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Opinion

'Systems approach' plant breeding illustrated by trees

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The linkage in new and creative ways of existing plant breeding methods responsive to different global trends and values provides a 'systems approach' to address a broad set of global production challenges more effectively. Here, we illustrate such an approach through its application to trees, chosen because of their extensive diversity in features, uses, users, production contexts, and domestication pathways. We coin the resulting strategy 'tree diversity breeding' and consider it with reference to trends and values related to participation, environment, biotechnology, and markets as examples. Features of the approach for trees are applicable to plant breeding more widely, as we seek to address complex problems through strategic biodiversity use.

Highlights

A 'systems approach' to plant breeding is increasingly recognised as required to address broad global challenges including the transgression of multiple planetary boundaries.

In this opinion piece we describe a systems approach to plant breeding that is based on advancing novel and creative linkages between existing breeding methods that are oriented to multiple global trends and values.

We illustrate our concept for how biodiversity can be mobilised strategically to address pressing global needs by considering the case study of tree genetic improvement.

We choose 'tree diversity breeding' as our example based on the increasingly crucial roles of trees in supporting continued human development and the environment, and because of trees' enormous diversity that provides significant opportunities for a systems approach to genetic improvement.

The need for 'tree diversity breeding' to respond to multiple global challenges and trends

A key **wicked problem** (see Glossary) of the 21st century is how to step back from multiple planetary boundaries, some already transgressed [1], while supporting continued human development. Trees have a crucial role to play [2]. Among other positives, they mitigate climate change, restore soils, serve as ecological matrices to conserve biodiversity (they also represent massive biodiversity themselves), and provide resilience and choice for human consumption as sources of foods, fuels, fibres, timbers, etc[i]. The over 60 000 tree species [3] supporting these roles occupy many different production contexts, spanning monocultural wood plantations and fruit orchards to highly diverse multifunctional forests and complex agroforests, and are domesticated to different extents, from being wild to fully dependent on humans for regeneration [4]. They also frequently have large **gene pools**, with high genetic variation within natural stands (e.g., [5]), that can be stewarded to enhance their beneficial roles, though these genetic resources are often threatened by forest clearing and the simplification of agricultural landscapes [6].

To travel toward meaningful solutions, wicked problems demand systems-oriented approaches that acknowledge the interconnectedness of the challenges faced and forge collaborations among stakeholders. In this opinion piece, we choose trees to illustrate a systems approach to plant breeding to help humanity address broad global challenges. Our choice of trees as a case study is motivated by their vast diversity of features, uses, users, production contexts, and domestication pathways that can support biodiversity-based breeding. It is also because the importance of using broad diversity in tree improvement and deployment is recognised (e.g., [7,8]), even if appropriate measures have often not been applied.

It is for example widely known that, at the species level, communities of mixed trees often provide more stable total productivity [9], can sequester more carbon [10], and frequently overyield single species stands [11]. Furthermore, at the intraspecific level, experience has shown that, because many tree species are outcrossing, they suffer from inbreeding depression when mating occurs

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between closely related individuals [12], a problem which can be avoided through deliberate widescale deployment of genetic diversity. In addition, compared with genetically-uniform stands, genetically-diverse 'treed' landscapes are known to often provide better habitat matrices for other organisms [13], give longer-term stability to agricultural and other ecosystems [14], and support greater adaptation to climate change [15].

The essential feature of a systems approach to tree improvement, which we call '**tree diversity breeding**', is an emphasis on maximising novel, creative linkages between existing tree breeding methods that are responsive to different global trends, thereby aligning breeding with multiple values to support broad progress. In the approach as we describe it, we build bridges between four key global trends that are more or less aligned with the four directions for breeding identified for (annual) crops by Edith Lammerts van Bueren and her colleagues [16]. Our chosen trends, their underlying values, and the existing tree breeding methods already aligned with them, are described in Box 1. These trends, namely the call for broader participation, increased emphasis on the environment, advances in biotechnology, and the evolution of markets, are also illustrated

Box 1. Global trends and responsive breeding methods

The call for broader participation, increased emphasis on the environment, advances in biotechnology, and the evolution of markets are key global trends to which existing approaches to tree improvement already at least partially align. These trends, their associated values, and aligned breeding methods, are described in this box. Though the comparison is inexact, in parentheses after the title of each trend below is the most closely aligned breeding orientation defined by Lammerts van Bueren *et al.* [16] for (annual) crop breeding.

