











OPINION

Human management of ongoing evolutionary processes in agroecosystems

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Societal Impact Statement

Agricultural sustainability depends on the adaptation of crops to their local environment. Smallholder farmers who save seed provide an essential “evosystem” service by growing locally adapted seed varieties that can recruit biodiversity to enhance their growth and defense. While professional plant breeding has diverted evolutionary processes away from local adaptation, smallholder farmers, particularly those in centers of origin for crops, benefit society by selecting and propagating diverse crop varieties that allow local adaptation processes to perpetuate. Given that smallholders support society through the generation of evosystem services, changes in policy and practice are needed to support the livelihoods of smallholder farmers in ways that mitigate risk and recognize their important contributions to agricultural sustainability. To enhance the reach of this work, a Spanish language version of the paper is available in the Supporting Information (see Translation_ES). [Correction added on 18 June 2024, after first online publication: The preceding sentence has been added in this version.]

Summary

Long-term food security and agricultural sustainability depend on protecting the evolutionary processes that select for local adaptation in crops. Since seed systems structure how people acquire seed, institutional and social changes influence evolutionary processes within agroecosystems. Since World War II, the rise of professional breeding has bifurcated seed systems into traditional and formal systems, which has negatively affected agrobiodiversity, crop evolution, and agricultural sustainability. In traditional seed systems, farmers often save seed from plants that best provide desired qualities, selecting landrace crop varieties to adapt to local environmental conditions. In formal or centralized seed systems, farmers buy seeds bred primarily for maximizing yield under ideal conditions. When farmers source seeds externally, evolutionary processes underlying local adaptation are disrupted. Here, we argue that traditional seed systems provide important *evosystem services*, or the evolutionary

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processes resulting from the maintenance and use of genetic diversity that benefit society. We present a framework on how seed systems influence the evolutionary processes that enable local adaptation, which is necessary for sustainable agriculture. We discuss how changes in human values underlying traditional and formal seed systems can alter evolutionary processes that underlie local adaptation. We conclude that developing policies that support people in managing ecological and evolutionary processes within seed systems is needed to address current and future challenges of global food security and agricultural sustainability.

KEYWORDS

agriculture, agroecology, biodiversity, ecosystem services, evolution, insects, landrace, seed systems

1 | INTRODUCTION

The domestication and continuous selection of crops is a human-mediated evolutionary process that has fundamentally changed the relationship between people and their food supplies. For over 10,000 years, people domesticated crops to fulfill their dietary and cultural needs (Meyer et al., 2012), while selecting them to adapt to different environmental conditions and human preferences (Chen et al., 2017). From the start, people have influenced crop evolution through **seed selection** (blue terms are defined in Box 1) and by modifying the environment to support crop **cultivation** (Smith, 2007). These practices changed relatively little for thousands of years, until the emergence of formal breeding and the subsequent privatization of crop seeds in the 20th century (Khush, 2001; Lyon et al., 2021). Due to the rise of professional breeding, there has been: (i) a shift in seed selection from farmers to plant breeders for major field crops (Louwaars, 2007), and (ii) increased use of synthetic fertilizers and pesticides (Rosegrant & Hazell, 2000). Although the Green Revolution successfully increased crop yield (FAO, 2004; Khush, 2001), it reduced direct farmer involvement in seed selection. Since traditional seed systems provide the genetic material for the evolutionary processes that enable local adaptation, they are critical for meeting future challenges of global food security and agricultural sustainability.

In this paper, we propose that changes in the social context have caused evolutionary processes to operate differently within traditional and formal **seed systems** (Figure 1). In traditional systems, farmers save seed from each cycle, while farmers in formal systems typically purchase seeds every cycle (Figure 1). Seed systems refer to how farmers obtain, manage, and select seeds, which can be broadly characterized into traditional and formal¹ (Box 2). In traditional seed systems, farmers select seed according to local and cultural preferences, allowing natural and human selection to act together, leading to local adaptation of different landraces (local varieties of a crop) across

¹While traditional seed systems have also been called informal or decentralized seed systems, we use the term “traditional” because it is the most commonly used term in the literature on seed systems. Similarly, we use the term “formal” to describe centralized seed systems because it is widely used by seed system researchers.

Box 1 Glossary

Seed selection – The set of practices that farmers or breeders use to identify, isolate, and retain the seeds of favorable crop plants for propagation.

Cultivation – The practices that people take to foster crop growth.

Seed systems – Seed systems describe how farmers obtain seed through time and space in a particular place and context.

Agroecosystem – A community of plants and animals that interact within environments modified by people to produce food, fiber, or other products for human use.

Intensive agriculture – Farming practices that focus on maximizing agricultural production with high inputs of labor and capital. Common techniques involve the use of HYVs, synthetic fertilizers, and pesticides.

Natural selection – Variation in phenotypic traits influences the likelihood of organismal survival and the transmission of genetic information.

Human selection – When humans and the ecosystem favor a set of traits, they influence the likelihood these traits are fixed and transmitted to subsequent generations.

heterogeneous landscapes (Figure 1a) (Bellon et al., 2018; Meyer & Purugganan, 2013). In contrast, formal seed systems centralize the breeding process, narrowing seed selection to breeding professionals who select seed in a limited range of environments. In this paper, we characterize traditional and formal seed systems distinctly, as a heuristic that helps to describe how evolutionary processes differ between these very different frameworks (Figure 1). However in practice, many farmers use seed from formal and traditional seed systems for different purposes, sometimes interacting with both seed systems on a single farm (discussed further in Box 2). We present a socio-environmental framework that explicitly links how people and their

Box 2 Seeds and seed systems

Seed systems describe how farmers obtain seed through time and space in a particular place and context. A seed system includes: (1) transactions determining how seed is obtained; (2) social relations defining from whom seed is obtained; (3) information and knowledge about identity, origin, and traits; (4) social rules that determine who can get seed and under what circumstances; (5) social structures enforcing those rules; and (6) practices of how seed is stored, selected, and transported.

Traditional seed systems are open, informal, decentralized, generally local, governed by cultural norms (i.e., reciprocity, fairness), and closely connected to smallholder and traditional agriculture. On the other hand, formal seed systems are centralized, driven by profits, specialization, and economies of scale. They are based on commercial transactions, homogenized products, and intensive usage of external inputs.

Seeds have both private and public characteristics and values: (a) private, those characteristics that cannot be consumed by, or values that cannot accrue to, two farm households at the same time; (b) public characteristics, those related to the seed genetic attributes that are available, and benefits that can accrue, to all those that have access to a particular type of seed.

While these definitions suggest that these seed systems as a “dichotomy”, they represent a gradient in centralization and specialization. Formal systems are associated with greater specialization and more specialized functions (breeding, seed production, etc.) and rely protection from formal law systems (e.g., UPOV, seed legislation). In contrast, traditional seed systems are decentralized, participants are not highly specialized (e.g., the farmer selects the seed while doing other things). While some seed savers may have a local reputation for seed selection, they usually have multiple other responsibilities and enterprises. The terms of engagement in formal seed system is based on customary rules and traditions, through which seed transactions are designed to be impersonal. On the other hand, seed transactions within traditional seed systems tend to be personal, mostly among people that know each other, but not always. While traditional seed systems have been around since the beginning of agriculture, formal seed systems are a relatively recent invention.

seed systems are fundamental to the generation of *evosystem services*, or, the evolutionary processes resulting from the maintenance and use of genetic diversity that benefit society (Faith et al., 2010). While the term ecosystem services describes the benefits that humans derive from nature including providing food, regulate Earth's processes, and

provide cultural value for people, it does not account for future yet-to-be described services (Faith et al., 2010, 2017). *Evosystem services* acknowledge the benefits from biodiversity that are derived from evolutionary processes, which include undescribed or novel adaptations/traits (Faith et al., 2010). *Evosystem services* are particularly prominent in human-managed *evosystems* (Faith et al., 2017), such as traditional seed systems in *agroecosystems* (Bellon & van Etten, 2013).

