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### **RESEARCH ARTICLE**

### Global modeling of the socioeconomic, political, and environmental relations of farmer seed systems (FSS): Spatial analysis and insights for sustainable development

Karl S. Zimmerer<sup>1,2,3,4,\*</sup>, Steven J. Vanek<sup>5</sup>, Megan Dwyer Baumann<sup>6,7</sup>, and Jacob van Etten<sup>8</sup>

Accessible, high-quality seed is vital to the agricultural, food, and nutrition sovereignty needed for justice-based sustainable development. Multiregion, interdisciplinary research on farmers' seed systems (FSS) can complement case-based and thematic approaches. This study's goals are to (1) provide a synthetic overview of current major FSS concepts; (2) design and evaluate a novel social- and political-ecological model of FSS using globally representative data from mountain agricultural areas of Africa, Asia, and Latin America; (3) model and evaluate FSS relations to socioeconomic, political, and environmental factors including main food crops (rice, wheat, maize, potato, and common bean); (4) generate new spatial, geographic, and demographic estimates; and (5) strengthen FSS for justice-based sustainable development of agriculture, land use, and food systems. The conceptual framework of FSS-related factors guided the global modeling of data from 11 countries in Africa, Asia, and Latin America. A multiple regression model explained FSS utilization ( $R^2 = 0.53$ , P < 0.0001), specifying the significant inverse relations to mean farm area (strong), per-capita Gross Domestic Product at the district level (strong), and urban distance (moderate). FSS showed strong positive relations to aridity and topographic ruggedness. FSS were positively related to elevation in a 5-country Andean subsample. Results estimated FSS utilization by 136 million farmers within the 11 countries. Novel insights to strengthen FSS policies and programs are the importance of FSS to extremely small farm-area subgroups and other distinct FSS stakeholders, global-region geopolitical distinctness of FSS-farm area relations, multidistrict FSS concentrations that enable extralocal FSS spatial connectivity, FSS capacities in climate-change hot spots, and high FSS encompassing periurban areas. Policy-relevant results on global geographic and demographic extensiveness of FSS and key spatial, socioeconomic, political, and environment relations demonstrate that globally FSS are key to supporting agrobiodiversity, agroecology, nutrition, and the sustainability of food systems. These advise strengthening FSS through pro-poor and linked urban-rural policies at regional scales in addition to expanding local initiatives.

**Keywords:** Farmers' seed systems (FSS), Informal seed systems, Local seed systems, Sustainable development, Land use and food systems, Agrobiodiversity and biodiversity, Social–ecological systems and political ecology, Climate change, Urbanization, COVID-19, Spatial analysis

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### 1. Introduction

Accessible, high-quality seed of food crops is vital to justice-based sustainable development and the combined quality and sovereignty of agriculture, land use, food, nutrition, and livelihoods. Potential seed-centered transformations advancing these goals are open-source seed and seed commons (van Etten, 2011; Girard and Frison, 2018; Scoones et al., 2018; Montenegro de Wit, 2019); community seed activism and seed organizations practicing care ethics (van Zwanenberg, 2018; Aistara, 2019; Isbell et al., 2021; Baumann, 2022); seed networks (Zimmerer, 2003; Helicke, 2015; Wencélius et al., 2016; Labeyrie et al., 2021); seed movements, public institutions, and policy support (de Boef et al., 2010; Almekinders et al., 2019b; Sperling, 2020; Sperling et al., 2020b; Zimmerer and de Haan, 2020; Lyon et al., 2021); freelance breeders, community seed hubs, and seed banks (Song et al., 2021); seed systems for strengthening gendered, smallholder and indigenous food, nutrition, biodiversity, and agroecological capacities (Delaquis et al., 2018; Nyantakyi-Frimpong, 2019; Zimmerer et al., 2020; Otieno et al., 2021); endogenous development, biocultural, and heritage approaches (Graddy, 2013; Thomas and Caillon, 2016; Nishikawa and Pimbert, 2022; Swiderska and Argumedo, 2022); seed-system underpinning for biosafety approaches involving new biotechnology (Montenegro de Wit, 2020; Rock, 2023); and biodiversity conservation (Curry, 2019).

"Farmers' seed systems" (FSS) refer to interlinked land use and farm-based seed production and care (including seed selection and storage), processing, distribution and exchange, and procurement of propagating materials. This definition is a synthesis of elements in previous works (Almekinders and Louwaars, 2002; de Haan and Thiele, 2005; McGuire, 2007; Louwaars, 2017; Westengen et al., 2018; Baumann, 2022). Additional defining FSS practices are the governance of propagating materials (e.g., informal institutions for seed quality) and capacities for adaptation, change, and innovation. The use or utilization of seed is highlighted in the FSS perspective (Westengen et al., 2018, p. 11). FSS are also termed local, informal, traditional, and farmer-managed seed systems (Almekinders et al., 1994; Louwaars and De Boef, 2012; McGuire and Sperling, 2016; Labeyrie et al., 2021) and they incorporate farmer seed saving (Tin et al., 2011; Kansiime and Mastenbroek, 2016). Local FSS provide extensive socioeconomic, nutrition, agroecological, and agrobiodiversity benefits (detailed in the next section), thus fueling the ongoing production of the great majority of the global biodiversity of food in land use and agriculture ("agrobiodiversity"; Louwaars, 2017; Zimmerer and de Haan, 2017; Zimmerer et al., 2019). Local FSS initiatives can potentially become expanded in global programs, institutions, and policies on biodiversity, food and nutrition, agriculture, and cityregion agri-food systems (Díaz et al., 2018; e.g., Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]; Consultative Group on International Agricultural Research [CGIAR]; UN panels and organizations on food, nutrition, and agriculture), which serves as a main motivation for this study.

FSS occur globally yet comparable, large-scale estimates across multiple global regions have been lacking. Analyzing FSS across a globally representative sample of African, Asian, and Latin American countries with significant tropical and subtropical mountains areas, this study estimates approximately 136 million FSS-utilizing farmers (detailed in the following). This demographic estimate of FSS utilization across Africa, Asia, and Latin America offers novel global region-level support of high FSS-utilization reported in case and theme-focused research (Almekinders et al., 1994; Food and Agriculture Organization of the United Nations, 2016; McGuire and Sperling, 2016). Finally, as noted in other studies, significant FSS utilization has continued to persist even where the formal seedsystem is common (e.g., Mexico maize farming, Hoogendoorn et al., 2018), thus reflecting the current continuation of high FSS demand (Almekinders et al., 2019a).

This study addresses a series of five related gaps in current research on FSS, which is defined to include systems of informal, local, and traditional seeds. First, we provide a focused synthetic overview of evolving FSS conceptual themes that guides the design of a broad-scale FSS framework. Second, global modeling and spatial analysis are undertaken using data from 11 countries representing tropical and subtropical mountain areas of Africa, Asia, and Latin America. This modeling and analysis focuses on five major foods (rice, wheat, maize, potato, and common bean). Multiple data sources, including agricultural surveys and census reports, are used to model FSS utilization in relation to the framework's socioeconomic, political, and environmental factors. Global representativeness of this FSS analysis is a novel complement to extensive local, within-region, and case and thematic studies (Almekinders and Louwaars, 2002; McGuire, 2007; De Boef et al., 2010; Louwaars and De Boef, 2012; McGuire and Sperling, 2016; Westengen et al., 2018; Sperling et al., 2020b). Third, this study is novel in its model-based testing and specification of FSS relations to a suite of globally common socioeconomic, political, and environmental factors. Fourth, it provides original spatial, geographic, and demographic estimates of FSS across countries of Africa, Asia, and Latin America. Fifth, this study offers new largescale insights to strengthen FSS for the justice-based sustainable development of food systems, land use, agriculture, and biodiversity.

The next section (Concepts) outlines thematic areas and design elements that guide the identification of socioeconomic, political, and environmental factors to model and estimate FSS relations (Study Design and Methods). The Results section presents the findings on the tested relations of these predictive factors to FSS utilization using the sample of multiple countries and crops across global regions. Comprehensive results of our model of FSS utilization are then evaluated at the end of the section. The Discussion interprets results and compares them to related research in identifying ten areas of significant new insights to strengthen FSS policy and program recommendations. These insights focus on FSS utilization for sustainable development and as responses to the COVID-19 pandemic and climate change. The Conclusion distills the principal research results and major recommendations for policy and programs to strengthen FSS.

#### 2. Concepts

The term FSS is chosen based on several rationales introduced briefly above and detailed here: (1) current FSS definitions (Almekinders and Louwaars, 2002; de Haan and Thiele, 2005; McGuire, 2007; Kansiime and Mastenbroek, 2016; Westengen et al., 2018) are consistent with a nonteleological perspective, whereas "informal" can suggest lesser status; (2) FSS highlights the overlap, rather than dichotomy, of the existing seed systems and future scenarios; and (3) FSS is compatible with the data sources used in this study.

