patterns of adaptive divergence (Jordan *et al.*, 1998; Fu & Somers, 2011; Fu & Dong, 2015). Indirect approaches to measure change in genetic diversity have also been employed, including coefficients of parentage and related metrics used to compare pedigrees (e.g. Bowman *et al.*, 2003; Martynov *et al.*, 2005, 2006). Within-variety diversity research has also included investigations of changes in phenotypic variation, often focusing on agronomic traits (e.g. Nersting *et al.*, 2006; van Heerwaarden *et al.*, 2009; Schouten *et al.*, 2019).

These crop diversity analyses have been conducted at a wide range of geographic scales, from local (e.g. farm, population or genebank accession), to community and agroecological landscape, to country, region and globe. The time frames for assessing change also vary widely, from short intervals to decades, and, more recently, aided by ancient DNA methods and for some clonally propagated crops, centuries or millennia (e.g. Gross *et al.*, 2014; Mascher *et al.*, 2016; Smith *et al.*, 2019). Intermediate time frame studies often compile and report diversity change at standardized intervals, such as the decade (e.g. Donini *et al.*, 2000; Duvick *et al.*, 2004; Fu & Dong, 2015).

As with other parameters, the sources of information used to document change in crop diversity also vary widely, and may be used in combination. Direct field observations provided the first lines of evidence for genetic erosion, and continue to be employed (e.g. Hammer & Laghetti, 2005; Nabhan, 2007). Local knowledge, gathered through interviews with farmers and their families, community meetings, and surveys, have been widely used to assay change and document farmers' perspectives (e.g. Bayush & Berg, 2007; Kombo *et al.*, 2012; McLean-Rodríguez *et al.*, 2019). Lists of cultivar names, seed inventories, catalogues, agricultural censuses, pedigrees and photographs have provided historical baselines against which to compare current diversity (Box 2). Biological specimens maintained *ex situ* or collected from the field have

Box 2 Change over time in crop diversity: what's in a name?

An oft-cited study based on varietal names compared the vegetable and field crop varieties listed in US seed catalogues in 1903 to the inventory of the national genebank in 1983 (Fowler and Mooney, 1991). The results indicated that only 3% of the 1903 varieties were still available in 1983. While the study accounted for synonyms, a reanalysis two decades later moved the number upward to 7.4%, due both to adjustments in synonymy and to the correction of a mathematical error (Heald & Chapman, 2009). The overall result held that more than 90% of historical varieties were no longer readily available.

One of the major challenges in investigating changes in crop diversity through such comparisons is considering not only the diversity that has been lost, but also what has replaced it. Heald & Chapman (2009) attempted this by also quantifying the total number of varieties presently available in US seed catalogues in 2004. Finding only a 2% decline in varietal richness compared to 1903, they concluded that no significant loss of US varietal diversity had transpired: 'If the meaning of diversity is linked to the survival of ancient varieties, then the lessons of the twentieth century are grim. If it refers instead to the multiplicity of present choices available to breeders, then the story is more hopeful.' (Heald & Chapman, 2009, p. 4).

A further challenge in name-based studies is that varietal names – even accounting for synonyms – may be poor proxies for genetic diversity (e.g. Busso *et al.*, 2000; Louette & Smale, 2000; Hoban & Romero-Severson, 2012; but see Quiros *et al.*, 1990; Martínez-Castillo *et al.*, 2008). Since biological materials from historical lists are rarely available in full for study, it is usually impossible to robustly compare these at the genetic level (Ford-Lloyd *et al.*, 2008; although see Le Clerc *et al.*, 2006; van de Wouw *et al.*, 2013). Furthermore, overall genetic diversity measures are not necessarily equivalent to the functional diversity of relevance to farmers' or market desires and needs, which are themselves constantly evolving (Brown, 1983; Fu & Somers, 2011; Vigouroux *et al.*, 2011). Moreover, significant losses in diversity can be difficult to distinguish from 'normal' levels of change in response to farmer, market or environmental drivers (Mercer & Perales, 2010). Finally, such studies rarely account for spatial change, such as in cultivated areas of different crop varieties or to weigh both richness and evenness.

provided materials for genotypic and phenotypic comparisons (e.g. Del Rio *et al.*, 1997; Diederichsen *et al.*, 2013; McLean-Rodríguez *et al.*, 2019). Remote sensing data have also been used, for example to predict changes in crop diversity impacted by climate change (e.g. Jarvis *et al.*, 2008b; Rhoné *et al.*, 2020).

III. Evidence for, and drivers of, changes in crop diversity over time

Here we present a synthesis of evidence regarding diversity changes in crop landraces on farms, modern crop cultivars in agriculture and crop wild relatives in their natural habitats (below), as well as crop genetic resources held in *ex situ* conservation repositories (in Notes S1). To review the literature on changes in crop diversity over time, we compiled studies investigating changes, as well as the reasons for such changes, across all geographies, scales, time periods, crops and their wild relatives, and methods, bringing together evidence on crop genetic erosion in the widest sense. Literature review methods and limitations are provided in Notes S2, with key attributes for 288 pertinent publications, including the 232 primary literature sources, given in Table S2, and their references in Appendix A1.

1. Changes in the diversity of crop landraces on farms

The original focus of genetic erosion concern – landraces – remains the most widely researched, with 139 articles published from 1939 to 2021 (Table 2). These provide information on changes mainly in annual cereal crops, namely maize, wheat, rice, barley and sorghum, with relatively broad geographic coverage globally and particular focus on East Africa, Mesoamerica, West Africa, South America, South Asia and Southwest Europe. More than three-quarters of these studies focus on the geographic origins and primary regions of diversity of crops. They predominantly assess diversity among landraces, but also include within-landrace and species-level diversity. Regarding scale, they mainly analyze regions within countries, as well as the country level. They employ a mixture of methods, with farmer and community interviews and surveys and field visits being the most common, but also including genetic, nomenclatural and phenotypic comparative analyses. Most publications assessed change from around the 1920s–2000s as a starting point to the 1990s–2010s as the end/current period, with a median time frame of 28 yr.

This literature documents widespread losses of landrace diversity over the past century, continuing to the present. Over 96% of studies found change in diversity over time, with more than 86% of the total documenting evidence of decline. These include the complete disappearance of specific landraces (e.g. Colunga-García Marín *et al.*, 1996; Laghetti *et al.*, 2009; Eticha *et al.*, 2010) and a few crop species (Hammer & Khoshbakht, 2005), declines in richness (Box 2) (e.g. Hammer *et al.*, 1996; Nabhan, 2007; Dyer *et al.*, 2014), and losses of within-landrace variation (e.g. Portis *et al.*, 2004; Trifonova *et al.*, 2021). Declines in the harvested area (e.g. Sharaf Uddin *et al.*, 2005; Rice, 2007; Gomes Viana *et al.*, 2020), or number of farmers/families (Teklu & Hammer, 2006; McLean-Rodríguez *et al.*, 2019; Mulualem *et al.*, 2020) or villages (Olodo *et al.*, 2020) cultivating specific landraces within a given area were also documented. The few studies assessing change in traditional knowledge related to crop diversity generally also indicated loss (Brush & Stabinsky, 1996; Benz *et al.*, 2000; Brush, 2004; Keller *et al.*, 2005).

As for reasons for landrace diversity loss, the most reported driver, both within and outside of the geographic origins of crops, was replacement with modern cultivars. In some regions and for some crops, this transition appears to be largely complete. For example, Brush (2004) documented the wholesale replacement of maize landraces in the US corn belt largely between 1925 and 1950. By contrast, maize landraces in Mesoamerica continue to be widely cultivated, with ongoing diversity loss but also maintenance and diversification (Fig. 3).

A wide variety of other drivers of loss were also documented, including agronomic, demographic, land use, environmental and market change, as well as development processes and seed system deficiencies (Tables 2, S3). The replacement of landraces with other crop species was also noted, for example sorghum with maize in Yemen (Varisco, 1985) and traditional with exotic vegetables in Tanzania (Keller *et al.*, 2005). Climate change has been reported to be a driver of loss of landrace diversity in recent decades and is predicted to lead to further declines (e.g. Mercer & Perales, 2010; Ureta *et al.*, 2012; Rhoné *et al.*, 2020; Labeyrie *et al.*, 2021).

Many of the drivers specifically highlighted in the literature are interrelated facets of agricultural and economic development, manifested through the extension and expansion of formal seed systems, globalization of markets and increasing availability of agricultural technologies, with national and international policies and trade agreements enabling all the above (Robinson, 2018). Studies focused on areas increasingly connected to outside regions, allowing the faster dispersion of modern cultivars, agricultural chemicals and other inputs, as well as easier movement of produce to market, have documented substantial losses in landraces and also reductions in differences among those that persist, that is increasing genetic homogeneity across remaining landraces (Fig. 4) (e.g. Rice *et al.*, 2006; Thormann *et al.*, 2017a; Rojas-Barrera *et al.*, 2019; Olodo *et al.*, 2020).