Traditional seed systems provide important provisioning *evosystem services* that are critical for future global food security (Bellon et al., 2018). Landrace varieties selected *in situ* are particularly valuable, because they already possess plant traits that are adaptive to particular marginal environments (Ficiciyan et al., 2018). Traditional seed systems maintain the processes that generate genetic diversity useful for local adaptation (Bellon et al., 2018). Traits from landraces are valuable to breeders because they can increase stress tolerance in elite germplasm (Atlin et al., 2017). For example, traits like greater root water extraction at deeper soil depths and water use efficiency can advance the capacity of crops to tolerate stress when introgressed into breeding germplasm (Reynolds et al., 2007). In the face of rapid climate change, these types of *evosystem services* are critical for adapting crop germplasm to current and future stressors (Mercer & Perales, 2010; Vigouroux et al., 2011). Given that the majority of a crop's genetic diversity is found in crop landraces (Khoury et al., 2022), farmers that cultivate and save landrace seeds contribute to an important “maintenance of options” benefit for *evosystem services* (Faith et al., 2017).

The evolutionary processes that take place within formal seed systems fundamentally differ from traditional seed systems, because the focus is on maximizing yield and short-term profit for their users (Almekinders et al., 1994; Lyon et al., 2021). In formal systems, professional plant breeders select crops at research stations, prioritizing traits like higher yield, distinctiveness, uniformity, stability, and shelf life (Kingsbury, 2009). The focus on high yields has led to a rise in *intensive agriculture*, where synthetic inputs of fertilizer and pesticides are used to manage abiotic and biotic stress (Figure 2). Crop selection and seed amplification occurs in intensively managed research fields, which tend to be environmentally homogenous and limited in number. As a result, there is evidence that planting seeds from the formal system may have reduced genetic diversity over space and time (Bellon et al., 2018; Mastretta-Yanes et al., 2018), though the process is not linear and can be complex. While breeding within the formal seed system has successfully developed high-yielding varieties (HYVs) for major field crops (Evenson & Gollin, 2003; Pingali, 2012), considerable environmental externalities have resulted (Pretty, 2008). In order to achieve high yields, farmers growing HYVs have increased their use of irrigation, fertilizer, and pesticides (Liu et al., 2015). While intensive agriculture has contributed a remarkable increase in yield in a few major crops, it has intensified water scarcity and pollution, degraded soil quality, and eroded agrobiodiversity (Evenson & Gollin, 2003). Therefore, professional breeders have selected for crop plants that are adapted to intensive *agroecosystems* that are nutrient-rich and protected with pesticides.

By connecting historical policy trends and institutional changes with eco-evolutionary processes, we discuss how the increasing domination of formal seed systems threatens informal seed systems and

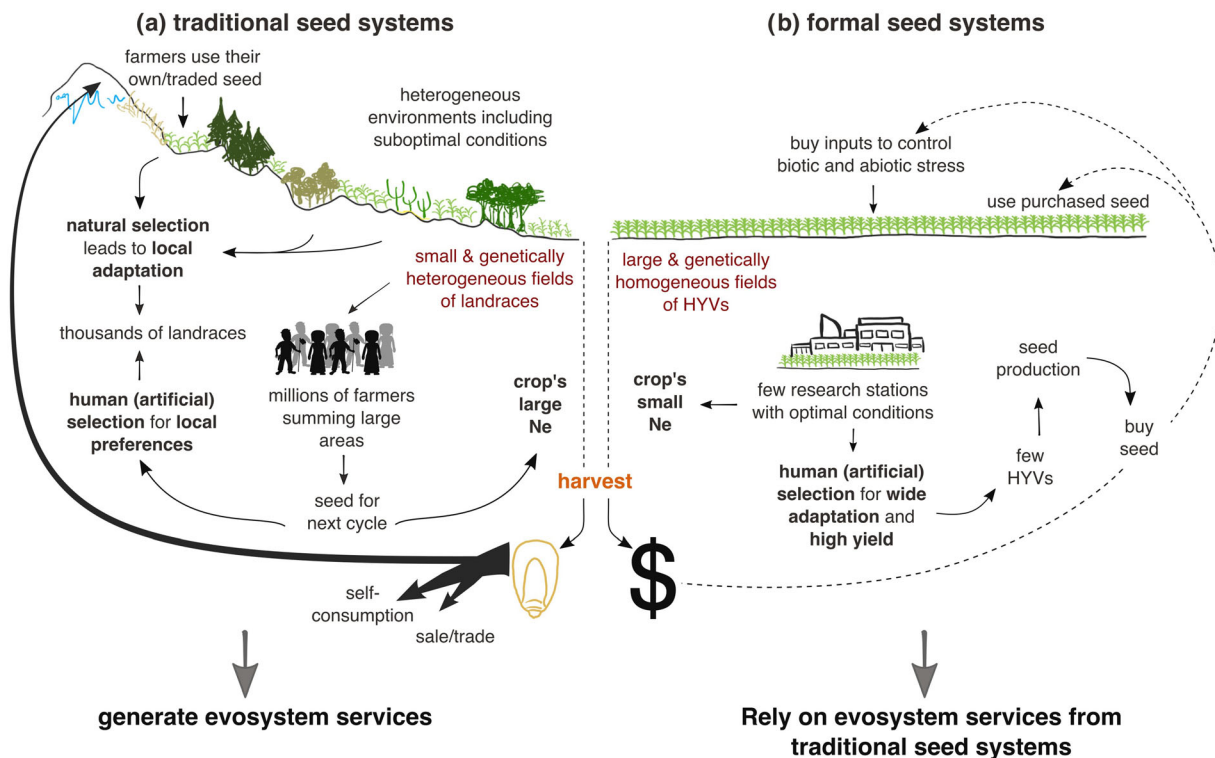


FIGURE 1 Evolutionary processes differ between traditional and formal seed systems. (a) Traditional seed systems typically consist of small fields of genetically heterogeneous landraces that are grown across a wide range of environments, including suboptimal conditions. Part of the harvest is used for self-consumption, traded or sold, but importantly, another part is saved and used as seed for the next cycle. The fields of traditional seed systems are owned by millions of individual farmers, who collectively cover large areas. Crop plants are grown over a broad area across a diverse habitat range, which has two implications. First, because millions of farmers save seed of individual plants, the number of genetically distinct individuals contributing to the next generation becomes large, thus generating a large effective population size (N_e) for the crop. Second, farmers select seed based on their local preferences (artificial selection) and at the same time, they save seed of the plants that performed the best under local conditions (natural selection). Seeds are grown again in the same environment the next year, promoting local adaptation. Thousands of landraces emerge from the interaction of natural and artificial selection across millions of farmer fields. Since large n_e also promotes the emergence and conservation of genetic diversity, traditional seed systems produce ecosystem services. (b) In formal seed systems, large fields of high-yielding crop varieties (HYVs) are grown for commercial sale. No seed is saved from the harvest, instead farmers buy seed using the profits from the previous year. The acquired seeds were developed by research stations, where breeders select plants for high yield and wide adaptation. Then, the seeds are amplified under optimal environmental conditions in intensive agroecosystems, which are agronomically managed to minimize biotic and abiotic stressors. Breeders develop a few HYVs that are adapted to optimal conditions. Since few genetically distinct individuals are used to produce seed, the n_e of the crop becomes small and there is little genetic diversity. Therefore, in order to source variation for breeding, formal seed systems rely on the ecosystem services produced by traditional seed systems.