Participation (community-based breeding)

In support of cultural values and equitability, an important concern in plant breeding has become the fair sharing of the benefits of genetic improvement with the local communities who have long stewarded genetic resources[ii]. For fruit trees, one successful sharing arrangement with forest-bordering communities has been **participatory domestication** [43]. In Central Africa, for example, the approach has been used to select and clone polygenically-controlled fruit traits [44], with participating communities benefiting through increased yields, higher profits, and the greater recognition of the cultural roles of indigenous tree foods in diets [45].

Environment (ecosystem-based breeding)

In support of current global commitments to tree-based climate change mitigation, ecosystem restoration, biodiversity conservation, and other ecosystem service provision[iii], calls to better define 'what trees to plant where', adapted to site and purpose, are being heeded through exploring genotype-by-environment interactions (GxE) in multilocational field trials [46]. These trials include **breeding seedling orchards (BSOs)** [47] that not only evaluate GxE but provide locally-adapted seed for growers, for example native timber trees crucial for forest landscape restoration in East Africa[iv].

Biotechnology (trait-based breeding)

Whether or not justified objectively, funding once channelled to 'conventional' plant breeding is now increasingly directed to biotechnological methods, including for African 'orphan' tree foods [48]. Such evolving interests of investors are complemented by researchers' priorities to dissect the genetics of traits through biotechnology use [18], with a range of traits being targeted by matched biotechnology methods. Genomic selection, which carries particular advantages in trees because of their long generation intervals, is applied to complex, quantitative traits such as wood production for 'forestry' species [49], while **CRISPR/Cas9 gene editing** use is being explored for targeting putative major domestication genes for food production in 'horticultural' species [50].

Markets (corporate-based breeding)

To counter current dominant global markets focused on a few business-profitable staple crops that have had detrimental impacts on human nutrition, biodiversity, and sustainability [51], it has been recognised that a broader range of market competitive, context-specific plant cultivation options is needed [39]. Breeders are increasingly paying attention to market-oriented traits for new business opportunities in a wider array of tree species, such as for commercial food spread production from African rainforest trees exhibiting large genetic variation in edible oil yield [52].

Glossary

Breeding seedling (seed) orchard (BSO): this is a tree planting design to explore GxE (see definition later), support selection, and multiply seed. Each BSO is generally composed of multiple tree provenances, each represented by several families (progeny from individual 'mother' trees). BSOs are replicated across environments, with each used to provide locally-suitable seed.

Citizen science breeding: this involves communities of people beyond formal breeders in the genetic improvement. 'Citizen science' has been widely associated recently with smartphone use by 'citizens' to report observations to 'scientists'.

CRISPR/Cas9 gene editing: this biotechnological approach targets and edits specific DNA sequences to introduce genetic mutations. In less-studied and/or newly-cultivated plants, orthologues of known genes from model plants can be targeted to see if expected phenotypic effects are achieved. 'Knockout' CRISPR/Cas9 gene editing disables gene function, a process typical in the initial stages of plant domestication, meaning the approach may be of particular relevance for developing 'new' tree crops, if technical and social constraints to application can be overcome.

Gene pools: the genetic variation within a species and its relatives. As tree species are generally little domesticated and still exist widely in the wild, they often have large extant gene pools.

Genotype-by-environment interactions (GxE): classically, these manifest as a change in ranking of the performance of tree provenances across different environments. The extent of GxE varies by tree species and trait, but can be large, with important implications for the matching of planting materials to locations.

Genome-wide association studies (GWAS): an approach that looks for associations between phenotypic trial data and genome-wide marker data. Markers 'linked' to phenotypic traits can be identified and used in selection. Multi-environment GWAS compares associations across trials situated in different environments, and identifies genomic variation associated with adaptation and adaptability.