The first guiding insight is that extensive FSS utilization benefits seed accessibility, affordability, versatile procurement via varied networks (including markets), and wide-ranging sourcing of diverse seed at individual, network, community, and multicommunity scales (Sperling and McGuire, 2010; Smale et al., 2012; Gill et al., 2013; Coomes et al., 2015; McGuire and Sperling, 2016; Sperling, 2020; Sperling et al., 2020a; Labeyrie et al., 2021). This study is critically cognizant through the perspectives of seed, food, and social justice that FSS utilization is usually sharply differentiated spatially, socioeconomically, and culturally (e.g., wealth and gender differentiation; Zimmerer, 2003; Helicke, 2015; Violon et al., 2016; Wencélius et al., 2016; Tadesse et al., 2017; Delaquis et al., 2018; Nyantakyi-Frimpong, 2019; Sperling et al., 2020a; Labeyrie et al., 2021; Mulesa et al., 2021; Otieno et al., 2021). FSS benefits underpin its widespread role in participatory plant breeding, farmer field schools, community seed banks, and citizen-science approaches as well as grassroots and benefits-sharing governance (Cleveland, 2014; Westengen et al., 2018; Mushita and Thompson, 2019; van de Gevel et al., 2020; Tsioumani, 2021; Ceccarelli and Grando, 2022). This study's global modeling and spatial analysis are a novel focus and complement that we integrate with the robust array of existing FSS research that tends to be case study- and local knowledge-based (e.g., van Etten et al., 2017; Baumann, 2022).

FSS benefits for vulnerable smallholders specifically can address global political-ecological crises. These include: (1) FSS benefits to address the gendered povertyand policy-induced crises of the COVID-19 pandemic and postpandemic that include disrupted seed and foodgrowing supplies (Sperling and McGuire, 2010; Adhikari et al., 2020; Jumba et al., 2020; Sperling et al., 2020b; Zimmerer and de Haan, 2020; de Boef et al., 2021), (2) increased distribution and spatial connectivity of adaptive agrobiodiversity to respond to climate change (Halewood et al., 2016; Kansiime and Mastenbroek, 2016; Ravera et al., 2019; Westengen et al., 2019; Zimmerer et al., 2019; Acevedo et al., 2020), and (3) FSS-utilization for sustainable development including gender, food, and nutrition goals (Croft et al., 2018; Shayanowako et al., 2021). FSS benefits are also shown for conflict/postconflict societies with displaced communities (Tamariz and Baumann, 2022) and social movements recognizing FSS as an international human right (Food First Information and Action Network International, 2021; Kuhlmann and Dey, 2021; Lokhandwala, 2022).

The second conceptual theme that guides our study is the supportive yet complex relation of FSS to agrobiodiversity and agroecology (Toledo and Barrera-Bassols, 2017; Barrett et al., 2020). FSS "nourish" agrobiodiversity through mutual benefits that lead FSS to account for the seeds of most biodiversity in global food, land use, and agriculture (Zimmerer and de Haan, 2017; Zimmerer et al., 2019). FSS also supply "improved varieties" derived from modern breeding. In Nepal, only 15% of farmers acquired wheat seed through formal systems even though "improved varieties" yield 78% of national wheat production (Garapaty et al., 2021). Numerous modern varieties have been locally adapted in FSS for local conditions (e.g., "creolized" maize, Bellon et al., 2006). That a substantial share of FSS seed originates from modern breeding has been confirmed by DNA fingerprinting (Floro et al., 2018; Hodson et al., 2020; Jaletta et al., 2020; Garapaty et al., 2021). Overall, versatile and wide-ranging FSS are vital for agrobiodiversity, thus motivating this study's goal to open policy-relevant dialogues about FSS support and focus in global programs and policies (e.g., IPBES, CGIAR, UN Panels and organizations on food, nutrition, and agriculture) in addition to expanding local initiatives.

The third insight informing this study is that FSS are notably important to certain global geographic areas while previous studies suggest potentially high levels of spatial variation. Case studies of tropical and subtropical mountains illustrate this tendency in case studies of the highlands of East Africa (Westengen and Brysting, 2014; Westingen et al., 2019), the Himalaya and uplands of South and Southeast Asia (Bisht et al., 2007; Sthapit et al., 2010), and the Andes and other mountainous areas of Latin America (Thiele, 1999; de Haan and Thiele, 2005; Badstue et al., 2006; Bellon et al., 2011; Arce et al., 2018; Chambers and Brush, 2010). FSS benefits are shown to be potentially extensive and varied among individuals, households, communities, and regions in these mountain environments. This focus of our study reflects the authors' participation in mountain-based projects that can potentially include and expand FSS support through these innovative organizations (e.g., Bioversity, Carasso Foundation, and, recently, the Andes Community of Practice [2023]).

The fourth insight is centered on extensive FSS cooccurrence and interaction with formal seed. The latter is tested, evaluated, certified, and sold by commercial seed companies and agribusiness (Almekinders et al., 1994; Almekinders and Louwaars, 2002; Sperling and McGuire, 2010; Louwaars and De Boef, 2012; McGuire and Sperling, 2013). It includes hybrid seed in major crops such as maize and sorghum. The context-dependent linkages of FSS to formal seed (including high-quality seed becoming adopted in informal seed systems; Ahmad et al., 2022) are extensively illustrated (Almekinders et al., 1994; Jones et al., 2001; Almekinders and Louwaars, 2002; Zimmerer, 2003; de Haan and Thiele, 2005; Bellon et al., 2006; Louwaars and De Boef, 2012; Pautasso et al., 2013; Coomes et al., 2015; Croft et al., 2018; Fadda et al., 2020; McEwan et al., 2021; Mulsea et al., 2021; Sperling et al., 2021). Policy and program designs for an "integrated seed system" are a principal goal of Ethiopia's 2017 Pluralistic Seed System Development Strategy (Mulesa et al., 2021). Seed developed in the formal system can become selectively adopted and strengthen FSS (Ahmad et al., 2022).

At the same time, FSS are often marginalized in government programs and formal, private-sector seed systems including campaigns for certified "improved varieties" and hybrid seed (Waldman et al., 2017; Hoogendoorn et al., 2018). Other threats to FSS are transforming intellectual property rights and seed enclosures (Wattnem, 2016; Montenegro de Wit, 2019). Conversely, FSS co-occurrence can be facilitated by integrated initiatives such as Quality Declared System and farmers' rights (Tripp et al., 2007), including protection of Article 9 of the International Treaty on Plant Genetic Resources for Food and Agriculture (Kuhlmann and Dey, 2021). The extents and type of FSS interactions are influenced further by country-level and international seed policies and legislation (Visser, 2016; Visser et al., 2019). For this reason, the interactions of FSS that are subject to potential biotechnology impacts, such as introductions of genetically modified and geneedited seeds (Cleveland et al., 2005; Scurrah et al., 2008; Mercer et al., 2012; Visser et al., 2019; Rock et al., 2023), need to inform national and international biosafety regulations. More generally, the inaccessibility of formal seed systems to smallholder farmers globally (e.g., Maredia et al., 2019) is a consequence of both the neoliberal privatization of seed production and markets (Louwaars and De Boef, 2012) and the decline of public-sector seed programs (Pingali, 2012).

#### 3. Study design and methods

The study was designed to construct and evaluate a model of FSS relations to socioeconomic, political, and environmental factors applied to a sample of countries representing global regions with substantial tropical and subtropical mountains and uplands. Guidance for study design was provided through FSS case studies, identification of specific factors that are potentially influential (first and third through sixth columns of **Table 1**), and relevance to sustainable development. Thematic categories of the FSS model variables were guided by the conceptual orientations described in the preceding section and integrative social-ecological and political-ecological approaches applied to FSS and agrobiodiversity (e.g., the Agrobiodiversity Knowledge Framework; Zimmerer et al., 2022b). Finally, the public availability of data also influenced the choices of model factors and countries in the tropical and subtropical mountains of Africa, Asia, and Latin America.

The abovementioned inputs led to the specification of seven types of variables for the FSS model (**Table 1**). These were as follows: average farm size, association with global region, Gross Domestic Product (GDP) per capita (district scale), distance from major city, crop type (for foodproducing crops), aridity, elevation, and the variation of topography (ruggedness). Four of these variables represent socioeconomic and political factors (farm size, association with global region, GDP per capita, and distance from major city). The final three variables are environmental factors. Crop type was distinct since its role in FSS reflects both socioeconomic and political factors that determine seed-sector development, plant-level traits associated with FSS (e.g., crop breeding system), and environmental influences. The hypothesized directionality of each of the seven variables as a positive or negative influence is shown in Table 1 (third column). Also noted are the examples of the webs of influences on each variable (fourth column) and the general relevance of each variable's relation to FSS for sustainable development (fifth column).

The abovementioned criteria led to the selection of 11 countries in the three world regions of Africa (Ethiopia,

Uganda, and Rwanda), Asia (Nepal, Laos, and Cambodia), and Latin America (Colombia, Peru, Ecuador, Nicaragua, and Bolivia). At least 30% of the national territory of each of these countries consists of tropical and subtropical mountains and uplands. Each country had completed an agricultural survey or census report specifying the levels of FSS utilization at the geographic scale of subnational administrative units (henceforth districts; **Table 2**). In total, the number of districts across all censuses with usable data was 265.

Study design was focused on FSS for each crop as specified in the surveys and census reports, leading to the focus on 5 major food-producing species—rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize (*Zea mays*), potato (*Solanum tuberosum*), and common bean (*Phaseolus vulgaris*; **Table 2**). Each crop is a vital, major producer of foods for the nutrition and energy of large populations. Finally, the 11 census reports were also chosen because they co-occurred in the 5-year period of 2008–2013 (**Table 2**). Agricultural census reports incorporating FSS estimations at the district level have not been available since this time for a sample of countries with similar size and scope.

The estimates of FSS-utilization rates were based on information in country-level agricultural surveys and census report (sixth column, **Table 2**). These estimates were then used to construct FSS as a response variable in hypothesized relations to the socioeconomic, political, and ecological predictors. The surveys and reports, as well as other data described in the following, were used to estimate the values of FSS utilization and the seven variables at the levels of the subnational administrative units referred to here as districts. Subnational districts were defined at one or two geographic levels below the national level and depended on actual census units.