the ecosystem services that they generate. We argue that the emergence of formal seed systems has altered the evolutionary processes by which crop populations generate new mutations and maintain adaptive variation for managing abiotic and biotic stress. In order to provide the historical context on seed systems, we briefly introduce how formal seed systems arose, focusing on the political economic transitions since World War II. We present four propositions on how ecosystem services differ between traditional and formal seed systems. While some propositions are more supported than others with evidence, the overall framework linking seed system structure with the ecology and evolution of agroecosystems is original and, to our knowledge, not been discussed elsewhere. First, we discuss how people participating in traditional and formal seed systems value different types of ecosystem services, which influences evolutionary

processes and the adaptive outcomes. Second, traditional and formal seed systems differ in the selection and generation of adaptive genetic diversity. Third, traditional seed systems provide ecosystem services by retaining crop traits that support plant competition and stress tolerance. Finally, traditional seed systems provide unanticipated ecosystem services by retaining crop traits that interact mutually with other species to meet their nutrient and defense needs. Therefore, the rise of the formal seed system has put new pressures on farmers that may challenge a broad set of ecosystem values, thus endangering the ongoing evolutionary processes that contribute to local adaptation in agroecosystems. By uniting decades of research isolated across natural and social sciences, we develop an integrated rationale about how changes in have altered evolutionary processes within agroecosystems.

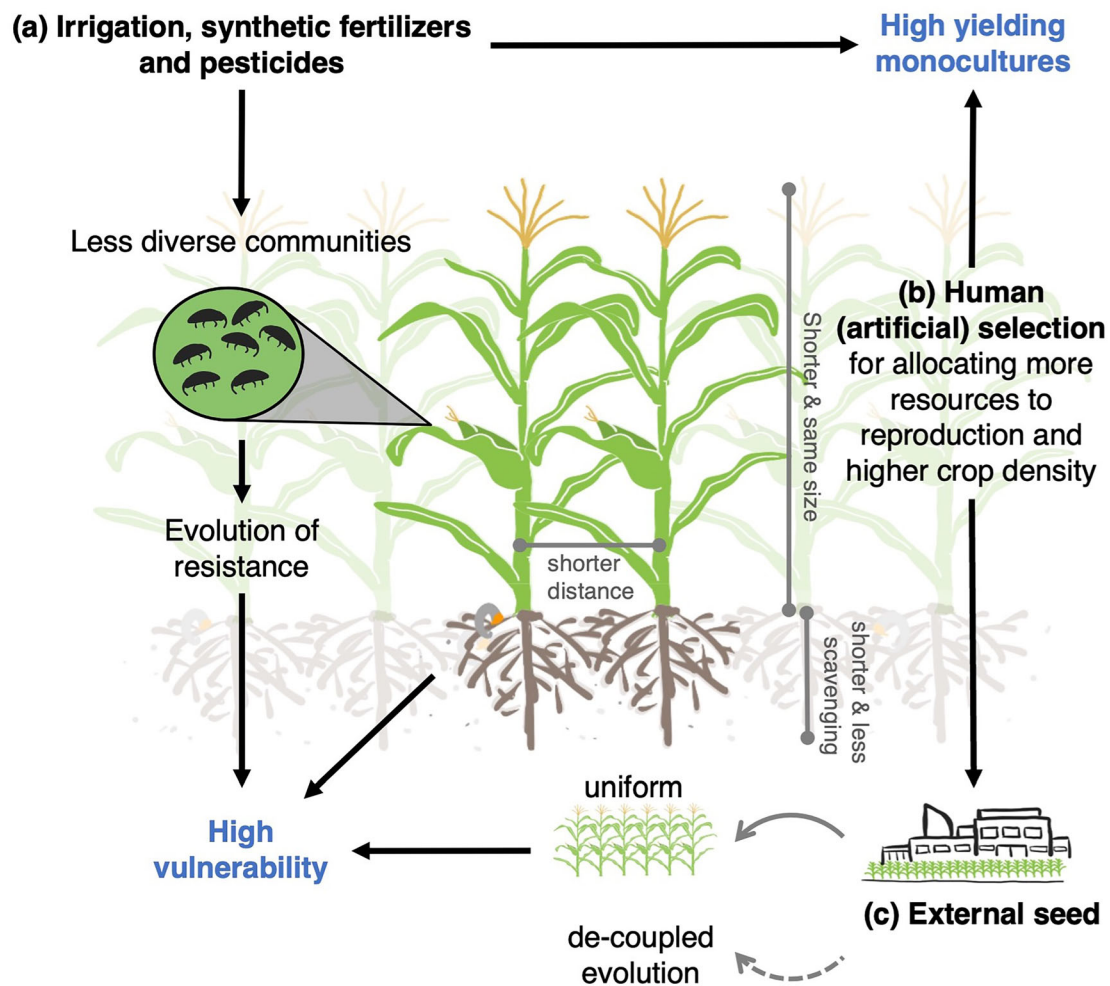


FIGURE 2 In the optimal environments of intensive agroecosystems, high-yielding varieties (HYVs) tend to achieve high yields of monocultures, but they are more vulnerable to insects, diseases and environmental change. In intensive agroecosystems, (a) farmers create optimal environments by controlling water availability, soil fertility, and pests with irrigation, synthetic fertilizers, and pesticides. The use of pesticides kills also the predators of pests, reducing biodiversity and increasing the likelihood of pest resistance and weediness. (b) because water availability is optimal, human selection can focus on shorter plants, shorter root length, and limited scavenging ability, thus allocating more resources to reproduction (yield). By selecting for less competitive plants, crop plants can be grown at a higher density, which results in higher yield because fertilizers are provided. (c) Seed selection occurs externally on research stations and are usually purchased each cycle. As consequence, crop evolution is decoupled from the rest of the agroecosystem. Since HYVs are also genetically homogeneous and usually grown as monocultures, fields are more vulnerable when new pests emerge or environmental conditions change.

2 | HOW HUMANS CONSTRUCTED SEED SYSTEMS

As the networks by which people access planting materials, seed systems arose from social interactions, governed by non-market and market institutions (Jones & Tobin, 2018). Since crops were first domesticated (Meyer et al., 2012), natural and social processes have shaped crop adaptation to diverse local environmental conditions and human preferences (Bellon et al., 2018; Chen et al., 2017) (Figure 1). Traditional seed systems likely arose as farmers developed and adhered to cultural norms around seed exchange, which occurred based upon trusted social networks among neighbors, relatives, and/or distant strangers (Pautasso et al., 2013). Farmers value crop qualities that are underemphasized in formal seed systems, such as

taste, cultural heritage, and stress tolerance (Graddy, 2013; Jackson et al., 2007; Tobin et al., 2018). Accordingly, farmers living in marginal rainfed, arid, or saline areas often prefer landraces over HYVs for tolerance of environmental stress (Ficiciyan et al., 2018). It is important to recognize that millions of farmers continue to rely on traditional seed systems (Bellon et al., 2018; Tobin et al., 2018). With estimates that traditional seed systems provide 80%–90% of seeds for smallholder farmers (Sperling & McGuire, 2010), we calculate, based on Samberg et al. (2016), that over 300 million farming households participate in traditional seed systems across Latin America, sub-Saharan Africa, and Asia.