The literature demonstrates the importance of particular environmental and social conditions in driving landrace diversity change. Farmlands with characteristics amenable to agronomic practices associated with modern cultivars, for example flat, irrigated plots, have shown more severe declines in landrace diversity than rainfed or marginal areas (Chambers *et al.*, 2007). Major changes in labor availability and other demographic shifts have led to losses for landraces with intensive labor requirements (Zimmerer, 1991, 1992; Negri, 2003). Demand and market changes have resulted in reductions in the cultivation areas of specific landraces (Rice, 2007; Gomes Viana *et al.*, 2020). Periods of instability, whether civil strife (Sperling, 2001) or environmental change (Shewayrga *et al.*, 2008), have led to rapid losses, although not in all cases (van Etten, 2006). These are not solely recent phenomena; Clement (1999) linked loss of traditional crop diversity with Indigenous population decline following the arrival of Europeans in the Americas after 1492.

While the body of literature clearly documents extensive declines in landrace diversity, it also provides important context and caveats

Table 2 Summary of crop genetic erosion research characteristics and findings.

Topic	Crop landraces on farms	Modern crop cultivars in agriculture	Crop wild relatives in their natural habitats	Crop genetic resources held in conservation repositories	All literature
Number of articles	139	105	33	28	232
Dates of publication	1939–2021	1984–2021	1988–2020	1995–2021	1939–2021
Journals/media	*Genetic Resources and Crop Evolution* (28), *Plant Genetic Resources: Characterization and Utilization* (7), *PLoS ONE* (4), *PNAS* (4), *Economic Botany* (4), *Theoretical and Applied Genetics* (4); 71 other journals/media with 3 or fewer articles	*Theoretical and Applied Genetics* (16), *Crop Science* (12), *Genetic Resources and Crop Evolution* (11), *Euphytica* (7), *Russian Journal of Genetics* (5); 41 other journals/media with 3 or fewer articles	*Genetic Resources and Crop Evolution* (4), *PLoS ONE* (2), *PNAS* (2), *Theoretical and Applied Genetics* (2); 23 other journals/media with 1 article	*Genetic Resources and Crop Evolution* (5), *Theoretical and Applied Genetics* (4), *Crop Science* (3), *Evolutionary Applications* (2); 14 other journals/media with 1 article	*Genetic Resources and Crop Evolution* (37), *Theoretical and Applied Genetics* (21), *Crop Science* (15), *Euphytica* (8); *Plant Genetic Resources: Characterization and Utilization* (8), *PNAS* (7), *PLoS ONE* (7); 96 other journals/media with 5 or fewer articles
Crops covered	Maize (18), wheat (16), rice (14), barley (9), sorghum (8), potato (5), bean (4); 28 other crops with 2 or fewer articles each; 31 additional articles with multicrop focus	Wheat (40), barley (8), maize (8), rice (8), oat (4), potato (3), soybean (3); 14 other crops with 2 or fewer articles each; 12 additional articles with multicrop focus	(Crop wild relatives of) Rice (4), maize (3), coffee (2), barley (2); 8 other crops with 1 article each; 12 additional articles with multicrop focus	Rice (4), wheat (4), barley (3), bean (3), maize (3), potato (2); 6 other crops with 1 article each; 3 additional articles with multicrop focus; 23 articles focus on cultivated materials (23 on landraces, 7 on modern cultivars), 8 on crop wild relatives	Wheat (50), maize (24), rice (24), barley (16), sorghum (9), potato (7), oat (5); 38 other crops with 4 or fewer articles each; 44 additional articles with multicrop focus
Regions covered	Americas (C America and Mexico (18), S America (11), N America (9)), Africa (E Africa (20), W Africa (12), N Africa (6)), Asia (S Asia (11), W Asia (9), SE Asia (7)), Europe (SW Europe (13), NW Europe (8)), Global (10), Pacific (1)	Europe (NW Europe (21), SW Europe (13), NE Europe (10), SE Europe (7)), Americas (N America (26)), Asia (S Asia (10), E Asia (8)), Global (8), Africa (2), Pacific (2)	Asia (E Asia (3), W Asia (3), SE Asia (2)), Americas (C America and Mexico (5), N America (3)), Africa (E Africa (6), W Africa (3), C Africa (2), S Africa (2)), Global (6), Europe (SW Europe (2))	Americas (N America (4), C America and Mexico (3)), Europe (NW Europe (4), NE Europe (2)), Asia (E Asia (3), W Asia (2)), Africa (3), Global (3)	Americas (N America (33), C America and Mexico (19), S America (14)), Europe (NW Europe (25), SW Europe (23)), Asia (S Asia (17), E Asia (14)), Africa (E Africa (22), W Africa (13)), Global (16), Pacific (3)
Countries covered	Ethiopia (15), Mexico (15), Italy (10), USA (9), Peru (6), India (4), Philippines (4); *c.* 50 other countries covered in 3 or fewer articles. Mostly (111 (80%)) inclusive of primary regions of diversity of crop(s)	USA (16), Canada (13), France (9), UK (8), China (7), India (6), Russian Federation (5); *c.* 35 other countries covered in 3 or fewer articles. Mostly (73 (69.5%)) outside of primary regions of diversity of crop(s)	Mexico (6), China (3), Ethiopia (3), Kenya (3), Tanzania (3), USA (3), Italy (2), Jordan (2), Senegal (2), Thailand (2); *c.* 15 other countries covered in 1 article. All inclusive of primary region of diversity of CWR	USA (4), Germany (3), China (2), Czech Republic (2), Mexico (2), Ethiopia (2); *c.* 10 other countries covered in 1 article. Mostly (23 (82.1%)) inclusive of primary region of diversity of crop	USA (23), Mexico (17), Ethiopia (17), Italy (14), Canada (13), China (12); *c.* 80 other countries with 7 or fewer articles. Mostly (145 (62.5%)) inclusive of primary region of diversity of crop
Geographical scale	Subcountry (88), Country (28), Region (11), Global (8), Community (4)	Country (62), Subcountry (18), Region (17), Global (7), Community (1)	Subcountry (17), Country (6), Global (6), Region (4)	Subcountry (16), Country (8), Global (3), Community (1)	Subcountry (106), Country (86), Region (24), Global (12), Community (4)
Timeframe	1920s–2000s (4000 years before common era (BCE)) to 1990s–2010s (2099). Median length of study period 28 yr	1900s–1970s (1200) to 1990s–2000s (2014). Median length of study period 59 yr	1950s–1990s (1927) to 2000s–2010s (2089). Median length of study period 17.5 yr	1950s–1990s (1831) to 1990s–2010s (2017). Median length of study period 31 yr	1900s–2000s (4000 BCE) to 1990s–2010s (2099). Median length of study period 40 yr
Diversity levels	Varietal (100), within-varietal (52), species (42)	Within-varietal (85), varietal (34), species (11)	Species (18), within-varietal (within population) (18), varietal (population) (16)	Within-varietal (23), varietal (8), species (3)	Within-varietal (129), varietal (120), species (52)

Table 2 (Continued)

Topic	Crop landraces on farms	Modern crop cultivars in agriculture	Crop wild relatives in their natural habitats	Crop genetic resources held in conservation repositories	All literature
Methods	Social/field survey (82), genetic (41), nomenclatural (33), phenotypic (20); 101 S; 38 M	Genetic (75), nomenclatural (13), social/field survey (13), pedigree (10), phenotypic (8); 93 S; 12 M	Social/field survey (17), genetic (13), nomenclatural (8), phenotypic (3), predictive modeling (3); 23 S; 10 M	Genetic (20), Phenotypic (8), Social/field survey (8), Nomenclatural (4); 17 S; 11 M	Genetic (112), Social/field survey (89), nomenclatural (42), phenotypic (28), pedigree (10), modeling (4); 185 S; 47 M
Baseline data	Farmer knowledge (60), biological materials (52), published information (28), field observations (27)	Biological materials (77), published information (16), pedigree information (11), farmer knowledge (9), field observations (5)	Biological materials (14), field observations (11), farmer knowledge (5), published information (6), remote data (3)	Biological materials (24), published information (4)	Biological materials (124), Farmer knowledge (60), Published information (38), Field observations (33), pedigree information (11), remote data (6)
Evidence of change in diversity	96.4% (134)	93.3% (98)	97% (32)	100% (28)	95.3% (221)
Evidence of loss of diversity	86.3% (120)	67.6% (71)	90.9% (30)	85.7% (24)	79.3% (184)
Evidence of maintenance of diversity	33.8% (47)	43.8% (46)	18.2% (6)	42.9% (12)	37.1% (86)
Evidence of increase/ appearance of new diversity	23.7% (33)	47.6% (50)	15.2% (5)	28.6% (8)	29.7% (69)
Proximate drivers of change	Replacement with modern varieties, agronomic change, replacement with other crops, demographic change, land use change, climate change, development, environmental change, market change, farmer selection, seed system deficiencies, War	Plant breeding	Land use change, climate change, agronomic change, environmental change, development	Genebank practices (regeneration, processing, storage, etc.)	Plant breeding, replacement with modern varieties, land use change, agronomic change, replacement with other crops, climate change, demographic change, development, market change, genebank practices, environmental change, farmer selection, seed system deficiencies, war
Evolutionary drivers of change	Replacement/removal, drift, selection, gene flow	Drift, gene flow, selection	Replacement/removal, drift, gene flow	Drift	Replacement/removal, drift, gene flow, selection