The estimation of FSS utilization was calculated as the proportion of farm households in a district utilizing sources other than the ones providing seed recognized as certified, hybrid, improved, and modern varieties seed—all major examples of the formal seed system (Almekinders et al., 1994; Almekinders and Louwaars, 2002; Sperling and McGuire, 2010; Louwaars and De Boef, 2012; McGuire and Sperling, 2012). FSS utilization was then specified as 100 minus the percent households responding they used at least some seed recognized as sourced through the formal system or as improved varieties.

This estimation provided a lower-level estimate of FSS utilization since, as mentioned above, the seed types recognized as certified and hybrid as well as improved or modern varieties can in fact be a part of FSS. Also, if any such seed types were utilized, then the household was characterized as non-FSS. The tendency in our methods to create a lower-level estimate of FSS was consistent with a focus on FSS functions that contain local and agrobio-diverse seed. Overall FSS utilization for each subnational administrative unit was calculated by incorporating the data across all crop types and taking the weighted average of the proportion of FSS for each specific crop. The

# Table 1. Socioeconomic, political, and environmental predictors of farmer's seed systems (FSS), hypothesized influence on the utilization of FSS and relevance to sustainable development derived from supporting research studies

Predictor Variable	Type of Variable	Hypothesized Effect on FSS Utilization (With Predicted Sign)	Concept and Con- text of the Predic- tor Variable (From Literature)	Relevance of FSS Variable to Justice- Based Sustainable Development	Supporting FSS Research (Case Studies and Overviews)
1. Mean farm area	Continuous	FSS common among larger size producers within smallholder category (+ within smallholder category)	Variation of FSS utilization within the heterogeneous category of small- scale farmers (smallholders)	FSS-utilizing smallholders vulnerable to COVID-19 pandemic, climate change, and development failure such as food insecurity	Almekinders (1994); Almekinders and Louwaars (2002); Etwire et al. (2016); McGuire and Sperling (2016); Nagarajan and Smale (2007); Wencélius et al. (2016)
2. GDP per capita	Continuous	Farmers in areas with lower values of socioeconomic resources rely more commonly on FSS utilization (–)	Potential interaction effects with farm area associated with development change (e.g., part- time farming)	Poor farmer reliance on FSS in multiple strategies, including food and nutrition security, and in specific responses to climate change and COVID-19	Etwire et al. (2016); Stromberg et al. (2010); Tadesse et al. (2017); Wencélius et al. (2016); Zimmerer (1991, 1996, 2003)
3. Distance from major large city	Continuous	Farm area at larger distances from major cities rely more commonly on FSS (+)	Periurban and short- distance rural areas less well-known since case studies and overviews to- date focus on conventional rural areas	Distance from major city can be associated with differing levels of need for FSS seed aid and support of rural return migrants in contexts such as the COVID-19 pandemic	Coulibaly et al. (2014); McGuire and Sperling (2013); Mulesa et al. (2021); Nagarajan and Smale (2007); Sperling et al. (2020a); Stromberg et al. (2010); Wencélius et al. (2016); Zimmerer et al. (2022a)
4. Type of major food crop	Categorical	Crop breeding system and influence of non-FSS seed sector contribute to higher or lower FSS (±)	Complex webs of institutional, economic, and political influence on seed development and non-FSS versus FSS determinants in major crops	FSS utilization in major crop types and sources of local food sources in need of multicrop comparison across global regions	Almekinders et al. (1994); Almekinders et al. (2019b); Bellon et al. (2011); Forbes et al. (2020); Garine et al. (2018); de Haan and Thiele (2005); Hoogendoorn et al. (2018); McGuire and Sperling (2016)
5. Aridity Index	Continuous	Farmers in more arid areas rely to a distinct degree (either more or less commonly) on the utilization of FSS (±)	Basic research needed since FSS utilization has not yet been analyzed across aridity gradients	higher aridity, such as occurs more widely and frequently under climate change, exerts impacts that can either rely on FSS utilization (if adaptive capacity exists) or,	Acevedo et al. (2020); Bellon et al. (2011); Kansiime and Mastenbroek (2016); McGuire (2007); Nagarajan and Smale (2007); Otieno et al. (2021); Ravera et al. (2019); Waldman et al.

(continued)

Predictor Variable	Type of Variable	Hypothesized Effect on FSS Utilization (With Predicted Sign)	Concept and Con- text of the Predic- tor Variable (From Literature)	Relevance of FSS Variable to Justice- Based Sustainable Development	Supporting FSS Research (Case Studies and Overviews)
				alternatively, expand non-FSS utilization	(2017); Westengen and Brysting (2014); Westengen et al. (2019)
6. Elevation	Continuous	Farmers in environments at higher elevations rely more commonly on the utilization of FSS (+)	Research needed on FSS utilization across elevation gradients in multiple world regions	Agriculture at higher elevations, such as occurs under climate change, can exert influence associated with either low or high levels of FSS utilization	Arce et al. (2018); Bellon et al. (2011); Bisht et al. (2007); de Haan and Thiele (2005); Samberg et al. (2013); Zimmerer (2003)
7. Variation of topography (rugged- ness)	Continuous	Farmers in areas with more rugged topographic conditions rely more extensively on FSS and, in the case of seed aid, require FSS- sensitive interventions (+)	Basic research needed since FSS utilization has not yet been analyzed across gradients of topographic variation (ruggedness)	Rugged topography can influence the types of locally suitable crop species and varieties; can also influence the feasibility and type of seed and food aid in contexts such as the COVID- 19 pandemic	Arce et al. (2018); Bisht et al. (2007); de Haan and Thiele (2005); Hellin et al. (2014); Samberg et al. (2013); Zimmerer (2003)

#### Table 1. (continued)

weighted average was calculated as the proportion of farms growing the specific crop in the subnational district.

Mean arable farm area (Ha) was estimated as a predictive factor (detailed conceptualization of this factor and others in Table 1) using the national surveys by dividing the estimate of arable farm area across the surveyed district by the number of surveyed farms. Additional spatial, socioeconomic, political, and ecological predictors were estimated for each of the districts in the 11-country sample. Per-capita GDP of districts was estimated in US\$ as mean purchasing power parity (PPP) using data from the Organisation for Economic Co-operation and Development, World Bank, and national sources. These were adjusted to 2011 value as a standardized time point representing the mean date of the agricultural survey and census data, by using the annual trends in national-level, percapita GDP (World Bank, 2016). We assessed distance from the nearest large city by spatially determining the centroids of district polygons in a Universal Transverse Mercator projection using QGIS open-source software and then calculating the Euclidean distance in kilometer to the nearest city with a population greater than 500,000 persons.

Mean elevation and mean topographic ruggedness index (Riley et al., 1999) were also calculated over each

district polygon using QGIS software and the NASA Shuttle Radar Topography Mission digital elevation model data at 500-m resolution. Aridity index (AI), an integrated measure of rainfall and evapotranspiration potential of climate that assesses drought stress on agriculture, land use, and natural vegetation, was assessed as the average value for each district polygon using the CGIAR Global Aridity and Global Potential Evapotransporation (PET) databases (https://cgiarcsi.community/data/globalaridity-and-pet-database/).

Multiple linear regression was used as the principal approach to analyze the relationship of FSS utilization to hypothesized predictor variables (**Table 1**). Methodologically similar approaches to the spatial-demographic analysis of environmental and agricultural outcome variables include Hird and Reese (1998), Hubal et al. (2022), and Zheng et al. (2021). We used this approach to assess the potential relation of FSS utilization at the district level to mean farm area as a factor emphasized in the thematic and case study-based literature (**Table 1**), while controlling for the district-level effects of per-capita GDP, distance to larger cities, aridity, elevation, and ruggedness. Added variable plots (Gallup, 2020), also called partial regression plots, were created for these geographic and climate covariates to examine their effects on FSS utilization while

Country	Survey Date	Survey and Census Sources for FSS Estimation	Districts Per Country	Individual Crops or Combined	Seed Categories in Survey or Cen- sus (FSS Marked With *)	Estimated Rural Popula- tion in 2011 (1,000s)	Mean FSS Proportion Across Dis- tricts (%)	Estimated FSS Users in 2011 (1,000s)
Ethiopia	2013	ETHIOPIA. (1995–present). Agricultural sample survey. Volume I. Addis Ababa, Central Statistical Authority.	40	Combined	"Improved" versus "indigenous"*	74,076	82.7	61,261
Uganda	2008	https://www.ubos.org/wp-content/ uploads/publications/03_ 2018UCACrop.pdf	10	Combined	"Improved" versus "traditional"*	28,110	79.0	22,198
Rwanda	2008	https://www.statistics.gov.rw/ publication/national-agricultural- survey-report-nas-2008	30	Combined	"Improved" versus "common"*	8,735	89.6	7,825
Nepal	2012	https://nada.cbs.gov.np/index.php/ catalog/53/study-description	75	Potatoes, maize, wheat, and rice	"Improved" and "hybrid" versus "local"*	22,652	73.5	16,653
Laos	2011	http://www.fao.org/fileadmin/ templates/ess/ess_test_folder/ World_Census_Agriculture/Country_ info_2010/Reports/Reports_4/LAO_ ENG_REP_2010-2011.pdf	17	Rice	"Improved" versus "local"*	4,391	65.2	2,862
Cambodia	2013	https://microdata.nis.gov.kh/index. php/catalog/29	20	Rice	"High yielding variety" versus "local variety"*	11,534	80.7	9,303
Colombia	2011	https://dane.gov.co; data collection for FSS utilization undertaken via a microdata request fulfilled by DANE-Colombia	13	Potatoes, maize, and beans	From formal supplier, certified and local market, not certified, versus from another producer and from own farm*	10,054	42.2	4,248
Peru	2012	http://censos.inei.gob.pe/cenagro/ tabulados/	14	Potatoes and maize	Based on classes of varieties distinguished in census	6,959	77.7	4,383
Ecuador	2013	https://www.ecuadorencifras.gob.ec/ encuesta-de-superficie-y-produccion- agropecuaria-continua-espac-2013/	23	Potatoes, maize, and beans	"Certified" and "improved" versus "common"*	5,638	49.5	3,444