Although farmers continue to interact within traditional seed systems, formal seed systems are also increasingly accessible, as they have increasingly penetrated rural regions over the last century. The

co-existence of formal and traditional seed systems has led to interesting blends between these systems. For example, farmers in Peru rely on traditional seed systems to cultivate native potato landraces for home consumption in their highland plots while growing improved potato varieties for commercial activities (Tobin et al., 2018). In Mexico, farmers commonly adapt hybrid maize to local conditions by saving and replanting those seeds over several generations to produce what are called “acriollados” (Bellon et al., 2006). Research approaches seeking to integrate aspects of traditional and formal systems also exist. For example, trials of participatory plant breeding and varietal selection involve large numbers of smallholder farmers in phenotyping crops across large regions (Sperling et al., 2001). More recently, seed saving is growing in prominence in regions long dominated by the formal seed system like the United States and Canada, where community seed research, small-scale organic seed companies, and seed libraries are gaining popularity (Lyon et al., 2021; Soleri et al., 2021).

In the mid-20th century, the Green Revolution catalyzed the development of formal seed systems (Louwaars, 2007), supported by major shifts in public policy and economic structures (Lyon et al., 2021). Prior to the 1930s, farmers had near complete autonomy over their seed usage due to the lack of government oversight regarding seed exchange (Kloppenborg, 2010). Beginning in the 1940s, concerns that hunger would plague food-deficit countries spurred plant breeders to increase agricultural production (Food and Agriculture Organization, 2003; Pingali, 2012). In the west, Keynesianism dominated economic thinking, which viewed public investment in international development as necessary to promote economic growth and orient food production toward efficiency and yield maximization (Goldman, 2005). By framing famine as a production problem (Sen, 1981), (inter)national agricultural research centers and US land-grant universities, in collaboration with philanthropic foundations (of private companies, such as the Rockefeller Foundation and Ford Foundation) promoted HYV field crops as a solution and supported dependency on subsidized inputs like fertilizers and pesticides sold by private companies (Patel, 2013; Pray, 1981).

Breeders focused on developing HYVs in annual field crops. In outcrossing species, particularly maize, the development of hybrid varieties derived from a cross of two inbred lines (or more in double hybrids) enabled HYV development. In hybrid varieties, the cross results in highly uniform progeny (F_1), where each individual plant is highly heterozygous (but all plants are similar or identical), resulting in higher productivity (Duvick, 2005). The replanted hybrid seeds segregate with different unstable combinations of inbred parent lines, so farmers need to access a new stock of seed annually. For selfing crops such as rice and wheat, crosses are often made early in the breeding cycle to combine traits from two parents. To create improved homogeneous lines, breeders often screen F_2 progeny for target traits, and select against the F_6 generation to develop more uniform progeny. In some predominantly selfing crops, such as rice, the discovery of cytoplasmic male sterility systems has allowed hybrid crop varieties to be developed, sometimes displacing varieties developed by other means (Louwaars, 2007; Sperling & McGuire, 2010). For selfing crops,

subsequent generations retain the high yielding traits of the parents. After HYV grain crops were first developed by plant breeders at international research centers (i.e. International Maize and Wheat Improvement Center [CIMMYT] and the International Rice Research Institute IRRI), formal seed systems were used as the conduits for their dissemination (Figure 1b). Partnering national agricultural research institutes (NARS) adapted the new HYVs to regional conditions and local preferences, before amplifying seed for release to farmers.

The Green Revolution initiated the decoupling of farmers from seed selection as government policies and institutions supported public breeding. The emergence of the formal seed system led to a spectacular doubling of global grain production in only 40 years (1960–2000) (Khush, 2001). The increased production and rise of an industrialized agrifood sector encouraged family farmers to transition to increasingly specialized production or to leave farming (Friedmann, 2005). The global debt crisis of the 1970s spurred a shift toward privatization, deregulation, trade liberalization, and austerity, eroding public investments in agriculture and public breeding programs (Kloppenborg, 2010). In capitalist countries, public involvement focused primarily on instituting policy frameworks that encouraged privatization, while divesting in the research and development of public entities that had enabled the first phase of the Green Revolution (Busch, 2010). As public funding declined and the role of public entities receded, the private sector filled the void for many field crops, focusing on the crops that generated profits.

For crops targeted by privatization, private breeders were able to further consolidate the genetic composition and breeding targets. Beginning in the 1980s, seed commercialization gained traction, as increasingly restrictive intellectual property rights elevated the rivalry and excludability (characteristics of private goods) of seeds and fostered private investment into seed research and development (Howard, 2015). As seed propagation became commodified, agrichemical corporations increasingly dominated formal seed systems, and strategies were developed by both the private and public sectors to limit seed saving (Thanopoulos et al., 2024). Legal protections developed for field crops helped consolidate private control of formal seed systems, targeting first HYVs and more recently, genetically modified (GM) varieties (Howard, 2015). Genetically modified varieties were developed using biotechnological methods that differ from the breeding of HYVs, because they contain genetic material that is derived from another organism and artificially inserted into the crop genome. For major outbreeding field crops like maize, GM and hybrids are similar as commodities due to the enhanced protections they give to seed producers. Hybrid seeds do not breed true, while utility patents protect GM seeds (Fuglie & MacDonald, 2023). In crops dominated by either hybrid or GM cultivars, these privatization efforts have resulted in market consolidation.

Agricultural policy borne out of these political economic trends encouraged farmers to shift away from traditional seed systems (Figure 1a) to formal seed systems (Figure 1b). The effect of these policies—whether farmers primarily source seed from public, private, and/or traditional sources—varies by country and crop species. For

example, since controlling cross-fertilization in maize is particularly easy, the economic incentive for breeding for novel targets is much greater for maize than for other staple crops (Spielman & Kennedy, 2016). While maize appears to be an extreme case where the seed system has shifted toward privatization, privatization may not occur to the same level in other field crops that are primarily selfing. For example, in Bangladesh, Pakistan, and Thailand, farmers acquire maize seed primarily from private/commercial seed systems, but they may acquire rice and wheat from public and traditional/informal sources more equally (Spielman & Kennedy, 2016). Since 2011, privatization has become so prominent that three firms control over half of the overall global seed market (Mooney, 2018). Regardless of whether improved varieties come from public (as was prominent during the first Green Revolution) or private breeding initiatives (commonplace since the 1980s), they both use centralized breeding processes.

3 | EVOLUTIONARY PROCESSES IN FORMAL AND TRADITIONAL SEED SYSTEMS

Seed selection is the key step for local adaptation to occur under domestication. The seed systems in which farmers operate influence how they manage their crops, leading to very different selective environments, influencing both crop evolution and species interactions in agroecosystems (Figures 1–3). Traditional seed systems tend to be associated with **traditional agroecosystems**, while formal seed systems are associated with **intensive agroecosystems** (Glossary 1; Box 1; Figures 2 and 3). By providing a broader framework, we discuss how these differences in human values and perception of ecosystem services alter **seed selection** and **agronomic management** affecting ecological and evolutionary processes in agroecosystems. While farmers clearly manage their fields with a wide variety of approaches,