Key characteristics and findings from the research on crop landraces on farms, modern crop cultivars in agriculture, crop wild relatives in their natural habitats, and crop genetic resources in conservation repositories. Counts provided in parentheses indicate number of articles.
General: articles may cover more than one crop, geography, timeframe and level of diversity, and use more than one method and baseline data, and find more than one major result, so counts and percentages provided in the table may not sum to totals. Data provided are predominant information; characteristics or findings reported in a small minority of studies may not be reported here. Data are generally sorted from most to least important.
Regions/countries: for crop genetic resources held in conservation repositories, these typically denote the location of *ex situ* repositories. Primary region of diversity of crops as per Khoury *et al*. (2016).
Timeframe: ranges denote where the greatest numbers of articles begin/end assessed timeframe. Dates in parentheses are earliest/latest dates in the dataset.
Method: social/field survey includes stakeholder interviews and surveys. Nomenclatural includes desk-based published information studies. S, single method used; M, multiple methods.
Evidence of change in diversity: note individual articles may find loss, maintenance and/or increase in diversity at different levels within the same study.

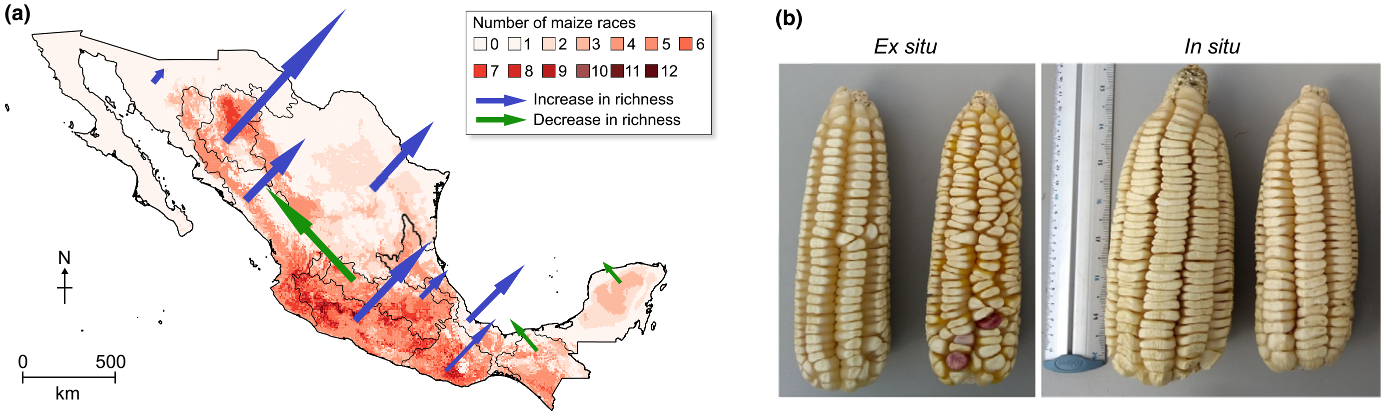

Fig. 3 Changes in maize landrace diversity in Mexico. Mexican farmers currently cultivate *c*. 8 million hectares of maize, 75% with farmer-saved seed (Bellon *et al*., 2018). While most farmer-saved varieties are landraces, some are advanced generations of modern cultivars or mixed (creole) varieties (Bellon & Risopoulos, 2001). Modern cultivars are largely absent in the highlands (> *c*. 2000 m asl), common in the lowlands (< *c*.1400 m asl) and rare at midelevations (Perales, 2016). (a) Perales & Golicher (2014) used genebank samples collected in *c*. 10 yr periods around 1950, 1975 and 2005 to examine changes in maize racial composition and richness in Mexico. All races were present at similar frequencies across time periods. Five of the 47 races were abundant and 20 were rare in all three sampling periods; rareness of some of these had already been noted in 1950 (Wellhausen *et al*., 1952). Distribution models showed richness generally increased over time, although possibly due to new racial designations; just three of 11 maize biogeographic regions showed a decline in richness over time (shown is maize racial richness based on distribution models for germplasm collected between 1975 and 2010 and relative change in modeled richness (%) by biogeographic region based on richness for < 1980 models, with blue arrows indicating an increase and green a decrease in richness, and size of arrows indicating the magnitude of change (maximums are +48% and −40%). By contrast, a case study from the Yucatan (Fenzi *et al*., 2015) confirmed an increasing dominance of longer season, higher yielding race Tuxpeño from 1999 to 2011, with (formerly common races) Dzit Bacal and Nal Tel maintained at low frequencies. At the landrace level, economic surveys by Dyer *et al*. (2014) have documented a decreasing landrace richness per household across Mexico, declining from 1.43 to 1.22 between 2002 and 2007. (b) At higher elevations, McLean-Rodríguez *et al*. (2019, 2021) examined maize landrace diversity in Morelos over 50 yr. Families still had the same seed lot for 15% of 93 accessions collected in 1966 and another 6% had a different seed lot of the same landrace. At the municipality level, racial types remained present in 65% of cases. When comparing the molecular genetic variation of historical and current samples from families still growing the same seed lot, they found diversity based on single nucleotide polymorphisms (SNPs) was similar – current samples had 3.1% fewer SNPs and lower pairwise genetic distances overall than historical samples, but similar heterozygosity; the sampling periods did not differentiate using clustering. Several loci appeared to be under farmer selection in the Ancho race (shown is a comparison of the historical (*ex situ*) collection and a current (*in situ*) collection from the same donor family in Morelos; photographs courtesy of McLean-Rodríguez), demonstrating ongoing evolution over the last 50 yr. Wide Ancho grains have greater commercial value for use in a specialty dish (Perales *et al*., 2003). The abundant literature on Mexican maize diversity shows complex trends, with farmer-saved seed exchanged intensely among households, communities and regions. Maize races grown in the 1940s remain extant, albeit with signs of decline in some locations, while some landraces seem to be evolving into new forms. This adaptive process could become even more essential under climate change and the declining economic importance of agriculture. However, the relationship between changes in landrace use and overall genetic diversity in this outcrossing species is not well understood and remains a research priority.

(described below, with gaps in existing knowledge further discussed in Steps needed to advance knowledge about crop genetic erosion section).

First, interchange and turnover of landraces have been demonstrated to be widespread and often relatively continuous characteristics of traditional agroecosystems for many crops (e.g. Louette *et al.*, 1997; Perales *et al.*, 2003; Martínez-Castillo *et al.*, 2012; Rojas-Barrera *et al.*, 2019), refuting early notions that landrace diversity is static and unchanging.

Second, while linear diversity declines when comparing wild species to landraces to modern cultivars have been documented, such as in sunflower (Tang & Knapp, 2003) and soybean (Hyten *et al.*, 2006), loss in overall genetic/genomic diversity has been shown to be less drastic or more gradual than expected in some crops, namely woody perennials including apple and grape (Miller & Gross, 2011; Gross *et al.*, 2014), common bean (Trucchi *et al.*, 2021), carrots (Iorizzo *et al.*, 2013) and sorghum (Mascher *et al.*, 2016; Smith *et al.*, 2019). More generally, regarding modernization diversity bottlenecks, crops lacking extensive formal scientific breeding and extension programs, and thus still primarily based on farmer-managed diversity, are less exposed to replacement by modern cultivars of the same species and less affected by associated reductions in landrace diversity.

Third, a considerable body of evidence for change or loss is based on landrace names. These are a way of describing crop diversity that farmers use and are thus relatively easily recorded through interviews and surveys (e.g. Teshome *et al.*, 2007; Bezançon *et al.*, 2008; Kombo *et al.*, 2012) and through inventories, catalogues and censuses (e.g. Fowler & Mooney, 1991; Hammer & Khoshbakht, 2005; Bayush & Berg, 2007). However, nomenclatural inconsistency, including the use of different names for genetically similar landraces (synonymy) and single names for genetically distinct materials (homonymy), complicates this approach (Jarvis *et al.*, 2008a; van de Wouw *et al.*, 2011; Volk & Henk, 2016). Further, the power of name-based genetic erosion studies is constrained by limited accounting for the diversity that replaced the landraces, challenges in distinguishing important or permanent vs minor or temporary change, limited documentation of accompanying spatial change, and poor correlation between name diversity and genetic diversity (Box 2).