Landscape genomics: approaches that explore correlations between genomes and the environments from

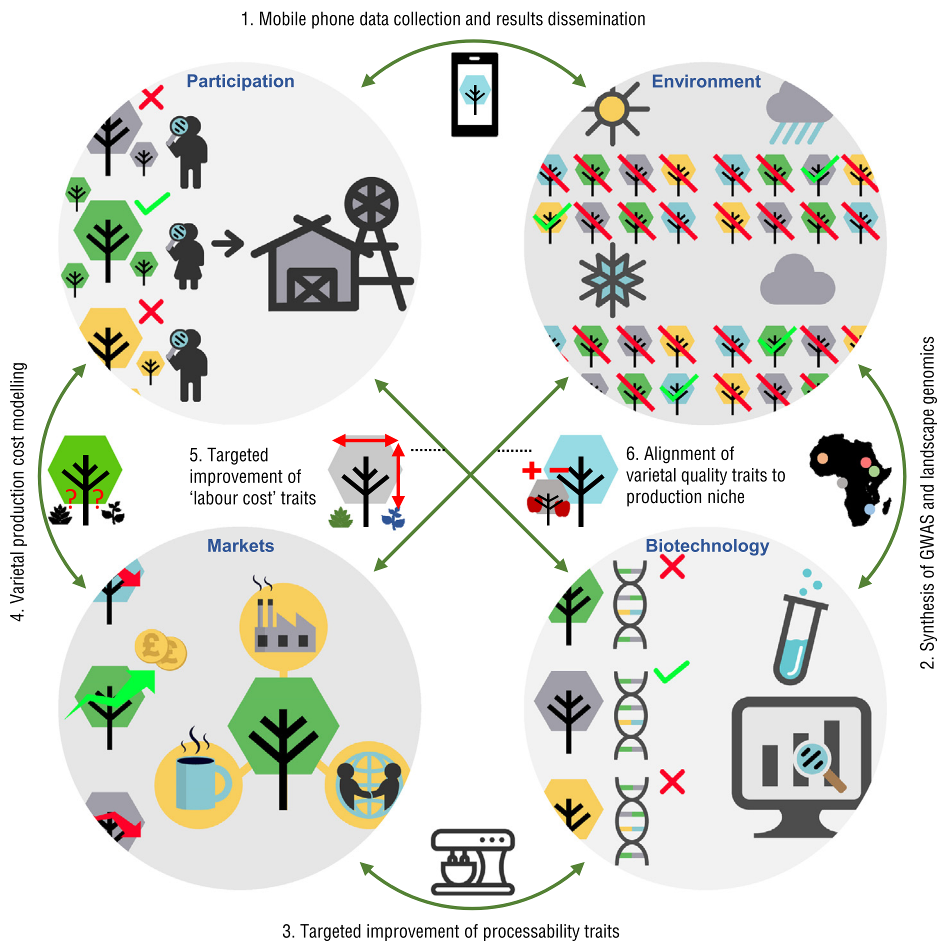

Figure 1. Schematic of the tree diversity breeding framework. Examples of novel linkages that constitute a systems approach to tree breeding, which we call tree diversity breeding, are indicated with arrows and summary headings. Shown are linkages between existing breeding methods responsive to four important global trends of participation, environment, biotechnology, and markets (see Box 1). (1) 'Mobile phone data collection and results dissemination' refers to the use of citizen science breeding approaches to bridge participation and environment trends; (2) 'Synthesis of genome-wide association studies (GWAS) and landscape genomics' refers to the use of new statistical approaches to support progress in the understanding of genetic adaptation to bridge environment and biotechnology trends; (3) 'Targeted improvement of processability traits' refers to the manipulation of orthologs of processability-related genes from model plants in trees to bridge biotechnology and markets trends; (4) 'Varietal production cost modelling' refers to advances in production system-level modelling for tree 'varieties' to bridge markets and participation trends; (5) 'Targeted improvement of 'labour cost' traits' refers to the manipulation of orthologs of architecture- and phenology-related genes from model plants in trees to bridge participation and biotechnology trends; and (6) 'Alignment of varietal quality traits to production niche' refers to the use of novel methods to explore genetic, product quality, and production system design relationships to bridge environment and markets trends. Numbers in the schematic indicate the order that linkages are discussed in the main text under the section 'Tree diversity breeding links trend-responsive tree breeding methods for transformative change'.

in Figure 1. As we describe in the next section, Figure 1 also illustrates the novel linkages between trend-responsive breeding methods that constitute the tree diversity breeding approach.