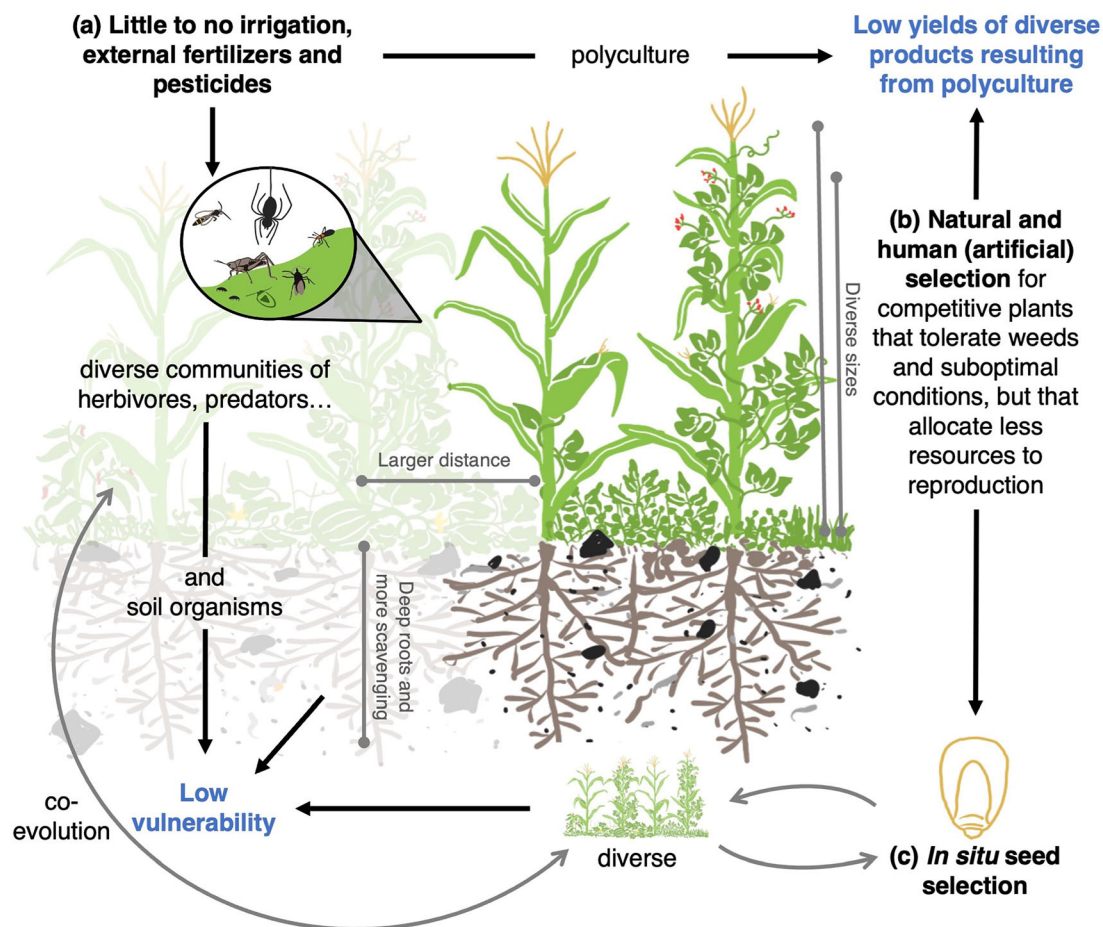


FIGURE 3 In traditional agroecosystems with suboptimal conditions, crop landraces tend to achieve low yields but are less vulnerable to insects, diseases and environmental change. (a) Little to no irrigation is provided, and synthetic fertilizers and pesticides are not used. Because pesticides are not used, traditional agroecosystems host diverse communities including predators that keep herbivores from becoming a pest, and a variety of soil organisms that can help with nutrient uptake and stress resistance. (b) Since water can be scarce, natural and human selection selects for deep root systems and scavenging ability. The resulting plants are competitive, and a low crop density is used to reduce intraspecific competition. Competitive and stress-tolerant plants reduce the allocation of resources to reproduction (yield), but can tolerate multicropping systems where diverse products can be harvested. (c) Seed selection occurs in situ with seeds of the previous cycle, leading to local adaptation to low water availability and low nutrient availability. Crop landraces are exposed herbivory and disease, as well as the rest of the biotic community. Crop landraces are genetically diverse, thus decreasing its vulnerability.

we present a simple model of traditional and intensive agroecosystems in order to present how the systems broadly differ.

3.1 | People value different ecosystem services in traditional and formal seed systems

People participating in traditional and formal seed systems value different types of ecosystem services, which influences how they acquire seeds, where they plant, how they save seed, and how they manage crop **cultivation** (Figure 1). Farmers who select landraces tend to value regulating, cultural, and provisioning services like crop nutrient efficiency, while breeders and farmers who select HYVs tend to solely value provisioning services. As a result, **natural** and **human (artificial) selection** act differently in traditional and formal seed systems, which influences what crops adapt to and the ecosystem services they generate. In traditional seed systems, many farmers participate in seed selection, as they plant and select seed in fields set in heterogeneous environments (Figure 1a). Farmers save seed to sow the subsequent crop, which directly influences how natural and human selection operate across diverse environmental and cultivated conditions. In formal seed systems, farmers are not directly involved in seed selection (Figure 1b). Professional breeders select crops using a particular set of breeding goals. For example, some breeders select for an ideotype, or ideal crop phenotype, that provides the high yields under optimal conditions, such as short stature in cereals (Donald, 1968). In formal seed systems, seed propagation happens in centralized locations, preventing natural selection from acting on locally adapted genotypes. When farmers source new seeds each season, crop populations do not adapt to local biotic, abiotic, and cultural preferences. Due to the breeding structure, HYVs are more adapted to the optimal conditions at research stations and seed amplification fields (Figure 1b).

In traditional seed systems, farmers select crops to adapt to their local field conditions. Farmers' seed saving and informal trade maintains the wide range of genetic and phenotypic diversity present in crop plants and generate new diversity upon which natural selection can act (Figures 1a and 3). By deciding what, where, and when to plant, smallholder farmers have selected crops to become locally adapted across diverse and often stressful environments (Vigouroux et al., 2011). For example, maize landraces are adapted to tropical highlands, lowland rainforests, temperate forests, and even deserts (Swarts et al., 2017). Similarly, sorghum landraces cultivated by indigenous Ethiopian farmers are the only ones that can be grown in the highlands (Tsehaye et al., 2009). Due to a more developed root system, landraces are also tolerant of drought and nutrient stress (Boudiar et al., 2019; Ficiyan et al., 2018). For example, farmers growing pearl millet in the drought-prone Sahel region of Niger prefer their own pearl millet seed to those found in markets (Ndjeunga, 2002). Similarly, smallholder farmers may also prefer landrace varieties because they are more pest resistant (Ficiyan et al., 2018). Therefore, farmers tend to prefer landrace varieties due to abiotic or biotic constraints in the environment.

Farmers also value traditional seed systems for reasons other than crop performance. Across diverse contexts, farmers maintain landraces for consumption, nutritional, and cultural reasons (Bellon et al., 2020; Graddy, 2013; Nordhagen et al., 2017; Tobin et al., 2018; Zimmerer, 2014). Farmers and consumers value landraces for taste, color, cooking time, storage qualities, or stover biomass (Bellon et al., 2006; Bidinger & Blummel, 2007; Keleman & Hellin, 2009; Pragnya et al., 2018), which they may prefer over higher yields. For instance, farmers in Peru prioritize culinary attributes and cultural significance when selecting potato landraces (Tobin et al., 2018). Increasingly, farmers and markets recognize the potential economic benefits of landraces. The sale of diverse crops is viewed as an important livelihood strategy to enhance food security (Sibhatu & Qaim, 2018), and landraces have been the target of value chain development initiatives to link smallholders with competitive markets (De Leeuw et al., 2017; Hellin et al., 2010; Hellin & Hignman, 2005).

In contrast, formal seed systems do not promote local adaptation because breeders select for general-purpose genotypes that perform well in nutrient-rich environments (Figure 1b). To deal with the lack of adaptation to local environments, breeders use two parallel approaches to ensure farmer acceptance. First, breeders promote "wide" adaptation (i.e. expanding the geographic area over which varieties can be grown) (Borlaug, 2007). They select plants that perform across multiple research stations, even if locally adapted varieties outperform them in some places. For example, Borlaug selected for broad disease resistance and day-length neutral flowering under high levels of fertilization (Borlaug, 2007). Furthermore, breeders selected for dwarfed grain crops, which caused plants to allocate energy toward larger seed heads rather than vegetative growth, increasing yields without lodging under fertile conditions (Figure 2) (Borlaug, 2007). As a result, the dwarfing caused plants to need a high input regime of water, synthetic fertilizers, and pesticides, which became standard use at agricultural research stations (Dawson et al., 2008). Hence, field crops such as wheat and rice HYVs outperform landraces under fertile conditions (Borlaug, 2007; Swaminathan, 1965).