Fourth, the disappearance of landraces, while potentially representing the extinction of unique genotypes and gene

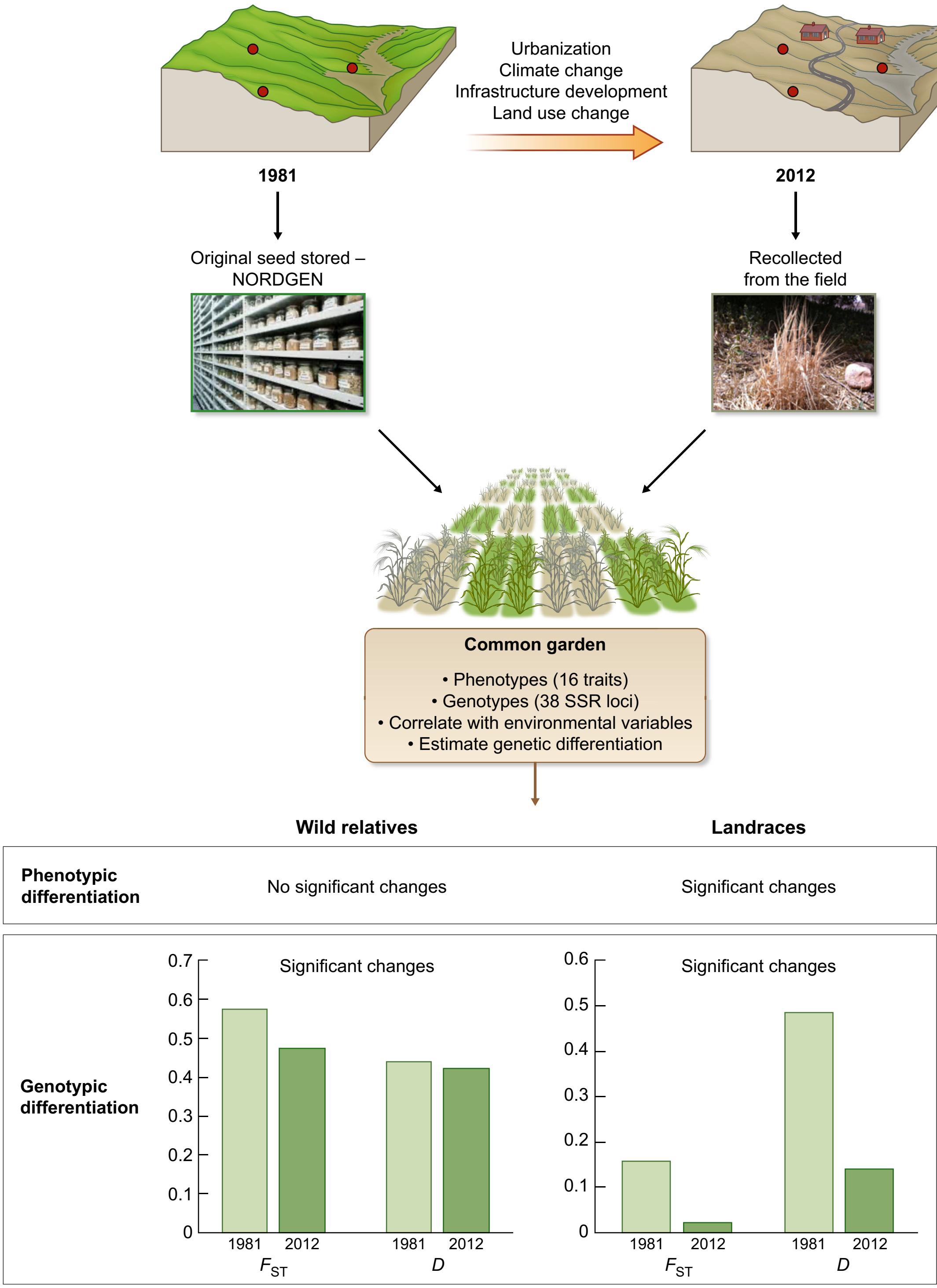

Fig. 4 Changes in cultivated and wild barley diversity in Jordan. Experimental design and results for evaluating temporal changes in genotypic and phenotypic diversity (Thormann *et al*., 2017a,b). Samples from a plant collecting mission in 1981 were stored as original seed at the Nordic Genetic Resource Center (NORDGEN) and used as baseline samples. Location notes were used to conduct a second collecting effort at the same sites in 2012, with the seed deposited at the National Center for Agricultural Research and Extension (NCARE) in Jordan and at the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Germany. Seeds from both collecting periods were grown in a randomized block design at the IPK in 2013 and individual plants were evaluated for 16 phenotypic traits. Phenotypes were compared as a multivariate composite of the 16 trait values using the first principal component. ANOVA was applied to these principal components to assess changes due to the collection year. In wild *Hordeum spontaneum* populations, there was no significant difference between collecting years. Phenotypic differences were significant for barley landraces. Tissue samples from individual plants were used as a source of DNA for microsatellite (simple sequence repeat (SSR)) genotyping at 38 loci. Genotypic changes, measured as standardized differentiation (Wright's F_{ST} and Jost's D), showed significant changes in genetic structure for both wild and cultivated barley, including significant reductions in differentiation among populations, reflecting an increase in genetic homogeneity across the landscape.

complexes, does not necessarily imply an overall decline in genetic diversity. Over a quarter of the studies documenting loss of landrace diversity also reported maintenance or even appearance of new diversity (e.g. Rice *et al.*, 2006; Bitocchi *et al.*, 2009; Orozco-Ramírez & Astier, 2017). Steele *et al.* (2009) found that replacement of rice landraces by modern cultivars in Nepal could increase overall genetic diversity if the adoption of modern varieties was limited to 65% of the study area. Vigouroux *et al.* (2011) found no major change in overall genetic diversity in pearl millet landraces in villages in Niger over 25 yr, despite significant shifts in adaptive morphological traits due to recurrent drought.

Finally, adoption of modern cultivars may not directly equate with landrace loss. Farmers commonly maintain landraces even as they incorporate modern cultivars into their systems (Brush *et al.*, 1981), and also interbreed the two to produce new varieties carrying useful traits from both parental backgrounds, a practice referred to as 'creolization' in Latin America (e.g. Bellon & Risopoulos, 2001; Perales *et al.*, 2003; Rojas-Barrera *et al.*, 2019).

Indeed, the continued generation of research publications on landraces to the present day demonstrates a level of persistence of traditional crop diversity unforeseen by the leading authorities predicting genetic wipeout in the early decades of the field (Fig. 1). This persistence can be traced in large part to the distinct values provided by landraces for local productivity, production stability and resilience as well as for dietary, specialized or high-value markets, and other cultural purposes in particular contexts and regions (Zimmerer, 1992; Brush & Meng, 1998; Negri, 2003; Perales *et al.*, 2003; Nabhan, 2007; Rice, 2007; Katwal *et al.*, 2015; Bellon *et al.*, 2017; Wang *et al.*, 2018).

Landraces continue to provide a viable manner by which farmers can optimize long-term production in heterogeneous and marginal environments, particularly in the absence of moderating technologies such as irrigation and soil amendments (Bellon *et al.*, 2006). In highlands, for example, landraces are more likely to be maintained in comparison to at lower altitudes and valley bottoms (Brush, 2004), in part due to varied soils (Bellon & Taylor, 1993), obstacles to road building and irrigation (Zimmerer *et al.*, 2017), and a lack of well-adapted modern cultivars (Mercer & Perales, 2010). Landraces can also better fit farm labor availability (Bellon *et al.*, 2017). Diversity among and within landraces thus provides option value (Brown, 1990) and risk management (Teshome *et al.*, 2007; Zimmerer, 2010), particularly to small-scale farmers lacking economic resources, credit opportunities and extension support (Baker & Jewitt, 2007; Nazli & Smale, 2016).

2. Changes in the diversity of modern crop cultivars in agriculture

Research into changes in the diversity of modern crop cultivars understandably began more recently than for landraces, but has been substantial, with 105 pertinent articles published between 1984 and 2021 (Table 2). As with landraces, the main crops studied have been annual cereals, namely wheat, barley, maize, rice and oats. Geographic focus has been quite uneven, with Europe and North America, and to a more limited extent South and East Asia, fairly well studied, while other regions have been poorly covered. The majority (69.5%) of research has focused on areas outside the geographic origins of the relevant crop(s). Most of the studies have been conducted at country, subcountry or regional scales, using genetic methods. These have focused mainly on changes in diversity within or among varieties, with a few assessing varietal richness (Stehno *et al.*, 1999; Heald & Chapman, 2012), or changes in cultivated area (Brennan & Fox, 1998; Aguilar *et al.*, 2015; Martin *et al.*, 2019). Often drawing on historical and contemporary materials maintained in genebanks, the literature generally analyzed cultivar diversity change from around the 1900s–1970s to the 1990s–2000s, with a median time frame of 59 yr.