Table 2. Information on farmers' seed systems (FSS) in the subnational administrative districts of 11 sampled countries in tropical and subtropical mountain regions of Africa, Asia, and Latin America (all estimates from sources as shown)

(continued)

Country	Survey Date	Survey and Census Sources for FSS Estimation	Districts Per Country	Individual Crops or Combined	Seed Categories in Survey or Census (FSS Marked With *)	Estimated Rural Popula- tion in 2011 (1,000s)	Mean FSS Proportion Across Dis- tricts (%)	Estimated FSS Users in 2011 (1,000s)
Nicaragua	2011	https://www.inide.gob.ni/Home/ dataBasesCENAGRO	14	Combined	Improved, certified, versus "criolla" (common or mixed)*	2,491	80.0	1,993
Bolivia	2013	http://anda.ine.gob.bo/index.php/ catalog/24/related-materials	6	Combined	"Certified" and "improved" versus "common"*	3,339	72.5	2,422
Totals			265			177,979		136,592

(continued)
2.
Table

	Sample Size ( <i>n</i> )	Range	Median	Mean	Standard Deviation
Independent variable					
FSS utilization	265	1.0–99.5	78.7	73.9	19.5
Farm size (Ha)	265	0.08-23.8	0.99	1.83	2.41
GDP per capita (US\$)	265	210–27,261	1,764	2,966	3,302
Distance from major city (km)	265	3–987	201	231	166
Aridity index (0–2.5)	265	0.04-2.22	0.95	0.96	0.38
Elevation (masl)-All countries	265	9–4,840	1,412	1,409	1,032
Elevation (masl)-Andean countries	63	58–3,936	1,609	1,676	1,146
Elevation (masl)-Africa	95	475–2,428	1,715	1,659	387
Elevation (masl)-Asia	117	9–4,840	746	1,176	1,247
Ruggedness (index, 0 to $\sim$ 150)	265	3–145	46	54	37
Percent FSS Use, By Crop					
Rice	117	17.7–98.7	81.2	77.4	16.1
Maize	138	1.0–99.0	81.1	71.0	26.8
Potatoes	112	7.7-100.0	76.0	68.9	24.7
Beans	22	33.0–98.1	88.1	78.2	20.2
Wheat	75	30.7–99.4	75.8	73.4	16.3
All crops	265	1.0–99.5	78.7	74.0	19.5

T	able	3. Descriptive	statistics f	or variables i	n this stu	idy's mode	l of the	utilization	of farmer's s	eed system
(1	FSS)	at the subnati	onal distric	t level of 11	countries					

n = number of districts.

controlling for the other predictors in the model. The interaction terms of mean farm area with world region and GDP per capita were assessed for significance since these combined effects can potentially influence FSS utilization (Delaguis and Almekinders, 2020). When the hypothesized variables were statistically insignificant (P > 0.15), they were removed from the model. The Akaike (1981) information criterion (AIC) was used to assess the addition of each term to this model to avoid overfitting (addition of terms stopped at the minimum AIC). The potential geopolitical influence of global region (Africa, Asia, and Latin America) was included in the models as a categorical term. In addition, the dependent variable of percent FSS-utilization was arcsine-square root transformed for assessing the significance of model terms to adjust for inhomogeneity of variance with data points clustered near to 100% FSS utilization.

The first regression analysis was conducted using survey data on the combination of all crops. A second analysis was completed using only the surveys with crop-specific data (**Table 2**) to examine whether there were any significant differences in FSS utilization among globally common staple food crops. Continuous predictors were assessed for significance using *P* values, while differences among categories such as crop types were assessed using Tukey tests for multiple simultaneous comparisons among all levels. Analysis focused on linear relationships as a first estimation of the relationships between potential drivers

and FSS utilization. The effect size of these linear trends was also assessed using standardized  $\beta$  coefficients with a heuristic for the effect size of  $\beta$  coefficients (Acock, 2014):  $\beta^* < 0.2$ , weak,  $\beta^*$  between 0.2 and 0.5, moderate, and  $\beta^* > 0.5$ , strong. Partial regression plots based on the overall regression analysis were used to visualize these linear relationships.

In addition to multiple linear regression, a betweenclass principal components analysis (BCA, Chessel et al., 2004) was used to visualize both linkages of FSS to different predictors and overall differences in these predictors among the 3 global regions that were examined in the study. After initial principal components analysis, BCA was used to rotate the ordination analysis to maximize variability among classes—in this case, the 3 world regions thus permitting a visualization of differences in relation to the combined predictor and response variables. This analysis was designed to yield results suited to visualization as a biplot of the first 2 components of variability created by this rotation. For the BCA analysis, variables with skewed distributions were transformed to better satisfy the requirements of normality.

### 4. Results

### *4.1. Multifactor model accounts for the majority of FSS variability across 11 countries*

**Table 3** gives the summary values and variation that are the results of the broad-scale modeling of FSS-utilization

			Ove	erall <i>P</i> Value	Variation Explained
Overall Multiple Linear Regression Model Results         P <		< 0.0001	$R^2 = 0.53$		
Predictor	Parameter Estimate	Units of Parameter	Effect Significance (P Value)	Magnitude of Change Over Min to Max of Predictor	Standardized β* Coefficients for Continuous, Linear Predictors
Farm size	- 17.9%	% Seed use/ LOG <sub>10</sub> (Ha) of farm area	<i>P</i> < 0.0001	-52.5%	-0.29
World region	- (categorical)	_	<i>P</i> < 0.0001	_	_
Farm area $ imes$ world region	– (interaction)	-	<i>P</i> < 0.001	_	-
GDP per capita (GDP as PPP US\$/yr.)	-14.0%	% Seed use/LOG <sub>10</sub> (per capita GDP)	<i>P</i> < 0.0001	-24.4%	-0.19
Farm area $\times$ GDP per capita	— (interaction term)	-	<i>P</i> < 0.0001	_	
Distance to nearest major city (>500,000 inhabitants)	-2.0%	% Seed use per 100 km distance	<i>P</i> < 0.001	-18.7%	-0.12
Aridity index	-13.4%	% Seed use per index unit change	<i>P</i> < 0.0001	-27.0%	-0.21
Elevation (all countries)	-2.0%	% Seed use per 1,000 masl	P = 0.12 NS	_	-0.10
Topographic variation/ ruggedness	0.147%	% Seed use per change in index (range is 0 to $\sim$ 140)	P = 0.0073	+19.7%	0.28
Elevation (Andean countries <sup>a</sup> )	7.8%	% Seed use per 1,000 masl	P = 0.008	+33.4%	0.27

### Table 4. Parameter estimates, significance, range, and effect-size measure ( $\beta^*$ coefficient) for model of farmer seed system (FSS) utilization in 11 countries of Africa, Asia, and Latin America

All predictors except for the elevation variable when applied separately to the 4 Andean countries were used within a single multiple linear regression to explain the dependent variable of percentage utilization of FSS.

<sup>a</sup>A separate regression analysis was conducted using only the Andean countries in the database to relate FSS utilization to the mean elevation of subnational districts.

and the predictor factors derived from data on 265 subnational administrative districts (hereafter districts) in 11 tropical and subtropical mountain countries of Africa, Asia, and Latin America. This global modeling of socioeconomic, political, and environmental factors demonstrated distinctive values and large ranges of these parameters across districts as well as specific subsets analyzed at the crop level and world region level (**Table 3**). With an  $R^2$ value of 0.53 and P < 0.0001, the overall model accounted for more than one half the variation in district-level FSS utilization across all districts of the 11 countries and 3 global regions (multiple regression results, **Table 4**). FSS utilization displayed distinct, significant statistical relationships with several predictor factors (**Table 4**), each described briefly in the following.

### 4.2. Farm area explains a significant proportion of the variability of FSS utilization

Low values of mean farm area characterized most districts across the sampled countries and global regions. Median and mean values were 0.99 hectares and 1.83 hectares, respectively (**Table 3**). Large divergences between mean and median farm-area values in addition to GDP per capita (reported in the following) reflected the skewed distributions of these district-level indicators of farm resources. Regression analysis showed the inverse relation of FSS utilization to mean farm area that was highly significant across countries and world regions (P < 0.0001, **Table 4**). Maximum FSS utilization was characteristic of the districts with the lowest values of mean farm areas (<1.0 hectares; **Figure 1a**). The axis showing mean farm area has been set



**Figure 1. Utilization of farmers' seed systems (FSS) in relation to (a) mean farm area and (b) interactions with global region.** Two plots showing the relationship of the utilization of FSS to mean farm area in 265 subnational administrative districts of 11 countries in Africa (Ethiopia, Rwanda, and Uganda), Asia (Cambodia, Laos, and Nepal), and Latin America (Bolivia, Colombia, Ecuador, Nicaragua, and Peru). Vertical lines represent the thresholds of mean farm areas of <1.0 Ha (small), between 1.0 and 5.0 Ha (medium), and >5.0 Ha for slightly larger mean farm areas. (a) Graph showing overall relationship and countries as indicated, as well as an overall fit line and  $R^2$  value for the overall trend. (b) Graph showing data categorized by global region, with trend lines for each region as well as region means (large diamond markers) and standard deviations indicated by error bars. Each point represents a district.

to display a log scale to visualize the low values below 1.0 hectares and between 1.0 and 5.0 hectares.