Farmers selecting HYVs tend to value yield and profit (Almekinders et al., 1994; Lyon et al., 2021), so they invest in intensive agriculture by applying more purchased inputs. Since HYV seeds are adapted to fertile conditions (Ficiyan et al., 2018), farmers cultivating them tend to use agronomic inputs to mimic the fertile conditions at research stations and seed amplification fields (Figure 1b; Baranski, 2015). Farmers are incentivized by profits to purchase seeds, fertilizers, and pesticides early in the season, prior to planting. Those farmers with better access to fertile land, agronomic inputs, and irrigation systems, are able to achieve higher yields with HYVs than poor farmers (Pingali, 2012). Therefore, farmers need to finance the inputs to grow HYVs, thereby incurring more debt when participating in formal seed systems (Monroy-Sais, unpublished data).

Aside from yield, farmers may value HYVs for specific provisioning reasons, which makes them important contributors for assaying HYV field performance. In some cases, farmers may select HYVs bred for specific disease resistance and larger grain size (Gamboa et al., 2018; Li et al., 2012; Sánchez-Toledano et al., 2017). Recent

breeding efforts have concentrated on reintroducing the traits for environmental stress tolerance (drought and salinity) and pathogen resistance. Since these traits may have been lost during the breeding process, breeding programs value screening traditional landraces and crop wild relatives for stress tolerance (Marone et al., 2021; Newton et al., 2009). Some breeding programs now seek to increase farmer participation in evaluating the performance and stress tolerance of varieties across large regions. Farmers submit the varietal performance and preference data to the breeders, who analyze the data to inform subsequent varietal selection (van Etten et al., 2019). While the varietal evaluation occurs using a decentralized approach, the actual varietal selection is still done by professional breeders (de Sousa et al. 2021).

How people value the ecosystem services of crop plants influences how ongoing evolutionary processes will continue in traditional and formal seed systems (Figure 1). By saving seed from crop plants that perform well in their fields and in use, farmers directly manage crop plants to adapt locally across heterogeneous environments and human preferences. In formal seed systems, the performance of a HYV crop plant in farmers' fields does not influence its fitness. Breeders are the only ones to select plants, so they adapt to the goals of the breeders, as well as fertile conditions of the breeding and seed amplification fields. While crop breeders clearly appreciate landraces for their tolerance to a wide range of stressors, most of the genetic diversity in landraces remains unknown and underutilized (Marone et al., 2021). In order to manage the crop evolutionary processes that support sustainable agriculture, it is important to understand the factors influencing human values, and how these values relate to seed selection and management decisions. However, empirical evidence is needed on how farmers' observations of ecosystem services specifically motivate how they grow seeds. Since seed systems deliver other important benefits to farmers aside from yield and profit, we expect that farmers who grow landrace varieties value a wider range of ecosystem services outside yield than those who primarily grow HYVs.

3.2 | Traditional seed systems provide ecosystem services by contributing to selecting and generating adaptive genetic diversity that has been reduced in formal seed systems

Traditional and formal seed systems also differ in their retention, selection, and generation of crop diversity. Crop genetic diversity is an emergent property of the seed system, as it depends on the generation of new mutations, size of the population, and the degree of gene flow or exchange of alleles among subpopulations (Figure 1). Seed systems are based on social networks, which determines among whom seed is exchanged, how frequently exchanges occur, how diverse the selective pressures are among farms, and the degree to which seeds are able to perform well in new habitats (Pautasso et al., 2013). Since the heterogeneous environments select for crop populations with unique adaptations, traditional seed systems can

retain higher population genetic diversity, where subpopulations have a different subsets of alleles (Figure 1).

In traditional seed systems, a multitude of farmers growing millions of plants increases a crop's **effective population size** (N_e) (Figure 1). The effective population size refers to how the population behaves genetically; it is smaller than the census size, because not all individuals reproduce or are genetically different. A large N_e increases the frequency of new mutations and reduces the loss of genetic diversity via drift, or the random changes in the frequency of genetic variants in the population (Bellon et al., 2018). Traditional seed system networks can be highly connected as smallholder farmers are known to regularly exchange seeds, trialing new varieties and crop combinations (Pautasso et al., 2013). For example, traditional (*campesino*) maize cultivation occurs across nearly four million ha in Mexico, which translates to an effective population size of about 500 million maize plants contributing seeds for the next cycle (Bellon et al., 2018). Unsurprisingly, the majority of maize genetic diversity comes from these four million ha (~10% of the maize acreage in North America) (Bellon et al., 2018). Although there are more maize plants in the US and Canada, their effective population size is smaller because they are genetically identical. The large effective population size in Mexico helps to explain the high level of genetic diversity that exists among different maize landraces (Arteaga et al., 2016). Therefore, smallholder farmers generate ecosystem services by collectively increasing the effective population size of crop populations (Figure 1a).

Crop evolution in formal systems typically occurs through selection by professional breeders, which can lead to losses of adaptive genetic diversity in the crop germplasm. The concentrated model of varietal development and dissemination (via formal seed systems) physically disrupts where seeds are selected from where they are produced (Figure 1b). Gene flow, or the movement of genetic alleles between populations is unidirectional. When particular plant strains perform well in a farmer's field, the seeds or progeny are harvested for consumption and none are retained for the next generation. The narrow focus on yield has caused losses in the genetic diversity for traits important to many smallholder farmers (i.e., storage quality, and culinary preferences) (Ficiciyan et al., 2018). Therefore, the overall crop genetic diversity is limited by the diversity of the breeding populations.

Since environmental stress can lead to novel mutations (Laland et al., 2014; Minow & Colasanti, 2020), we expect that traditional agriculture management approaches that are prevalent in traditional seed systems create more stressful conditions for crops, which cause higher rates of heritable changes through epigenetic modifications (Figure 3). Epigenetics refer to heritable changes in an organism's phenotype that are outside of a change in the DNA sequence, such as histone modifications or DNA methylation (Chang et al., 2020). The recent extended evolutionary synthesis emphasizes the importance of environmental stress in the generation of evolutionary novelty by elevating the likelihood of stress-induced epigenetic variation (Mojica & Kültz, 2022). Given that exposure to stress increases the generation of new genetic diversity, we postulate that human cultivation of crops in new stressful conditions helps to

generate new epigenetic and genetic mutations that underlie novel traits.

Farmer management affects the degree to which crops are stressed and the likelihood of stress-induced evolutionary processes. Unlike intensive systems, traditional agricultural systems are frequently rainfed and receive low external inputs, causing plants to experience more stress (Figure 3) (Zhu, 2016). In addition, crops grown without insecticides have higher exposure to biotic stress, such as insects and pathogens, which contribute to natural selection (Figure 3). Furthermore, seed exchanges expose crop populations to new environmental conditions, which can select on crop populations (Mercer et al., 2008). Crops grown in marginal environmental conditions have been shown to elicit epigenetic modifications, such as in low nutrient (Li et al., 2021), drought (Verkest et al., 2015), saline (Wang et al., 2021), and environmental stress conditions (Perrone & Martinelli, 2020). Epigenetic changes in DNA methylation, histone modifications, and small RNAs can be passed to subsequent generations, so crops retain a “memory” of environmental stress (Jablonka & Lamb, 2005). Therefore, by growing crops in stressful environments, farmer management continues as an ongoing selective force that contributes to rapid adaptive change. While epigenetic processes could occur within formal seed systems, they are only passed to the next generation if the seeds are saved. Thus, traditional agroecosystem generate epigenetic variation that is heritable by descendants.