This literature documents widespread and complex changes in modern cultivar diversity. More than two-thirds of the publications found evidence of decline in diversity over time, mainly as a result of plant breeding activities and associated with changes in public vs private industry dominance and intellectual property frameworks. Many of these studies compared the modern cultivars of a crop available within a geographic area, and also historical landraces from the same region, generally finding higher diversity in the landraces, with a decline in variation through the transition to modern cultivars and across cultivars over subsequent decades (e.g. Jordan *et al.*, 1998; Roussel *et al.*, 2004; Mir *et al.*, 2012). The multispecies review by Rauf *et al.* (2010) identified the highest rates of genetic erosion among modern cultivars, compared to that among landraces and wild materials.

Almost half of the publications also found increasing diversity among modern cultivars over recent decades, in some cases compensating for losses of overall genetic diversity found in historical varieties (Fig. 5) (e.g. Reif *et al.*, 2005b; Steele *et al.*, 2009; Schouten *et al.*, 2019). A meta-analysis of 44 publications on change in allelic evenness among modern cultivars of eight field crops released during the 20th century at regional levels found significant change over decades but no overall decrease in genetic diversity in cultivars over time (van de Wouw *et al.*, 2010). The researchers documented a reduction of allelic evenness in the 1960s compared to previous decades, especially in North America. After the 1960s and 1970s, however, diversity increased, perhaps because of greater access to genetic resources in genebanks, as well as wider use of crop wild relatives and other diverse resources in plant breeding.

Many of the publications surveyed reveal complexity in these trends. Fu (2006), in a review of 23 cultivar diversity publications, found that genome-wide changes in overall genetic diversity were not significant over time, but allelic diversity loss at individual chromosomal segments was substantial. Duvick (1984), in a survey of plant breeders, reported an assessment that the genetic base of modern cultivars of major crops was increasing, but was still not sufficiently diverse. van de Wouw *et al.* (2013) reported an increasing number and uniqueness of lettuce cultivars available from French and Dutch companies after a genetic diversity low in the 1960s, but also a dramatic decline in the number of breeding companies. A recent study on rice cultivars in China documented a diversity peak in the 1990s–2000s – aligning with reviews such as that of van de Wouw *et al.* (2010) – but also found significant decline in the most recent decade (Tang *et al.*, 2021).

Increasing genetic homogeneity among modern cultivars was also commonly reported (e.g. Cox *et al.*, 1986; Moon *et al.*, 2009; Gatto *et al.*, 2021). While van de Wouw *et al.*'s (2010) meta-

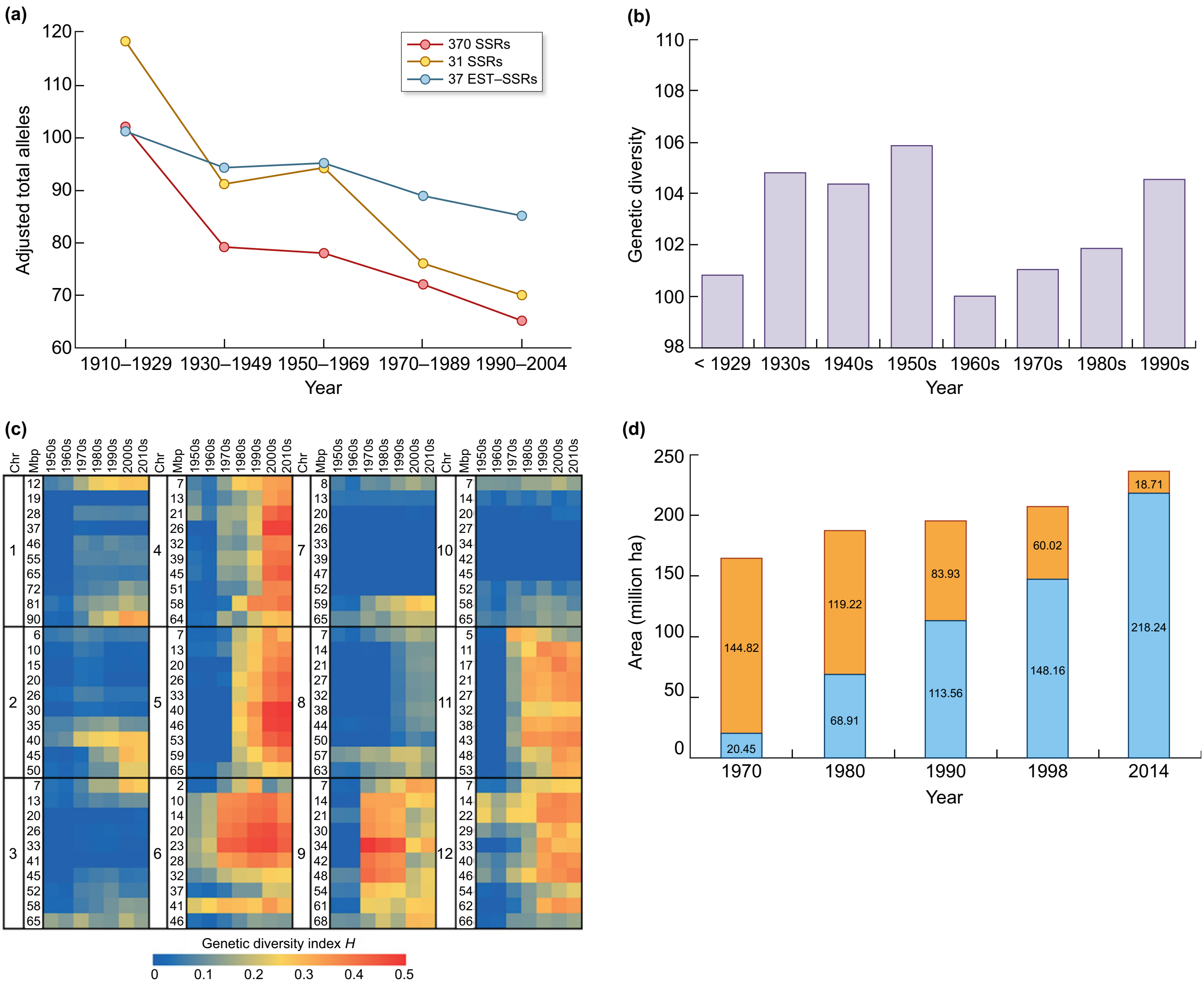

Fig. 5 Diversity trends in modern cultivars. (a) Among the most comprehensively studied pools of modern cultivars are those released in Canada over the 20th century. While the results have varied by crop and methodological tool, the overall trend has been one of declining diversity, including substantial allelic reduction at individual loci as well as genetic shift, particularly for wheat and oat cultivars (Fu & Dong, 2015). This figure demonstrates allelic diversity decline in 75 wheat cultivars and across three genetic methodologies. (b) Global analyses of genetic diversity within and among modern cultivars have documented both declines and increases in diversity. A metaanalysis involving 44 publications covering eight field crops, based on allelic evenness (Nei's *D*) in regional pools of cultivars released during the 20th century (van de Wouw *et al*., 2010) revealed declines in diversity especially around the 1960s–1970s, followed by increases in more recent decades, resulting in minimal overall loss over time. This figure depicts decadal diversity changes with results across studies weighted by sample size, number of loci and molecular marker system. (c) Analyses targeting changes in important traits are less frequent in the literature than those assessing overall diversity. Schouten *et al*. (2019) documented not only increasing genetic diversity over seven decades in registered glasshouse tomato cultivars in the Netherlands, but also higher proportions of exotic introgressions from crop wild relatives since the 1970s to increase resistance to diseases and pests, particularly for organic/low pesticide systems, as well as further genetic and phenotypic diversifications to meet consumer demand for fruit size, color, shape and flavor. The heat map depicts increases in genetic diversity (expected heterozygosity) across the crop's 12 chromosomes, with blue indicating low diversity and red high diversity per decade for chromosomal fragments. (d) Changes in the spatial diversity of modern cultivars are much less well researched than changes in pools of registered or available varieties. A recent analysis of trends in the Green Revolution expansion of improved cultivars of 11 cereal, pulse, and root/tuber crops in 44 countries in Asia and sub-Saharan Africa from 1970 to 2014 (Gatto *et al*., 2021) quantified the increasing proportion of total cultivated area dedicated to modern cultivars, especially in Asia (depicted here; orange depicts landraces, while blue depicts modern cultivars). They also documented the importance of modern 'mega-varieties' in driving spatial homogeneity. (a) Reprinted by permission from Springer International Publishing (*Genetic Diversity and Erosion in Plants*) (Genetic erosion under modern plant breeding: case studies in Canadian crop gene pools, Fu Y-B, Dong Y-B, 2015). (b) Reprinted by permission from Springer Nature (*Theoretical and Applied Genetics*) (Genetic diversity trends in twentieth century crop cultivars: a meta analysis, van de Wouw M, Hintum T, Kik C, Treuren R, Visser B, 2010). (c) Reprinted under CC-BY, © 2019 Schouten, Tikunov, Verkerke, Finkers, Bovy, Bai & Visser. (d) Reprinted under CC-BY, © 2021 Gatto, de Haan, Laborte, Bonierbale, Labarta & Hareau.

analysis found no net loss of genetic diversity at regional levels, they acknowledged that varieties may be more similar globally due to declining numbers of seed companies breeding varieties for different markets. Martin *et al.* (2019) documented greater spatial homogeneity across subcontinents over time in terms of richness of major crop commodities, while Aguilar *et al.* (2015) demonstrated increasing uniformity in crops cultivated within counties in the US. Both these studies illustrate crop specialization based on modern cultivars and may also point to the dominance of widely adapted varieties (Gatto *et al.*, 2021).