FSS utilization declined by 52.5% across the range of mean farm areas (**Table 4**), while the rate of this decline was just under 18% with each  $\log_{10}(Ha)$  change of farm area (**Table 4**). Even districts with values of mean farm areas that categorized as medium (1.0–5.0 hectares) demonstrated the predominant utilization of FSS. The prevalence of FSS is also notable, where mean farm areas are slightly larger than 5.0 hectares (**Figure 1a**). As a single predictor omitting other factors in the regression model, mean farm area accounted for approximately 22% of the variability of FSS utilization across the data set ( $R^2 = 0.217$ , **Figure 1a**). Within the overall linear regression, meanwhile, the effect of mean farm area on FSS utilization was moderately strong in terms of its standardized beta coefficient ( $\beta^* = -0.29$ , **Table 4**).

### 4.3. Global regions (Africa, Asia, and Latin America) differ significantly in FSS—farm area relationship

Regression analysis demonstrated that the relation of FSS utilization to mean farm area varied to a highly significant degree among the countries in Africa, Asia, and Latin America (P < 0.0001, **Table 4**). Equally significant was the interaction of world region with the values of the mean farm areas of districts (P < 0.001, **Table 4**; noting the farm area × world region interaction term), with FSS utilization typically the most high in the African countries followed by those of Asia and Latin America (**Figure 1b**; crosshair plots around the regional mean values; see also the alignment of African countries with maximum FSS utilization in Figure 5). **Figure 1b** highlights the steeper rates of FSS decline with estimated mean farm areas in districts of the countries of Africa (Ethiopia, Uganda, and Rwanda) and

Latin America (Colombia, Peru, Ecuador, Nicaragua, and Bolivia) compared to Asia (Nepal, Laos, and Cambodia).

### 4.4. Per-capita GDP adds significantly to explanation of FSS utilization

GDP per capita annually, estimated as PPP (see Methods), is characterized by a wide range of mean values in the sampled districts (US\$210–US\$27,261 per year: Table 2). The commonness of low values (mean US\$1,764 and median US\$2,966 per year; Table 3) reflects the characteristic, widespread poverty levels of tropical and subtropical mountain countries. LOG<sub>10</sub> transformation highlights this prevalence of low GDP per capita as clustered values at the left and middle of the plot (Figure 2a; note skewed distribution of GDP per capita as seen in difference of median and mean values in Table 3). FSS utilization declined in a highly significant way at the rate of 14.0%per LOG<sub>10</sub>(GDP per capita/yr; P < 0.0001; **Table 4**). A partial regression plot allows visualization of this FSSutilization decline with increased income levels (Figure 2a). This analysis, which controls for other predictive factors in the model, estimates the effect size of GDP per capita as near-moderate strength ( $\beta^* = -0.19$ ; **Table 4**).

The significant interaction of mean farm area and GDP per capita in association with FSS utilization (*P* < 0.0001, **Table 4**) was visualized through the comparison of districts with low and high values of low-capita GDP, in combination with low and high mean farm areas (**Figure 3**). Examples of low GDP per-capita units in the sample were Potosi and Beni in Bolivia; the Ngetta and Serere zones of north-central Uganda; Nariño and Cauca in Colombia; Xayabury, Luang Prabang, Phongsaly in northern Laos; and Huancavelica, Ayacucho, Huánuco, and Apurimac in Peru. Examples of high GDP per-capita units in the sample were



**Figure 2. Utilization of farmers' seed system (FSS) in relation to (a) GDP per capita, (b) distance to major city, (c) Aridity index, and (d) topographic ruggedness.** These graphs are added-variable (partial regression) plots for the regression model of the utilization of Farmers' Seed System (FSS) related to (a) per-capita GDP, (b) distance to major city (population >500,000), (c) Aridity index, in which arid-to-humid climates appear from left to right on the graph, and (d) topographic ruggedness, in which higher values are more topographically varied. See text for full definitions of variables. The partial regression plot indicates the variability associated with each predictor, controlling for other predictors in the multiple regression. Partial regression plots were created in which the adjusted values on the *x*-axis display the residual variability of the predictor variable regressed against all the other variables in the model and the adjusted values on the *y*-axis display the residual variability for FSS utilization for a model including all the variables except the predictor in question. The graphs are based on data from 265 subnational administrative districts in total of 11 countries of Africa (Ethiopia, Rwanda, and Uganda), Asia (Cambodia, Laos, and Nepal), and Latin America (Bolivia, Colombia, Ecuador, Nicaragua, and Peru). Each point represents a district.

Tarija in Bolivia, Valle de Cauca and Antioquia in Colombia, Mbarara district in Uganda, and Vientiane in Lao.

The visualization in **Figure 3** uses the 20th and 80th percentile of both GDP per capita and mean farm area as representing high and low values. **Figure 3** demonstrates that in the districts with relatively high values of mean farm area, the districts with high and low GDP per capita diverged significantly in terms of FSS utilization. Districts distinguished by the combination of larger mean values of farm areas and lower GDP per capita were found to have relatively higher levels of FSS utilization than those with

the combination of larger farms and higher GDP per capita (**Figure 3**).

## 4.5. Urbanization effects are related positively and significantly to FSS utilization

Estimated spatial distance of the district to the nearest major city with more than 500,000 inhabitants ranged from locations in proximity (3 km) to extremely distant (987 km; **Table 3**). Utilization of FSS corresponded inversely to this distance in a significant fashion (P < 0.001; **Figure 2b**). This FSS decline was estimated at the



**Figure 3. Interaction effect of the mean farm area of districts and the GDP per capita on the utilization of farmers' seed systems (FSS).** Interaction plot of the combined influence of the mean farm area and GDP per capita on FSS in districts of the 11-country sample of the global regions of Africa, Asia, and Latin America. The mean farm area and mean GDP per capita are set at low (20th percentile) and high (80th percentile) levels within the data set statistical model fit to evaluate effects at different rates of utilization.

rate of 2.0% of decreased FSS utilization with each 100 km of distance from the nearest major city (**Figure 2b**). This minor rate of decline meant that FSS utilization was slightly higher in the near-city districts located in periurban spaces, whereas FSS exhibited levels approximately 18.7% lower in the most remote districts that were characterized by the greatest distance from cities (**Table 4**). Although significant, distance to the nearest major city exerted standardized effect size that was relatively small ( $\beta^* = 0.12$ ; **Table 4**).

## 4.6. Crop type significantly influences FSS utilization

The mean rates of FSS utilization were determined to be high in each of the five major food crops (rice, wheat, maize, potato, and common bean) that were distinguished in the agricultural surveys and reports. The highest rates of FSS utilization characterized common beans (**Table 3**). Rank orders of FSS utilization in the five food crops were similar in value but not identical in the estimated ranges of both median values (75.8%–88.1%) and mean values (76.0%–78.2%; see the last 5 rows, **Table 3**). A separate regression analysis of FSS utilization applying crop type as a predictor showed that small yet significant variation of FSS utilization was found among the crops (P < 0.0001, Supplemental Table S1), with common bean and maize higher than potato and wheat, while rice was intermediate (means differentiation with Tukey's test at  $\alpha = 0.05$ ).

#### 4.7. Aridity correlates with higher FSS utilization

The estimated values of the AI in the sampled districts ranged from near zero (hyperarid climate) to 2.22 (high year-round rainfall and humidity) across the districts in the sample (**Table 3**). FSS utilization declined by 27% across this range in effective rainfall, being highest in districts of the lowest AI values (i.e., most arid climate; **Figure 2c**). Increased aridity, represented by smaller values of the AI, was shown to be significantly associated with higher FSS utilization (P < 0.0001, **Table 4**) and had a moderately strong effect size ( $\beta^* = -0.21$ ; **Table 4**). The value of this parameter was estimated as -13.4% of FSS per unit of AI.



Figure 4. Utilization of farmers' seed systems (FSS) in relation to elevation in Andean countries (Colombia, Peru, Ecuador, and Bolivia). Plots showing the utilization of FSS in relation to elevation in Andean countries (Bolivia, Colombia, Ecuador, and Peru): (a) partial regression plot showing the variability of elevation only, controlling for all other predictors in a multiple regression; (b) relationship of original elevation data and FSS utilization controlling for other predictors. Each point represents a district.

#### 4.8. Elevation relates to higher FSS utilization in Andean subsample, but not across the full sample

Mean and median elevation values (1,412 and 1,409 m above sea level, respectively) characterized mountain environments of sampled districts (Table 3). While FSS utilization did not vary significantly with elevation when considering the full model of 11 countries in three global regions (Table 4), the analysis of this relation in a subsample of the countries of the Andes Mountains (Bolivia, Colombia, Ecuador, and Peru) was undertaken because of the wide elevation ranges characterizing multiple crops and countries in this region.<sup>1</sup> The FSS-elevation relation showed significant statistical variation across crops in this subset of the Andean countries (P = 0.008; Table **4**). The standardized effect size of elevation as a predictor was moderate in this subset of countries ( $\beta^* = 0.27$ ; Table 4), where mean FSS-utilization increased more than 30% from near sea level to nearly 4,000 masl (Table 4: Figure 4).