Since environmental stress can induce changes that cause genomes to be less regulated and more prone to mutation (Mojica & Kültz, 2022), traditional seed systems may also generate more adaptive genetic variation as well. Physiological stress can cause DNA polymerases to make more mutations, induce higher rates of recombination, and compromise DNA repair mechanisms (Galhardo et al., 2008). Stress can cause changes in DNA methylation, which can deregulate transposable elements (TEs), or mobile DNA regions (Baduel & Colot, 2021). For example, nitrogen stress causes a widespread loss in DNA methylation of the genome, mostly in TE regions (Mager & Ludewig, 2018). Since DNA methylation functions to silence TEs (Miura et al., 2001), the loss of DNA methylation can allow TEs to mobilize, which can cause new genetic mutations (Baduel & Colot, 2021). In summary, traditional seed systems contribute ecosystem services by generating new genetic and epigenetic diversity.

3.3 | Traditional seed systems provide ecosystem services by retaining crop traits that support plant competition and stress tolerance

Due to differences in plant competitiveness, the choice to plant a landrace or HYV variety leads to entirely different plant communities that provide different ecosystem services (Figure 2 and 3). Traditional and formal seed systems have selected for different crop growth strategies that have shifted the focus from the individual to the stand performance. Traditional agroecosystems often host higher levels of interspecific and intraspecific plant diversity, while farmers practicing intensive agriculture prefer monocultures to reduce plant competition

and increase cropping efficiency. While a diverse assemblage of plants may be welcome or tolerated in traditional agroecosystems, non-crop plant species are considered weeds and targeted by herbicides.

Crop breeding has made gains in productivity by selecting for increased performance of the crop population (Denison et al., 2003). The discipline of crop breeding previously assumed that selection for higher individual fitness increased population yield (Weiner et al., 2017). However, natural selection favors plant traits that increase individual fitness (taller stature and better competitor) that are considered “selfish”, which increases individual fitness but reduces the overall stand yield (Weiner et al., 2017). Higher individual performance has been called a “Tragedy of Commons” (TOC) as it is associated with decreased group performance (Anten & Vermeulen, 2016). By selecting for dwarfed crops, breeding for higher yields during the Green Revolution occurred by reducing plant investment in stem and root biomass, which minimized individual competitiveness so that crop plants could be grown more densely (Figure 2) (Weiner et al., 2017; Zhu et al., 2022). The crop ideotype for high yield is a plant that it is a poor competitor (Donald, 1968). Therefore, crop breeding has been generally successful in selecting for traits that favor group fitness, which has increased crop productivity (Anten & Vermeulen, 2016).

Selection for stand performance has been coupled with a trade-off with stress tolerance, competitiveness, and efficient resource utilization. Due to a reduced investment in stem and root biomass, HYV plants are less capable of tolerating abiotic stress and competing with other plants (Figure 2). HYVs tend to be more susceptible to drought stress (Boudiar et al., 2019; Devnarain et al., 2016). For example, under low fertility conditions, shorter wheat HYVs are less able to uptake nitrogen compared to landraces and taller varieties (Newton et al., 2009). The root morphology of HYV wheat varieties tend to be simpler and less branched, spreading less laterally to reduce intraspecific competition (Zhu et al., 2019). Also due to their short stature, HYVs are less competitive aboveground, which allows for more dense plantings but reduces their weed suppression ability (Murphy et al., 2008). As a result, weeds need to be more strongly managed in intensive agroecosystems to avoid major yield losses.

Farmers' choice of seed systems influences resource utilization and cropping density in agroecosystems. Landrace varieties are more competitive individually, so they need to be planted at lower densities to reduce intraspecific competition (Figure 3). HYVs have been selected for reduced root systems, so they can be grown at higher densities (Figure 2). In terms of nutrient uptake, landraces are better at acquiring the macronutrients phosphorus and nitrogen (Newton et al., 2009), as well as scavenging for micronutrients (Figure 3; Schmidt et al., 2019). HYVs require fertile soils, so supplementation with fertilizer or cover crop amendments is often needed. Therefore, in order to reap the ecosystem service rewards, farmers manage the crops completely differently agronomically.

Landraces in traditional agroecosystems may benefit from growing in more diverse plant communities than HYVs in intensive agroecosystems. Some crop landraces have been selected in **polyculture**, which can result in unanticipated benefits. In traditional agroecosystems, other crop species (Brooker et al., 2015) or wild plants (Figure 3,

Bye Jr., 1981) may be welcome or tolerated. Different crop species that have been selected together may have more efficient shared resource utilization than **monoculture** systems, allowing interspecies crop combinations to be planted at a higher density than stands of single species (Murphy et al., 2008). Although growing crops in polyculture can lessen the yield of individual species, polyculture systems, such as in the *milpa* (Mesoamerican polyculture of maize, beans, and squash), can increase overall biomass production due to niche complementarity while mitigating risk failure (Zhang et al., 2014).

3.4 | Traditional seed systems contribute evosystem services by retaining beneficial traits that support mutualistic plant-biotic interactions

Following differences in selection history and agronomic management, landraces and HYVs interact differently with the biotic communities in agroecosystems, which generates different outcomes for evosystem services (Figures 2 and 3). As Figure 3 shows, traditional agroecosystems are typically managed with less inputs of water, fertilizer, and pesticides. Due to less pesticide use, traditional agroecosystems host a more diverse arthropod and microbial community (Figure 3; Altieri, 1999). Growing within a more diverse biotic community, landraces are able to mediate interactions between harmful and beneficial species. There is greater variation in the population in resisting pests and pathogens. In intensive agroecosystems, the use of water, fertilizer, and pesticides results in a less biodiverse community where pests outnumber beneficial species (Figure 2).

Due to decreased defenses and higher genetic uniformity of HYV fields, insect and disease outbreaks are more likely to occur in intensive systems (Ratnadass et al., 2012). As such, pesticides are widely used for pest control in HYV fields, which have wide-ranging negative environmental impacts (Van Der Werf, 1996). Farmers are reliant on pesticides to manage pests, which reduces the natural enemy population from regulating pest populations. As a result, pests managed in this way may evolve resistance to pesticides. The crop plant population is genetically uniform, so all plant individuals in the population lack resistance to pests and diseases. Intensive agroecosystems are more vulnerable than traditional agroecosystems (Figures 2 and 3), because both the plant traits promoting mutualistic interactions and the beneficial species are lost from the system. Therefore, we expect that, as an evosystem service, beneficial plant-biotic interactions are more likely to occur with landrace varieties than with HYVs.

Landraces retain traits that allow them to resist disease and pests, while recruiting beneficial species. Although poorly studied in most crops, many landraces possess important traits for managing disease (Figure 3; Ficiyan et al., 2018). For instance, oat and sorghum landraces show a higher degree of resistance to fungal and oomycete diseases (Patil et al., 2014; Sánchez-Martín et al., 2017). Landraces also defend themselves against insect herbivory through myriad ways. Landraces can release volatile compounds repelling insect herbivores from laying eggs (Tamiru et al. 2011). Landraces can produce higher levels of secondary defenses that kill or slow herbivore development (Costa

et al., 2018). They are also more tolerant of insect herbivory, meaning that they can incur more feeding damage without yield loss (Ferrero et al., 2020). In addition to direct responses of plants to herbivores and disease, landraces can also recruit beneficial species for defense. For example, when Mexican maize landraces are attacked by herbivores, they are able to recruit beneficial parasitoid wasps and predatory nematodes to protect them, which HYVs cannot do (Rasmann et al., 2005, Kollner et al., 2008, Tamiru et al. 2011). Overall, crop breeders value landraces for retaining traits that enable them to manage plant-biotic interactions, so they are a critical source for improving plant resistance to diseases and pests (Hajjar & Hodgkin, 2007).