While significant changes in modern crop cultivars are clearly documented in the literature, determining the overall impact of plant breeding on their genetic diversity and, further, on their genetic vulnerability remains a major challenge (Fu & Dong, 2015). Only a few of the studies targeted genetic diversity of known functional relevance (Jordan *et al.*, 1998; Fu & Somers, 2011), with the majority analyzing random genetic markers or overall diversity. Phenotypic studies of modern cultivars, on the other hand, have generally focused on agronomically important traits (e.g. Nersting *et al.*, 2006; Diederichsen *et al.*, 2013; Schouten *et al.*, 2019). The majority of these 'functional' diversity studies found significant decreases in variation.

Further, with only a few exceptions (Brennan & Fox, 1998; Bowman *et al.*, 2003; Gross *et al.*, 2014), these studies analyzed trends in the diversity of modern cultivars that were available, registered or bred in a given area, not in the extent of their cultivation (e.g. planted area) or the varietal turnover rate. Research focused on cultivation patterns following the Green Revolution transition documented increasing varietal homogeneity within 11 major food crops, particularly in Asia, through the spread of modern cultivars and especially due to the success of 'mega varieties' (Gatto *et al.*, 2021). More evidence of this sort is critically needed to form a comprehensive understanding of field- and landscape-level diversity changes in areas planted to modern cultivars, and the implications of these changes in terms of crop genetic vulnerability.

3. Changes in the diversity of crop wild relatives in their natural habitats

Research on changes in the diversity of crop wild relative species and their populations comprises a much more limited body of literature than that on landraces and modern cultivars, with 33 articles published between 1988 and 2020 (Table 2). These cover the wild relatives of rice, maize, coffee, barley and a handful of other crops, with relatively good regional spread, especially in East Africa, Mesoamerica, East and West Asia, West Africa, and North America. These studies mainly assessed changes in diversity at the subcountry scale, although research was also conducted at the country, regional and global levels. The research analyzed changes in entire species (e.g. Jarvis *et al.*, 2008b; Legesse, 2019), populations (e.g. Akimoto *et al.*, 1999; Kiambi *et al.*, 2005) and within-population diversity (e.g. Nevo *et al.*, 2012; Greene *et al.*, 2014; Rojas-Barrera *et al.*, 2019). Using field surveys, published list comparisons, genetic and phenotypic analyses, and predictive modeling, the analyses examined change from around the 1950s–1990s to the 2000s–2010s, with a median time frame of 17.5 yr.

This research largely documents severe negative impacts on many crop wild relative populations around the world over time, including on crop progenitor species. Across the literature, 81.8% of the articles found evidence of a decline in diversity, with another 9.1% predicting future genetic erosion. A few studies also noted genetic diversity increases at specific loci due to greater gene flow among wild populations (Fig. 4) (Thormann *et al.*, 2017b) or with associated crops (Akimoto *et al.*, 1999) because of habitat disturbance, both leading to greater genetic homogeneity among wild relative populations.

Documented drivers of losses of crop wild relatives in their natural habitats included changes in land use, climate, agronomic practices (regarding wild relatives occurring in traditional agricultural fields) and environment (Table S3). Modeling of future climates has predicted major negative impacts to cowpea, peanut, potato (Jarvis *et al.*, 2008b) and maize wild relatives (Ureta *et al.*, 2012). Vincent *et al.* (2019) projected varied but often major impacts to a wide range of wild relative taxa worldwide.

Threat assessments for wild plants, such as IUCN Red Listing (IUCN, 2021), may include analyses of change over time when data are available, typically of range and population sizes. These studies are not covered in full in this review. Many crop wild relatives lack recent assessments, even in regions with active conservation programs (Khoury *et al.*, 2020). Haruntyunyan *et al.* (2010) Red Listed nine wild wheat progenitor (*Aegilops* L.) species in Armenia and determined four to be threatened, mainly due to expansion of agriculture, urbanization and uncontrolled grazing. European Red Listing efforts for 572 wild relatives in 2011 estimated at least 11.5% of species to be threatened (European Commission, 2019). Preliminary threat listings for wild chile peppers (Khoury *et al.*, 2019b), pumpkins (Khoury *et al.*, 2019c) and for 600 wild relative taxa native to the USA (Khoury *et al.*, 2020) identified many species as potentially threatened due to small population and range sizes. An analysis of the drivers of threats to North American native crop wild relatives included the following as the main concerns: natural system modifications, residential and commercial development, agriculture, invasive species, and pathogens and crop-wild gene flow (Frances *et al.*, 2018).

IV. Steps needed to advance knowledge about crop genetic erosion

The hundreds of pieces of research considered here, published over more than 80 yr and spanning an even longer study time frame, represent a tremendous global effort to understand the magnitude, trajectory and drivers of change in crop diversity worldwide. Yet many questions remain. In this section, we outline persisting gaps and challenges regarding conceptualizing, measuring and determining the agricultural and societal significance, as well as conservation implications, of crop genetic erosion. We discuss steps needed to further advance knowledge about changes in crop diversity.

1. Breadth, complexity and inclusiveness of crop genetic erosion research

While crop genetic erosion research has provided extensive information on annual cereals and a few other crop types, very little is known about changes in the diversity of pulses, starchy roots and tubers, vegetables, fruits, oil crops, and sugar crops, much less forage and feed crops, fibres, medicinals, ornamentals and other cultivated plants. While some knowledge may be transferable across crop types, differences in reproductive strategy, mode of propagation and other characteristics lead to marked differences in genetic variation (Miller & Schaal, 2006; Mckey *et al.*, 2010; Camadro, 2012). The literature on woody perennial crops has indicated that long-term diversity trends may differ from those of annual staples (Gross *et al.*, 2014; Diaz-Garcia *et al.*, 2020). While these taxonomic and trait biases persist for both landraces and modern cultivars, even less is currently known about their wild relatives.

Regarding geographic coverage, large areas on every cultivated continent, including regions historically recognized for diversity in major crops (Vavilov, 1926; Khoury *et al.*, 2016), remain to be comprehensively studied. There is scant published information, for example, on changes in the diversity of wheat in the Fertile Crescent, maize in the Andean mountains or in sub-Saharan Africa, sorghum in South Asia, common bean in Mesoamerica and in the Andes, soybean in East Asia, potato in Europe, and tomato in Mesoamerica and South America. Some of these deficiencies, such as wheat in the Fertile Crescent, are for crops in their centers of domestication, but significant stores of diversity are also known to have existed in secondary centers, such as Andean maize. In terms of study scale, more research is needed at landscape and even larger levels to quantify change across the metapopulations and trade networks understood to be the most relevant spatial units within which diversity flows (McLean-Rodríguez *et al.*, 2019). At the same time, more information is needed about crop diversity typically ignored in larger geographic-scale studies, such as that cultivated in homegardens (Aguilar-Støen *et al.*, 2009; Galluzzi *et al.*, 2010; Hernández-Andrade *et al.*, 2019).

Further, the evidence base for changes in many other forms of agricultural diversity needs to be bolstered, for example for livestock, pollinators and soil organisms (Potts *et al.*, 2010; Garibaldi *et al.*, 2013; Bruford *et al.*, 2015; Sprunger *et al.*, 2020). Advances in genetic sequencing should enable a deeper understanding of change in less visible forms of associated diversity, such as for associated endosphere and rhizosphere microorganisms (Fahner *et al.*, 2016). Ideally, genetic erosion research will become more holistic by integrating assessments across the multiple crops and associated biota within the study area (Lopez-Ridaura *et al.*, 2021).

Finally, while the expertise of crop diversity researchers/authors is quite varied, including agronomy, plant breeding, genetics, anthropology, conservation science and more, noticeably absent among this community are farmers themselves. This shortcoming in the diversity of voices in this conversation has undoubtedly limited the world's understanding of how diversity has changed, and perhaps even more so the reasons for change and the effects on farmers' lives. The call for greater inclusivity, which has begun to be voiced in research communities devoted to related existential challenges such as climate change (David-Chavez & Gavin, 2018), needs to be heeded in crop diversity conservation as well.

2. Robustness of the methods and underlying theory regarding crop genetic erosion

Crop genetic erosion research will always be limited by gaps in knowledge about the diversity that existed in the past (Box 2). Ancient DNA techniques will help to shed further light on long-term change, and where biological materials can be found and defensibly matched to current diversity (Mascher *et al.*, 2016; Smith *et al.*, 2019). However, these are indirect comparisons with inherent uncertainty and many caveats (Lynch & Ho, 2020).