# *4.9.* Topographic ruggedness significantly strengthens the model's prediction of FSS utilization

Values of topographic variation reflected in the index of topographic ruggedness were found to range widely from 3.1 (nearly flat) to 145 (extremely rugged topography such as in the high valleys of Nepal) in the sampled districts (**Table 3**). FSS utilization showed statistically significant increase with topographic ruggedness at

a per-unit rate of 0.147% (P = 0.007; **Table 4**). The partial regression plot of FSS to ruggedness values in **Figure 2d**, controlling for other factors, indicates district-level values that are distributed widely in relation to different degrees of varied topography. Overall, the effect size of this predictor factor is moderately strong ( $\beta^* = 0.28$ ; **Table 4**).

## 4.10. Clustering occurs among predictor variables and global regions in explaining FSS utilization

Between-class PCA analysis of the six predictor factors possessing continuous variables in addition to the dependent variable of FSS utilization showed degrees of relatedness and global-region level clustering in Figure 5. This analysis visualizes predictor and response variables as vectors within the two-dimensional plot. Districts are shown as the data points that are grouped by world region. Proximity of districts and world regions to vectors denotes influential variables. As shown in Figure 5, the socioeconomic and political factors of mean farm area and GDP per capita were most related to one another in the most important first axis of variation (Figure 5, horizontal axis or PC1), and in opposition to FSS utilization, as displayed in the lower left quadrant. In other words, mean farm area and GDP per capita were the most important clustered predictors explaining FSSutilization among global world regions.

The environmental factors representing by the mean values of ruggedness, elevation, and aridity were aligned with a second axis of variation (**Figure 5**, vertical axis or PC2). A correlation matrix shows *r* values among the 6 factors (Supplemental Table S2). The between-class PCA analysis most strongly distinguished between the

<sup>1.</sup> By contrast, the range of elevation is less in scope in the sample of African countries; in Asia, only one country shows a wide range of elevation (Nepal).



Figure 5. Between-class principal components analysis (BCA) of farmers' seed systems (FSS) model variables in relation to global regions of Africa, Asia, and Latin America. This graph shows the BCA of the FSS model variables used in this study in relation to world region (Africa, Asia, and Latin America). The first two principal components of variation in the 7 variables (PC 1 and PC2) are rotated to maximize the separation of the 3 regional classes. The BCA is based on data from 265 subnational districts in 11 countries of Africa (Ethiopia, Rwanda, and Uganda), Asia (Cambodia, Laos, and Nepal), and Latin America (Bolivia, Colombia, Ecuador, Nicaragua, and Peru). Each point represents a district.

countries of Latin America and those of Africa with the Asian countries as intermediate (**Figure 5**). The differentiation of these global regions in the multivariate ordination was statistically confirmed at a level of P < 0.001 by the result of a Monte-Carlo test using the ADE 4 package of the R statistical platform.

### 5. Discussion

### 5.1. FSS global modeling is strategically situated and shows robust results in research comparisons

This section uses the insights of our FSS results to (1) situate results in the existing FSS research (including the

closely related research on informal, local, and traditional seed systems); (2) interpret the FSS-related mechanisms and processes contributing to the FSS results; (3) discuss how to strengthen FSS, including policy and program recommendations, using this study's insights; and (4) use results to reflect on FSS capacities to address the current issues of justice-based sustainable development, climate change, and the COVID-19 pandemic/postpandemic.

Overall, this study is situated in a vibrant, rapidly expanding research community—both highly interdisciplinary and notably transdisciplinary—on FSS in agriculture, land use, and food systems. This study made use of 100+ works that were referenced in the first 2 sections alone of this study. These works abound with contributions to multiple facets of sustainable development (e.g., SDGs 1, 2, 3, 5, 10, 15, 16) and powerful synergies with social justice. Moreover, this study's socioeconomic, political, and environmental model was robust in explaining substantial variability in FSS utilization ( $R^2 = 0.53$ ; P < 0.0001). This explanatory level equals and exceeds the existing FSS case-study models of household-level FSS utilization (Wencélius et al., 2016) and non-FSS variety adoption (Okello et al., 2016). This study's FSS model and analysis thus contribute the first large-scale modeling of FSS utilization in countries across multiple global regions.

### 5.2. FSS serve a dominant proportion of smallholder subgroups across the global sample and concentrate among often-overlooked smallest farms and women-headed households

This study demonstrated high FSS utilization among the heterogeneous group of famers referred to generically as smallholders whose populations predominate in the 11country sample of tropical and subtropical mountain countries representing the global regions of Africa, Asia, and Latin America. Generally distinguished as farms less than 5.0 hectares (Berdegué and Fuentealba, 2011; Zimmerer et al., 2015), smallholders are globally central to sustainable development given their social-ecological and demographic importance (Gill et al., 2013; Scoones et al., 2018) as well as key functions and adaptive capacities (e.g., climate change; Acevedo et al., 2020). This study's identification of the predominance of FSS-utilizing smallholders aligns with the dominance of smallholders, including many women-headed households, among the 1.5-2.0 billion persons employed in agriculture that are categorized as extremely small scale (<2.0 hectares). It also corresponds to many of the 1.1 billion persons living in moderate or extreme poverty while working in agriculture and the additional 119-163 million persons impoverished by COVID-19 pandemic-related shocks (Rapsomanikis, 2015; Zimmerer et al., 2015; Castañeda et al., 2018; Lakner et al., 2021).

Globally, the prevalence of FSS-136 million farmers are estimated in the 11-country sample of this study (Table 2)—combines with the extreme social and ecological precarity and widespread importance of smallholder populations including many women-headed households. These conditions urge the prioritization and fast-track development of policies and programs to strengthen FSS among these populations. Specific insights below detail these insights. Moreover, our findings recommend that the strengthening of smallholder FSS become a foundation for understanding and assessing new biotechnology impacts including the potentially expanding and quickly evolving biotechnology impacts of genetically modified and gene-edited seeds (Scurrah et al., 2008; Mercer et al., 2012; Montenegro de Wit, 2019; Visser et al., 2019; Montenegro de Wit et al., 2020; Rock et al., 2023). Specifically, results highlight that biosafety risks may potentially become concentrated among FSS-utilizing places and households, which in many cases will include severely land-poor and highly vulnerable populations (see the following discussion).

Results of this study demonstrated the preponderance of FSS utilization in districts characterized by the smallest farms (mean farm area <0.5 hectares) in each of the studied countries and global regions (Figure 1a and 1b; Tables 2 and 3). These results contradict the study's hypothesis (Table 1) of predicted variability in FSS-farm area relations associated with the range of landholding sizes in smallholder agriculture and land use. Studies to-date generally recognize FSS (including informal, local, and traditional seed systems) as crucial to smallholders en toto and vice versa (Almekinders and Louwaars, 2002; Etwire et al., 2016; McGuire and Sperling, 2016). But the existing studies focused on farm extent have tended to emphasize the role of smallholders with relatively medium-size and larger landholdings due to their importance to FSS production, distribution, and networks (Almekinders, 1994; Nagarajan and Smale, 2007; Wencélius et al., 2016). This study's results therefore offer a novel insight on the most highly concentrated importance of FSS for the populations of smallholders that are extremely land poor and economically marginalized (see the following).

Consideration of potential mechanisms leading to these results on FSS relations to farm area suggests a pair of predominant processes. First, the widespread and extreme poverty of districts populated by those with the lowest values of farm area often restricts access to seed other than FSS since the latter is typically most affordable and available. This factor was most probably a principal mechanism behind this study's finding of district-level differences revealing the within-smallholder variability of FSS-utilization rates. Influences likely impacting the places with populations having somewhat higher values of mean farm area (e.g., mean farm area >5.0 hectares) presumably included production characteristics such as increased use of agricultural machinery and other input technologies that can result in reduced FSS utilization.

This study's FSS-farm area results provide key insights to strengthen FSS policies and programs. FSS utilization across smallholder populations is aligned with broadbased international legal frameworks and global smallholder social movements supporting FSS such as the 2018 Peasant Rights Declaration and Via Campesina. At the same time, concentrated FSS utilization in districts characterized by populations with the lowest values of mean farm area and often most gendered and extreme poverty indicates the need to strengthen their capacities using collective-action initiatives and inclusive pro-poor policy and sustainability approaches (McGuire and Sperling, 2016). FSS seed and care initiatives (such as seed-andcooking groups) need to tailor approaches for the extreme resource poverty and social-ecological vulnerability of subgroups (Healy and Dawson, 2019; Mulesa et al., 2021), rather than assuming generalizable capacities of broad social categories such as smallholders sui generis.

Additional insight to strengthen FSS stems from the finding on 60% or more FSS utilization characterizing

districts with mean values of smallholder farm areas as large as 5.0 hectares. These districts often represent concentrated farming populations of relatively powerful social actors that can promote FSS utilization and leverage benefits economically and politically (Etwire et al., 2016). Therefore, one policy challenge to strengthen FSS is to harness the capacities of this subgroup while supporting the more concentrated FSS utilization of places with populations characterized by the smallest-scale and often poorest producers.