Landrace crops interact mutually with microbes that influence plant and soil health (Rodríguez et al., 2019). Particular microbial species contribute to plant nutrition and soil regeneration (Aguirre-von-Wobeser et al., 2018). Since changes in bacterial groups correlate with plant genotype, human selection on crops can influence microbial community composition (Mendes et al., 2018). For example, with more support from microbial mutualists, landraces are more able to scavenge macronutrients than their HYV counterparts (Figure 3; Beebe et al., 1997, Van Deynze et al., 2018). Landraces also support microbial mutualists that support plant nutrition in less fertile conditions. For example, a landrace maize variety in the highlands of southwest Mexico hosts nitrogen-fixing bacteria on its aerial prop roots (Van Deynze et al., 2018). Also, soybean landraces associate with more effective rhizobia symbionts for nitrogen fixation than improved soybean varieties (Kiers et al., 2007). Therefore, traditional agroecosystems retain interactions with beneficial microbial species that intensive systems do not (Pérez-Jaramillo et al., 2019). However, no definitive study has isolated the relative roles of crop selection history, local environmental variation, and agroecosystem management in the recruitment of beneficial microbial communities in a center of origin (Pérez-Jaramillo et al., 2019).

Given that some landrace crops may have been selected in polyculture systems, they may have traits that recruit beneficial species that can only be observed in these systems. Polyculture functionally alters biodiversity and the accompanying ecosystem services. For instance, polyculture systems collectively enrich for a different functional microbiome network that may be absent in monocultures. Polycultures support particular co-occurrence patterns of microbial species (Rebollar et al., 2017), increasing beneficial bacteria (Walters et al., 2018) and enhancing symbiotic bacteria-plant interactions (Pueppke, 1996). Although milpas and other polyculture systems have been grown for thousands of years (Maezumi et al., 2018), mutualistic interactions within polyculture systems remain poorly studied. Given that the expression of particular plant phenotypes can depend on the environmental conditions, more studies on how landraces perform within polyculture may reveal unanticipated evosystem services.

Both the breeding of HYVs and intensive agriculture have disrupted the plant-microbial mutualisms and the benefits they provide. HYV's are reliant on mineral fertilizers, which reduces a crop's ability to associate with microbes that support nutrient acquisition. Selection for high yield disrupts crops from forming mutualistic relationships with microbial species (Porter & Sachs, 2020). For instance, in soybean,

breeding has reduced host plant benefits from rhizobia (Kiers et al., 2007). HYVs exude simpler sugars than landraces, which support faster growing microbial species (Gutiérrez-García et al., 2019). Since commercial breeding has clearly disrupted plant-microbial symbiosis (Porter & Sachs, 2020), landraces retain more mutualistic interactions with beneficial species compared to HYVs (Pérez-Jaramillo et al., 2019).

Landraces grown in traditional agroecosystems can host a rich community of organisms that mutualistically support plant growth and growth. Alarmingly, HYVs have lost the ability to defend against pests and associate with beneficial species. Therefore, they are unable to provide the ecosystem services that landraces do. Accordingly, we expect that, when grown under low input or stressful conditions, landraces associate with more microbial species that support nutrient scavenging, plant defense, and crop growth compared to HYVs. Landraces should also be better defended against insect herbivores and better able to recruit natural enemies to attack crop pests. There is still much yet to be discovered about how agrobiodiversity contributes to the functioning of agroecosystems. Overall, the species diversity found within agroecosystems is an emergent property that depends upon crop selection history and cultivation. Thus, differences in seed selection between traditional and formal seed systems can scale up to affect the ecosystem services within agroecosystems.

4 | CONCLUSION

We present a heuristic framework linking farmers' engagement with seed systems with social and evolutionary processes. Assuming that future research supports the propositions of our framework, we expect that the benefits from ecosystem services such as locally adapted seed are more prominent in traditional seed systems than in formal seed systems. The shift from traditional to formal seed systems threatens the process of adaptation and limits the exploration of unanticipated future uses of crop genetic diversity. The Kunming-Montreal Global Biodiversity Framework, adopted in December 2022 during COP15, explicitly targets the conservation of genetic diversity within and between populations of wild and domesticated species to maintain adaptive capacity. While the framework explicitly targets crop populations from traditional seed systems, these seed systems will continue to erode should seed (and agricultural) policy continue to overlook (or undermine) traditional seed systems.

Ecosystem services are under threat as the formal seed system continues to expand. Farmers in different regions are increasingly reliant on the formal seed system for sourcing seed (Spielman & Kennedy, 2016). Farmers who plant hybrid seed need to buy seed each season for consistent yields. In selfing crops such as rice and wheat, farmer seed saving is more common as seeds will breed true to their parents, but depending on the country, farmers purchase 2%–96% seed from the private sector anyway (Spielman & Kennedy, 2016). Depending on the crop species, the impact of the formal seed system may differ on traditional seed systems.

We contend that the farmers and the ecosystem services that emerge from traditional seed systems urgently need to be supported in order to advance sustainable agriculture and protect our food supply amidst a rapidly changing environment. Formal seed systems are dependent on traditional seed systems for ecosystem services because breeders use the genetic diversity from crop landraces to improve crop stress tolerance. While traditional seed systems select for the plant traits that meet the livelihood needs and preferences of smallholder farmers, they have been undervalued in research, breeding, and policy. Therefore, we need to reevaluate how economic and policy supports have favored formal seed systems at the expense of traditional seed systems and the ecosystem services they provide.

Farmers who save their seed are central for maintaining the evolutionary processes that enable crops to adapt to future conditions (Bellon & van Etten, 2013). Yet, viewing farmers as singularly responsible for the maintenance of ecosystem services overlooks the broader systems and structures that influence their management. Farmers have to respond to the social and natural forces that affect their livelihoods and fields. If governments directly value ecosystem services, they could provide a new set of opportunities to alleviate what farmers currently confront: an agrifood system that prioritizes formal seed systems and the HYVs that circulate within them. Accordingly, government policies could adjust policies to directly support traditional seed systems, by encouraging the planting and seed saving of landraces. While farmer management of ecosystem services produces a global public good, farmers will only continue growing landraces if the landraces provide local and private benefits to them (Bellon et al., 2014). Without a rigorous appreciation of how ecosystem services are generated and maintained, we risk losing the ecosystem services that are crucial to global food security and agricultural sustainability. By presenting this framework, we hope to spur researchers, policymakers, and the public to value and support the farmers managing the evolutionary processes that select crops to rapidly adapt to changing conditions.

AUTHOR CONTRIBUTION

A. Mastretta-Yanes, D. Tobin, and Y. H. Chen jointly drafted and edited manuscript. M. Bellon and A. S. Monroy-Sais provided input on smallholder farmer values, beliefs, and practices. E. von Wettberg, A. Cibrián-Jaramillo, and A. Wegier advised the discussion on crop breeding, plant genetics, and plant-microbial interactions. Nancy Gálvez-Reyes, and J. Ruiz-Arocho contributed to the discussion plant-biotic interactions. A. Mastretta-Yanes developed the conceptual figures. Y. H. Chen edited the full manuscript while soliciting input from other authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study. Please find a Spanish language version of the manuscript in the Supporting Information. Una versión en español de este artículo se encuentra disponible como Material Suplementario.

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