More sophisticated, larger scale, direct comparative methods are needed. These will surely build on established methods and protocols, but may also be supplemented by new applications, such as crowd-sourcing farmer knowledge using mobile phones and social media (Fadda *et al.*, 2020), the organization of local events to engage farmers in research (Mainali *et al.*, 2020), and the greater use of remote sensing tools (Hutchinson & Weiss, 1999). The establishment of useful baselines for crop diversity through the creation of a network of collaborative observatories in appropriate sites around the world and the development and application of robust, semistandardized methods to document change, as has been done to provide a research resource regarding impacts on native plants due to climate change (Franks *et al.*, 2008), would provide an invaluable resource for further crop genetic erosion research (Mercer *et al.*, 2019).

Even when comparing diachronic variation in the same populations and same locations, the dynamism of agricultural diversity presents major challenges in quantifying change. Crop diversity data need to be interpreted in their historical contexts; for example, rules of naming or registering varieties have changed over time (Appa Rao *et al.*, 2002; Jarvis *et al.*, 2008a). Permanent change needs to be better distinguished from relatively minor or temporary variation (Brush, 1999; Zeven, 1999; Brown, 2008), requiring multiple time points over sufficient duration and relatively broad geographic scale. Methods themselves may need further analysis; similar studies have produced different results depending on the crop and method (Le Clerc *et al.*, 2005; 2006; Zhao *et al.*, 2006; Fu & Dong, 2015).

With a few exceptions (Jordan *et al.*, 1998; Fu & Somers, 2011), genetic methods have tended to assess neutral alleles or to measure overall diversity rather than focus on agronomically valuable traits. This is partly due to the inherent challenge that many important traits, such as yield, are quantitative and thus highly complex. Phenotypic studies generally have targeted agronomically or culturally important traits (e.g. Nersting *et al.*, 2006; Diederichsen *et al.*, 2013; Schouten *et al.*, 2019). A few of these studies have used both genetic and phenotypic methods, but none integrated them fully by assessing changes in genes for the specific measured phenotypic characters. Increasing information on the functional relevance of genes (Leroy *et al.*, 2018) should enable genetic studies to better assess the diversity that matters to agricultural productivity, sustainability, resilience, evolutionary potential and adaptive capacity (Hufford *et al.*, 2019). On the other hand, limitations in our ability to predict traits important to future agricultural needs and demands, especially given the uncertain impacts of climate change, imply that genome-wide analyses will ptobably remain relevant despite their deficiencies (Teixeira & Huber, 2021).

While genetic research has provided considerable data on changes in overall allelic diversity, more information is needed about the apparent increasing homogeneity trend, at least for some crops and in some regions, not only for modern cultivars but also for landraces and crop wild relatives. A better understanding of increasing similarity among varieties, including by documenting associated factors such as cultivar turnover rate and pesticide use, should contribute to deeper insights into crop genetic vulnerability at field and landscape scales.

A particularly important methodological hurdle that, if overcome, would generate a deeper understanding of the implications of crop diversity change is the integration of temporal and spatial trends (Bonneuil *et al.*, 2012; Aramburu Merlos & Hijmans, 2020; Fenderson *et al.*, 2020). The research to date provides much more information on appearance/disappearance and numbers (richness) of varieties than it does on changes in their geographic extent. Better spatial data, for example through agricultural censuses, are needed. Remote sensing and crop modeling may help to fill this gap at the crop species level (Benami *et al.*, 2021), while greater openness to data sharing by seed industries would aid in a better understanding of spatial change in modern cultivars.

3. Relevance of crop genetic erosion to society

Only a very limited number of studies have investigated crop diversity change in ways that provide insights regarding human nutrition (e.g. Davis *et al.*, 2004; Fan *et al.*, 2008). The association between crop production diversity and dietary diversity, while generally considered at least marginally positive, is complex, with crop diversity potentially contributing to diversified diets through both subsistence- and income-generating pathways (Remans *et al.*, 2011; Jones, 2017; Gupta *et al.*, 2020). Lopez-Ridaura *et al.* (2021) found that traditional polycultures in the highlands of Guatemala better provided 14 essential nutrients, and were also more productive, than maize monocultures. On the other hand, farm- and district-level specialization (i.e. lower species and varietal diversity) has been linked to productivity in some contexts, potentially leading to higher incomes and the increased capacity to purchase more nutritious diets (Kurosaki, 2003). Increased yields of staple crops brought about by modern cultivars and related agronomic practices are posited to have freed up arable land for other (potentially more nutritionally dense) crops. For example, in various Asian countries, the total cultivated area of rice has declined since the 1970s, while diversity as measured by crop species evenness has increased (Dawe, 2003).

There is scant published information on changes over time in diversity within food supplies, trade systems or diets, particularly at scales useful for understanding crop trends. Assessing changes in the diversity of crops contributing to national food supplies globally over the past 50 yr, Khoury *et al.* (2014) documented an increasing richness of internationally traded crop commodities in national food supplies, and greater evenness in the contribution of the individual commodities to supplies, including a diminished dominance of the formerly most important staple, as a result of economic development, demographic change and globalization. Oil crops in particular increased in their availability in food supplies, while regionally important staple cereals and starchy root and tuber species became further marginalized. These shifts have led to greater similarities (i.e. homogeneity) among national food supplies around the world, probably accompanied by losses of locally unique crop species diversity. Diversification of commodity crop species in national food supplies has been attributed primarily to increased dependence on international trade (Aguiar *et al.*, 2020), even as diversity in import partners has narrowed (Kummu *et al.*, 2020), potentially indicating both increasing interconnectedness among, and vulnerabilities within, national food systems.

Measuring dietary diversity and understanding its impact on human health also continue to be challenging. De Oliveira Otto *et al.* (2015) found that while the richness and evenness of dietary components were (weakly) positively correlated with diet quality, and diet quality was associated with lower risk of type 2 diabetes, dietary diversity itself was not associated with lower diabetes or obesity. Bernhardt & O'Connor (2021) determined that increasing species richness of aquatic foods did a better job in providing multiple micronutrients and essential fatty acids to the human diet, but did not affect protein, and also increased concentrations of toxic metal contaminants.

Furthermore, dietary diversity is generally measured at the food group and sometimes at the food (i.e. crop or species) levels (Remans *et al.*, 2014), but only extremely rarely at varietal levels, despite evidence of significant variation in micronutrient quantities and other nutritional factors among varieties (Marles, 2017; de Haan *et al.*, 2019). These nutritional factors may have also changed over time due to plant breeding and farming practices (Davis *et al.*, 2004; Fan *et al.*, 2008) although the temporal changes may not be significant in relation to overall variation among varieties and species (Marles, 2017).

4. Conservation implications of crop genetic erosion

While the urgency of conserving crop diversity has taken historical precedence over detailed documentation and theoretical analysis, gaps in our understanding of crop genetic erosion impact the effectiveness of conservation. This is partly a result of the historical lack of integration among research, monitoring and conservation efforts. Research combining genetic erosion assessments and conservation guidance appears to be gradually increasing (e.g. Martínez-Castillo *et al.*, 2008; Legesse, 2019; Mulualem *et al.*, 2020).

Further progress in making research findings more relevant to conservation can be made by conceptualizing the full extent of extant crop diversity, for instance for a crop in a region, through baseline documentation of the diversity of landraces, modern cultivars and crop wild relatives, both *in situ* and *ex situ*, and subsequently identifying those areas undergoing (or most likely to undergo) rapid change. While these methods have been proposed and partly elaborated upon under the rubrics of threat assessments, early warning systems, conservation gap analyses and hotspot analyses (e.g. Ramírez-Villegas *et al.*, 2010; Pacicco *et al.*, 2018; Khoury *et al.*, 2019a; Ramirez-Villegas *et al.*, 2020), they have yet to be fully developed and widely implemented, particularly regarding temporal change aspects.

V. Conclusion: mitigating, stemming and reversing losses of crop diversity

After over a century of warnings about crop diversity loss, more than 50 yr of concerted conservation efforts, and many decades of active genetic erosion research, the cumulative evidence indicates that enormous change in, and loss of, crop diversity have occurred and continue to occur. Over 95% of all the crop genetic erosion articles analyzed here reported diversity change, and almost 80% found evidence of loss, the magnitude varying by species, taxonomic and geographic scale, and region, as well as analytical approach.

Major reductions of diversity of landraces in farmers' fields and of crop wild relatives in their natural habitats continue to transpire, although substantial landrace diversity continues to be cultivated. Cycles of decline and recovery in the overall genetic diversity of modern cultivars are evident. Increasing homogeneity has been documented among cultivars, landraces, wild relatives and national food supplies. While there is little evidence for markedly reduced diversity at the crop species scale globally (Hammer & Khoshbakht, 2005; van de Wouw *et al.*, 2009; Khoury *et al.*, 2014), a lack of resolution in documentation probably masks losses of various locally cultivated crops. Change in the diversity of genetic resources held in *ex situ* conservation repositories, including loss of genetic variation, is common.