# 5.3. Differences of FSS-farm area relations among global regions suggest correspondence to capital intensity and labor availability

Results on the geographic dimensions of the FSS relation to mean farm area indicate significant differences among the geopolitically designated global regions (Figure 1b). The highest FSS rates associated with districts having the lowest values of mean farm area occurred among the smallholder populations in the African countries of this study's analysis (90%–95% in Ethiopia, Uganda, Rwanda, and Figure 1b; see also Scoones and Thompson, 2011; McGuire and Sperling, 2016). Lesser though still high rates of FSS utilization were similar among the lowest value, farm-areas districts (70%-75% in **Figure 1b**) in the countries of Asia (Nepal, Laos, and Cambodia: see also Gill et al., 2013: Delaguis et al., 2018) and Latin America (Colombia, Peru, Ecuador, Nicaragua, and Bolivia; see also Bellon et al., 2005; de Haan and Thiele, 2005). This result is interpreted as documenting the general importance of FSS among smallholder populations that is globally widespread yet significantly varied among these three global, geopolitical regions.

Moreover, the distinctness of the overall shapes of FSSfarm area relations as displayed in the three curves of Figure 1b (Africa, Asia, and Latin America) is interpreted to reflect the variation of global region-level influences of capital intensity and labor availability. Agriculture in districts with the higher values of mean farm area that are common in Latin America, for example, are usually characterized by relatively higher capital intensity (e.g., farm machinery) and less labor availability. This difference is interpreted as a geopolitical-historical influence of colonial latifundia in Latin America, in which the present-day prominence of large landholdings is seen in the prevalence of mean farm areas >5.0 hectares in Figure 1b. It contributes to Latin America's steeper drop-off of FSS utilization in the districts with higher values of mean farm areas (Figure 1b). By contrast, high FSS-utilization rates are maintained in districts with greater values of mean farm area in Africa and Asia (Figure 1b). The latter reflect a reduced degree of the political-historical impact of settler colonialism. Strengthening the policies and programs of FSS requires understanding its distinct relations to land resources and access in each global region.

Finally, results on the widespread geographic occurrence of high FSS highlight the potential viability of FSS-utilizing connectivity approaches to support sustainable development and pro-poor climate resilience through medium- and long-distance seed flows (Zimmerer, 2003; van Etten and de Bruin, 2007; Chambers and Brush, 2010; Wencélius et al., 2016; Garine et al., 2018; Porcuna-Ferrer et al., 2020; Sperling et al., 2020b; Labeyrie, 2021; Otieno et al., 2021; Zimmerer et al., 2022a). Strengthening crossdistrict FSS connectivity at landscape, region, multicommunity, and village-area scales needs to become an FSS policy priority to address development and climatechange challenges (described further below). This study's results on multidistrict FSS prevalence are evidence of strong existing viability of potential FSS connectivity initiatives at intermediate geographic scales that are needed to complement policy and program emphasis todate on local FSS spaces (e.g., individual community and agroecosystem) and national programs (Almekinders and Louwaars, 2002; Hodgkin et al., 2007; De Boef et al., 2010).

Variability in FSS-utilization relates to interactions of GDP per capita and mean farm area, highlighting distinct smallholder subgroups for FSS interventions and policy. Results demonstrating the significant correspondence of maximum FSS utilization to low GDP per capita (Table 3; Figure 2a) confirm this study's hypothesis (Table 1) and align with its findings on farm-area effects (see previous subsections). This study's results across global regions offer important similarities and differences in comparison to existing research case studies based on a single site or region. The latter are used here to reflect on FSS in relation to income (Etwire et al., 2016), wealth estimates (Tadesse et al., 2017), and socioeconomic status (Wencélius et al., 2016). Other case-study comparisons are drawn from research on FSS-based agrobiodiversity using income measures (Stromberg et al., 2010) and resource-level estimates (Zimmerer et al., 2019).

The above case studies show the important relations of FSS to individuals and groups of smallholders at the ends of the spectrum of extremely reduced and greater wealth and resource status. This study's results in **Figure 2a** are similar since there are several points showing the latter tendency (areas characterized by populations of greater GDP per capita related to greater FSS utilization) while they differ since the significant relation is toward the most concentrated FSS utilization at the lowest GDP levels. To strengthen FSS, these results counsel the importance of significant yet varied FSS utilization among districts characterized by subpopulations of smallholders whose percapita GDP ranges severalfold (**Table 3**; **Figure 2a**).

The interaction results highlight further dynamic influences of these first two predictive factors (mean farm area and GDP per capita; **Figure 3**). Divergence of their interaction occurs where higher than expected FSS utilization distinguishes the districts with combined low GDP per capita and relatively larger mean values farm areas. This combined effect can potentially strengthen FSS through further tailoring policies and programs to account for influential interactions.

#### 5.4. Novel results on the positive relation of urbanization to FSS reveal new insights and opportunities for policy and interventions

Urbanization-focused results demonstrating the inverse relation of FSS utilization to distance from the nearest major city (**Table 3**; **Figure 2b**) countervail the hypothesized higher rates of FSS utilization as urban proximity declines. These results reflect the important role of FSS markets and traders located in urban and periurban spaces, which has been described in case-study research (Nagarajan and Smale, 2007; Stromberg et al., 2010; McGuire and Sperling, 2013; Sperling et al., 2020a; Mulesa et al., 2021) and a recent urbanization-agrobiodiversity conceptual framework (Zimmerer et al., 2021).

These results can be interpreted to offer specific geographic recommendations for strengthening FSS in relation to urbanization. First, we interpret the influences of urbanization as a powerful force of global change that encompasses the extensive areal coverage of periurban spaces including large numbers of FSS-utilizing smallholders in mixed land use (Zimmerer et al., 2022a). Socialand political-ecological approaches for FSS support need to be expanded and modified to build a focus on these periurban spaces of mixed smallholder farming. Second, the sizeable concentration of FSS among smallholder farmers in closer proximity to urban areas suggests the important role of smallholders whose livelihoods are distinguished by part-time farming (on the increase and widespread importance of part-time farming to FSS; see Zimmerer et al., 2015; Arce et al., 2018). This result recommends new FSS-support and policies for smallholders in periurban and adjoining rural landscapes. Third, these urban-influenced populations of smallholders include social movements focused on FSS (e.g., the Red Andaluza de Semillas or Andalucian Seed Network, in southern Spain; Zimmerer et al., 2022a) that can offer new partnerships well-suited to the support of FSS policies, programs, and initiatives.

### 5.5. Extensive and varied FSS utilization in major foods underpins global food production (rice, wheat, maize, potato, and common bean)

This study's results on the rates of FSS utilization among five major types of food crops (rice, wheat, maize, potato, and common bean) offer a first comparative analysis using spatially extensive data from countries across multiple global regions. These results show predominant FSS utilization in each of these staple food sources, with high rates of FSS at approximately 75% and above. The geographic scope of the crop-type results representing three major global regions across the Global South is novel, building on existing crop-type comparisons of seed systems offered in multicountry studies in Sub-Saharan Africa and fieldbased, case-study and survey data (Almekinders et al., 1994; McGuire and Sperling, 2016; Garine et al., 2018). This study's focus on the FSS of multiple crop types further complements FSS research to-date on single-crop FSS. Finally, focus on major crops is a complement to FSS research on important, the so-called minor crops (also referred to as underutilized, and orphan crops; Mabhaudhi et al., 2019).

Based on the literature referenced above—see also row 4 in **Table 2**—this study's results on different FSS-utilization rates among crop types, especially common bean and potato, are interpreted to reflect factors of the

non-FSS seed sector (least influential in common bean) and crop breeding system (e.g., clonal and selfpollination in potato and common bean, respectively). Together, these factors contribute to our results that show relative rates of FSS as higher (common bean and potato), intermediate (rice), and lower (maize and wheat). These results suggest strengthening FSS by recognizing key variation and differentiated FSS dynamics among major foodcrop systems, including root and tuber crops such as potato (Bentley et al., 2018; Almekinders et al., 2019b). Our results highlight that the production of key nutritional crops such as common bean is highly dependent on FSS (Zimmerer et al., 2020). Also, crops such as maize can depend significantly on FSS in certain geographic areas such as tropical and subtropical mountain countries even though this crop is generally prone to lower FSS utilization rates (Hoogendoorn et al., 2018). These results can be used to strengthen FSS policies and programs through early-stage design that anticipates the influence on FSS of crop-specific variation.

#### 5.6. Aridity effects reveal FSS importance for climate-change policy and interventions

This study's result revealing the Aridity Index as a powerful predictor of FSS-utilization rates is interpreted to reflect a significant degree of environmental influence on FSS exerted through effective precipitation. This focus of our research is engaged with expanding studies on FSS-based responses to aridity-stressed conditions and climate change (McGuire, 2007; Nagarajan and Smale, 2007; Bellon et al., 2011; Westengen and Brysting, 2014; Kansiime and Mastenbroek, 2016; Waldman et al., 2017; Ravera et al., 2019; Westengen et al., 2019; Acevedo et al., 2020; Otieno et al., 2021). Our interpretation leads to specific recommendations to strengthen FSS for the purpose of enabling responses to climate change. These recommendations encompass both FSS-based agroecological adaptation as well as FSS-based accessibility and suitability that can contribute to seed, climate, and social justice called for in transitions and potential transformations of sustainable development.

The first recommendation is to urge strengthening FSS across the wide gradient of arid environments utilizing FSS-based smallholder varieties. Attention to FSS-related environmental gradients and varietal types can provide both local agrobiodiverse varieties (landraces) and ones adopted into FSS from the formal sector (Nagarajan and Smale, 2007; McGuire and Sperling, 2013; Croft et al., 2018). Strengthening FSS of this type can support innovations that include new varieties and social–ecological adaptation capacities (Teeken et al., 2012). Second, this result can strengthen FSS by illustrating the smallholder use of FSS-based varietal types of the major crop species. Support for this FSS usefulness can strengthen policies and programs for justice dimensions of climate change combined with seed and food security and sovereignty.