A great many uncertainties remain regarding the significance of these changes. Quantifying marked change in functional traits linked to agricultural productivity, resilience and adaptive capacity, much less human nutrition, remains more an ambition than a standard protocol. While locally unique diversity has probably diminished, in many cases it has not fully disappeared, but rather been relegated to smaller cultivation areas, such as homegardens and marginal arable lands (Aguilar-Støen *et al.*, 2009; Galluzzi *et al.*, 2010; Hernández-Andrade *et al.*, 2019). Whether such pools of persisting *in situ* diversity mostly mitigate historical declines by continuing to provide for local nutritional and cultural needs, or serve as sources of diversity when larger cultivation areas are under stress, is largely unknown. Also unclear is whether the diversity of genetic resources currently maintained *ex situ* is sufficient to support crop breeding needs into agriculture's unpredictable future. The status of representation of crop diversity in *ex situ* and *in situ*/on-farm conservation systems, compared to that in farmers' fields, natural habitats and seed systems, remains to be fully assessed.

Future progress in documenting and addressing crop genetic erosion requires better recognition of complex, pluralistic and seemingly paradoxical findings. Crop diversity may be decreasing, being maintained and increasing, all at the same time, in different forms and at different scales. These trajectories constantly change due to a range of anthropogenic and environmental drivers, many of which cannot be easily predicted. Since change is constant, the focus should be on identifying the most consequential changes, including better understanding for what and to whom they are significant.

As we will never know the full scope of crop diversity in the past, and are unable to fully predict future threats, limits to our knowledge must also be acknowledged and managed. This uncertainty, however, should not undercut the conservation imperative (CBD, 1992). The individual passion and collaborative enthusiasm of crop diversity activists in the early days of the conceptualization of genetic erosion mobilized, despite limited information and documentation, one of the largest conservation 'rescue' efforts in human history (Mooney, 1983). These initiatives need to be continued in updated forms, incorporating the knowledge and lessons generated through decades of research and action.

Research suggests where changes are likely to occur and cause significant diversity loss. These include areas whose connectivity is rapidly increasing. They are regions where agricultural communities are undergoing demographic shifts, such as out-migration, and commercialization of land and labor; where climate change is most acute; and those affected by war and strife. Other areas where crop diversity loss is likely include where formal seed systems are losing public breeding institutions and seed companies are consolidating, and where conservation repositories lack stable funding and adequate infrastructure.

***Ex situ* conservation** Given ongoing losses of crop diversity from farmers' fields, natural habitats and seed systems, evident simplification and homogenization of the diversity persisting in these environments, and increasing anthropogenic pressures, including habitat destruction and climate change, caution dictates that continued efforts should be made to mitigate further loss by safeguarding crop diversity *ex situ*, where the methodologies and infrastructure are largely established and relatively cost-effective. Nevertheless, the capacities of conservation repositories to maintain crop diversity and minimize genetic erosion need further improvement (Lawrence, 2002), and safety duplication should continue to be a priority (Westengen *et al.*, 2013). This is important not only in terms of the potential of genebanks to maximize the option value of *ex situ* genetic resources as a contribution to present and future agriculture, but also to provide a historical record of crop diversity in this period of unprecedented global change.

It is also ever more important that *ex situ* collections are accessible to those working toward the productivity and sustainability of agriculture, including farmers, especially those cultivating in environments and for markets that still are not, and may never be, well served by formal crop breeding programs. Efforts to directly connect genetic resources maintained in national and international *ex situ* repositories with farmers are providing innovations (Westengen *et al.*, 2018; Ceccarelli & Grando, 2020; Fadda *et al.*, 2020). Community seedbanks should be further embraced for their important role in facilitating local access to diversity (Vernooy *et al.*, 2017). International and national policies regarding access and benefit sharing to genetic resources require further progress to support both plant breeding needs and farmers' rights to manage and exchange crop diversity (Halewood *et al.*, 2020).

***In situ* and on-farm conservation** *In situ* and on-farm conservation of crops and their wild relatives must be further embraced if this diversity is to continue to evolve alongside climate, pest and disease, and other pressures (Bennett, 1968; Berthaud, 1997; Bellon *et al.*, 2018), and if the evidence regarding the critical value of crop diversity to ecological processes, agroecosystem resilience and small-holder farmers' livelihoods (Mijatović *et al.*, 2013; Fenzi & Bonneuil, 2016; Sirami *et al.*, 2019) is to be embraced and translated into action. It is also essential that *ex situ* and *in situ* approaches are better integrated, providing links to holistically monitor crop diversity, fill gaps (e.g. through further collecting for conservation in genebanks and repatriation of genebank samples to farmers) and implement benefit sharing (Stenner *et al.*, 2016; Schwartz *et al.*, 2017; Mercer *et al.*, 2019; AGUAPAN, 2021).

Further development of on-farm conservation methods continues to be needed, with an emphasis on bolstering the conditions and processes that foster diversity (Brush, 2004; Bellon *et al.*, 2017; Guzzon *et al.*, 2021), and particularly through support for farmer-led efforts (Stenner *et al.*, 2016; AGUAPAN, 2021; Halewood *et al.*, 2021). Such autonomous, informal conservation processes, including the traditional seed systems which promote the exchange and influx of new diversity (Engels *et al.*, 2008; Thomas *et al.*, 2012), should be embraced for their strengths, regardless of the difficulties in quantifying their effectiveness due to their inherent dynamism.

On-farm conservation interventions may be warranted where there is evidence of ongoing or upcoming threats to important diversity or where there is demand for recovering diversity already lost. A range of pertinent community-based conservation tools have been developed, including diversity inventories and fairs, agrobiodiversity zoning and crop diversity park systems, specialized markets, participatory evolutionary breeding, and payments for agrobiodiversity conservation services (Tapia, 2000; Narloch *et al.*, 2011; Graddy, 2014; Fadda *et al.*, 2020). Options appropriate to location and culture should be identified based on participatory processes (de Haan, 2021).

For crop wild relatives, highlighting the importance of these species, developing inventories and monitoring, and implementing management plans for the protection of critical habitats and populations (potentially also including assisted migration) are essential. Large-scale efforts toward the expansion of natural area conservation, including 30 × 30 and Half-Earth, would, if implemented, probably enhance conservation of crop wild relatives. Recognizing the roles and the rights of Indigenous and agrarian peoples within such initiatives will be important to the survival of many crop wild relative populations, as well as to landrace conservation.

Formal seed systems For modern cultivars, continued advocacy for diversification of the genetic bases of commodity crops is important to avoid major production losses from genetic vulnerability (Cooper *et al.*, 2001; Penna *et al.*, 2019). Reinvestment in public breeding programs, providing prebreeding and other diversification services to formal seed systems, will probably be critical (Warburton *et al.*, 2006; Coe *et al.*, 2020). Farmer participatory breeding initiatives focused on modern cultivars have also shown potential to contribute to varietal diversification (Lammerts van Bueren *et al.*, 2018). Further critical assessments of seed sector consolidation, varietal release procedures and intellectual property tools (i.e. UPOV and patents), and advanced breeding technologies (e.g. genetic modification and gene editing) are needed to develop and implement strategies to minimize negative impacts on modern cultivar diversity (Kolady & Lesser, 2012; van de Wouw *et al.*, 2013; Howard, 2015).

Societal change Reversing the trajectory of crop genetic erosion requires more profound change – no less than reorganizing global agriculture, and food systems, and even the human societies they nourish, to become diversity-supportive processes (Ceccarelli & Grando, 2020; Clement *et al.*, 2021). Crop diversity must be valued not only as a genetic resource to be exploited, but just as much for its cultural and ecological values (Fenzi & Bonneuil, 2016). This implies a (re)integration of species, varietal and genetic diversity into agricultural systems, both temporally and spatially, as well as the (re) establishment of local autonomy and markets supporting the processes that foster the ongoing evolution of this diversity.

The importance of crop and other forms of agricultural diversity and their conservation need to become core messages in educational curricula and public awareness efforts (Esquinas-Alcázar, 2005; Khoury *et al.*, 2020). Ultimately, creating the conditions in which crop diversity can thrive within agriculture and food systems will necessitate widespread societal recognition that this diversity underpins our productivity, resilience and capacity to adapt to an ever-changing future (Hufford *et al.*, 2019; Pilling *et al.*, 2020).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Changes in the diversity of crop genetic resources held in conservation repositories.

Notes S1 Changes in the diversity of crop genetic resources held in conservation repositories.

Notes S2 Crop genetic erosion review methods and limitations.

Table S1 Definitions and descriptions of crop genetic erosion encountered in the literature, and their attributes.

Table S2 Crop genetic erosion literature matrix.

Table S3 Importance of drivers of crop diversity loss as documented in the literature.

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Appendix A1

References reviewed in the crop genetic erosion analysis

Included are the 288 crop genetic erosion references compiled; 232 of these were considered in the main analysis (see Table S2).

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