Finally, this result on the major role of FSS in arid environments and potential climate-change adaptation underscores the importance of supporting FSS capacities for medium- and long-distance seed exchange as well as potential population movements (Mwongera et al., 2014). Relatedly, the viability of FSS capacity at the extralocal scale is shown above in the subsection on FSS Utilization. Finally, it recommends strengthening the FSS of major crops in spatially coordinated policies and programs on climate change that complement focus on minor crops (Mabhaudhi et al., 2019) and non-FSS approaches (discussed in Acevedo et al., 2020).

### 5.7. Global-region contrasts in elevation effect yield insight for FSS utilization amid climate change

The results on FSS-elevation relations, which were statistically validated in the Andean countries though insignificant overall, are interpreted to reflect the role of agroecological and social factors on FSS. In the Andean countries, FSS prevalence increases in this way in the potato crop since seed quality improves in conjunction with the agroecology of disease and pest levels, including soil-borne nematode, virus, and bacteria infestations, that are reduced at the cooler temperatures of high elevations (Zimmerer, 2003; de Haan and Thiele, 2005; Arce et al., 2018; Forbes et al., 2020). In addition, high-elevation FSS-producing locales in the Andean countries are often located in relatively close proximity to mid- and lowelevation areas, so that high-elevation seed can be transported. The general FSS-elevation relation is probably applicable, albeit to lesser extents, to other specific global highland contexts such as maize in Mexico (Bellon et al., 2011) and diverse crops in East Africa (Samberg et al., 2013).

These results offer specific inputs to strengthen FSS policy and programs since climate change is impacting the role of elevation among smallholder agriculturalists and land users in tropical and subtropical mountains. Mountain-based food production utilizing FSS is generally shifting to higher elevations as a principal form of smallholder adaptation to global climate change (de Haan and Thiele, 2005; Bellon et al., 2011; Arce et al., 2018). Strengthening FSS in high-elevation environments will depend on utilizing both highly agrobiodiverse varieties as well as incorporating types associated with the formal seed sector. In the case of the Andean potatoes from lower elevation production, this versatility of FSS already exists and can be further strengthened. Additionally, the upslope movement of the production of other crops-such as maize and common bean in the Andes-requires strengthening the capacity of their high-elevation FSS as a key strategy for adaptations to climate change.

### *5.8. Role of topographic ruggedness is important to FSS policies and interventions*

This study's results demonstrating the positive relation to topographic ruggedness are interpreted to suggest that FSS is being utilized in association with the environmental and social conditions associated with this variation. The heterogeneity of soils, vegetation, and climate, as well as the predominance of smallholder agriculture and land use in these environments, is associated with high levels of FSS utilization. Several case studies have demonstrated or suggested this relation of FSS to topographic variation (de Haan and Thiele, 2005; Bisht et al., 2007; Samberg et al., 2013; Arce et al., 2018; Baumann et al., 2020; Zimmerer et al., 2020), though multicountry analysis has not previously been undertaken with this focus. These results recommend that strengthening this role of FSS can be combined with promoting sustainable development and humanitarian interventions in these kinds of places. They reinforce calls to strengthen FSS policies and programs in difficult-to-access place due to crises such as the 2015 Nepal earthquake (Gauchan et al., 2016; Joshi et al., 2020).

## 5.9. Identifying limitations of this study and promising future research directions

This study recognizes limitations as well as recommendations for policy and guidance for future research. One limitation is the circumscribed information on FSS in existing national agricultural surveys and census reports. We urge policymakers, governments, and civil-society groups involved in the design and implementation of this important information to consider FSS-utilization data that will enable policy and program support to strengthen FSS. FSS-related information should include FSS seed data (seed quality, affordability, access, and potentially such factors as seasonality) as well as information about FSS use and users that are necessary to strengthen FSS. While this study's model yielded a robust level of overall explanation relative to related research (as discussed above), other untested characteristics could potentially affect FSS.

Finally, future research can build upon this study's key findings of the global extensiveness and variation of FSS, multiple key FSS relations (socioeconomic, political, and environmental, as well other types of potential influences), and the complex linkages of FSS to agrobiodiversity, agroecology, nutrition, and urbanization. Here, this study recommends research on the policy-sensitive institutional capacity to innovate, share, and utilize new FSS knowledge systems, such as the ones highlighted in this study and its recommendations. Examples include strengthening FSS linkages beyond singular rural places to incorporate the multiscale connectivity of FSS exchange and flows, promote FSS for periurban and urban food producers, and facilitate FSS partnering with allied biodiversity and agroecology approaches (e.g., IPBES, CGIAR; Díaz et al., 2018). This study's results promote mixedmethods FSS knowledge approaches (e.g., Jones, 2017) that integrate global modeling and large-scale analysis with descriptive, comparative, local knowledge-based, and ethnographic research (e.g., Zimmerer, 2003; van Etten et al., 2017; Almekinders et al., 2019a; Baumann et al., 2020; Sperling et al., 2020b; de Boef et al., 2021). Other directions stemming from this study can further research how FSS support and analysis can serve as a new and expanded focus for global biodiversity, food, nutrition, and agriculture institutions (e.g., Díaz et al., 2018; IPBES, CGIAR, UN Panels, and organizations on food, nutrition, and agriculture).

### 6. Conclusion

The results of this large-scale research contribute new scientific understandings as well as specific recommendations for policies and programs. Synthesis of current FSS conceptual themes was used to productively guide the broad-scale, data-compatible model framework of the socioeconomic, political, and environmental relations of FSS in globally representative areas of tropical and subtropical mountains and uplands in Africa, Asia, and Latin America. This modeling yielded rigorous results, showing the significant inverse spatial relations of FSS to mean values of farm area (strong) and per-capita, district-level GDP (strong) as well as distance to major city (moderate). FSS showed strongly positive relationships to aridity and topographic ruggedness. FSS was positively related to elevation in a five-country Andean subsample. Overall, the multiple regression model was rigorous in explaining the variation of FSS utilization to a significant degree ( $R^2 =$ 0.53. *P* < 0.0001).

Additional highlights of the results are that FSS utilization was being undertaken by approximately 136 million farmers in the globally representative sample of tropical and subtropical mountain areas in 11 countries in Africa, Asia, and Latin America at the time of data collection. Detailed analysis demonstrated the extensive relations of FSS utilization to socioeconomic, political, and environmental predictors. These include: (1) different rates of FSS utilization among smallholder populations that range from places with extremely low values of mean farm area as well significantly higher values, (2) global region-level differentiation of FSS-farm area interactions (e.g., Africa, Asia, Latin America), (3) FSS and farm-area interactions with income variation that highlight the geographic associations of FSS with low-income smallholders that include many of the world's poorest people, (4) modeling results showing that FSS utilization is high for all crop types in the study though significantly varied among common bean and potato (highest) to rice (intermediate) and wheat and maize (significantly lower though still high), (5) inverse relations of FSS to the factor of distance from major city and thus high rates of FSS utilization in periurban spaces and surrounding nonremote locations, and (6) specific environmental associations (e.g., high importance in arid environments and hence climate change-prone contexts). We note the aforementioned conclusions are drawn from the first modeling analysis of its type using data from a globally representative sample of countries and major crops in Africa, Asia, and Latin America.

Finally, we conclude that our results have yielded several recommendations to strengthen FSS policies and programs including ones that respond to the COVID-19 pandemic/postpandemic and global climate change as well as goals of transitions and transformations toward justice-based sustainable development. For FSS to address these needs, we recommend identifying and directing policies and programs to vulnerable, FSS-utilizing smallholder populations and subgroups (particularly those with both extremely small and mid-size farm areas), accounting for global region-level distinctiveness of FSS- farm area relations, leveraging multidistrict connectivity through medium- and long-distance FSS connectivity, incorporating FSS relation to aridity to improve climatechange response capacities, and focusing on the urbanization-related effect of high FSS in periurban areas, adjoining spaces, and rapidly changing rural areas. Supportive FSS relations, which are interpreted as nourishing FSS (broadly defined), suggest the need for FSS projects and policies to incorporate periurban spaces and adjoining rural areas as well as the FSS of major crop types (complementing recently increased emphasis on underutilized crops), extremely small farm sizes, and arid and semi-arid environments.

Concluding recommendations argue for expanding the scope and strategic integration of interdisciplinary and transdisciplinary knowledge frameworks to strengthen FSS. This study illustrates convergent insights generated through the selectively integrated approaches of social– ecological systems and global modeling, political ecology and social justice, demography and spatial analysis, and the combined use of socioeconomic, political, and environmental data. We conclude that the knowledge integration and policy insights of this study establish the promise of future synthesis and dialogue using FSS analytical models, such as this study, together with the suite of diverse, vibrant FSS approaches currently being developed.

#### Data accessibility statement

The data used in the study are publicly accessible with accompanying metadata through the Pennsylvania State University Data Commons, 2023, doi:10.26208/7VBH-7B87.

#### Supplemental files

The supplemental files for this article can be found as follows:

Tables S1-S2. PDF

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#### **Competing interests**

The authors declare no competing interests.

#### Author contributions

Conceptualization: KSZ, SJV, MDB, JVE; methodology: SJV, KSZ, JVE, MDB; investigation: KSZ, SJV, MDB, JVE; data and analysis: SJV, KSZ, MDB, JVE; writing—original draft: KSZ, SJV, MDB, JVE; writing—review and editing: KSZ, SJV, MDB, JVE; funding acquisition: KSZ, JVE; visualization: SJV, KSZ, JVE, MDB; supervision: KSZ, JVE, SJV, MDB.

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Art. 11(1) page 23 of 28

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