We focus here on the application of tree diversity breeding to the global tropics (with an emphasis on Africa, a region of particular interest to the authors), as the tropics are where the greatest unrealised potential for tree planting lies and where biodiversity levels remain high, despite current

which genotyped samples originated. A correlation may indicate adaptation and could support a 'local sourcing' policy for tree seed. Landscape genomic approaches are particularly relevant for trees, as most still have wild stands where local adaptation has occurred.

Participatory domestication: as practiced in Central Africa, an approach to tree improvement that is implemented by growers, mentored by scientists, and supported by extension agents and other local institutions. It combines communities' knowledge of tree use and management with their priorities for cultivation, and with scientific advances in germplasm collection, selection, propagation, and planted tree management.

Processability traits: characteristics that influence the ability to make use of tree products and thus potential targets to address market requirements. Such traits may relate to food use (e.g., that allow tree fruit or extracted edible oil incorporation into processed food formulations) and/or other functional properties (e.g., ease of lignin extraction from wood).

Tree diversity breeding: as we define it, a systems approach to conserve and use inter- and intra-specific diversity in tree genetic improvement, to support and amplify biodiversity. The key feature is to link existing trend-responsive tree breeding methods novelly and creatively.

Wicked problem: a problem with complex interdependencies and no simple solution. Significant movement toward 'a solution' requires trade-offs considering multiple values, and multiple, coordinated changes in behaviour by several stakeholders.

erosion [6]. The tropics are also where there is a particular importance to deploying tree species and genetic diversity because, after improved tree planting material has been distributed to growers, replanting will often occur through the 'self-collection' of germplasm from these original trees, due to limited 'redelivery' infrastructure [17]; getting both species and genetic diversity out at the start is therefore essential for sustained, effective use.

Our concept of diversity breeding should help policymakers and practitioners support impactful breeding for multiple values, cognisant of the trade-offs inherent to a system with many different interrelated components. While we apply the approach to trees, our case study's relevance for creating cohesive approaches to plant genetic improvement more widely, encompassing the broad values that need to be addressed in an increasingly complex world, will be evident.

Tree diversity breeding links trend-responsive tree breeding methods for transformative change

By linking existing trend-responsive breeding methods in new and creative ways, tree diversity breeding endeavours to broaden the values considered in genetic improvement, to better steward biodiversity and enhance success on multiple fronts. In this section, we illustrate the approach by considering promising links (arrows in Figure 1) between the trend-responsive breeding methods for participation, environment, biotechnology, and markets described in Box 1. We include examples that focus on traits for genetic improvement that we identified in a previous review as necessary to support production diversification for human and environmental health, including traits that support tree product processability, the physical integration of trees in mixed production systems, and tree grower profitability [18]. In each scenario, we describe the bottleneck addressed (B), the innovation involved (I), how biodiversity is deployed (D), and the desired outcome (O).

Citizen science breeding to bridge participation and environment

Participatory tree selection and breeding trials have traditionally been implemented on a small scale that samples only a few environments because of the effort involved in communicating with grower/testers, thus limiting the applicability of findings for both existing and novel conditions (B). Novel **citizen science breeding** methods overcome this through the use of mobile phones to recruit trial participants, collect trial data, and disseminate location-specific findings (I) [19]. Even for annual crops, the use of mobile technology in this way has to date been limited in tropical nations [20,21]; but its applicability to trees is obvious. The functionality of smartphone apps already used by local communities to monitor tree restoration in the tropics (e.g., [22]) could be enhanced to enable reporting on the performance of grower-collected trees as well as that of researcher-chosen tree germplasm panels distributed to growers. Such work also presents the opportunity to expand the concept of performance to encompass a broader range of traits beyond production characteristics, such as environmental service provision traits (see, e.g., Table 1 in [23]). To support grower engagement, at least some of the chosen traits should be measurable in the early stages of tree growth (e.g., initial survival and early vigour). The result will be deployed tree genetic diversity better matched to variable environments, cultivation practices, and growers' uses (D), in support of more sustainable, context-tailored production (O).

New statistical approaches to bridge environment and biotechnology

Multi-environment field trials that quantify **genotype-by-environment interactions (GxE)** provide only a limited understanding of the processes behind adaptation, restricting the broader applicability of findings for new environments (B). Existing approaches that seek to bridge environmental and genomic data to provide greater insight include multi-environment **genome-wide association studies (GWAS)** [24] and **landscape genomics** [25]. In trees, however, where adaptation is generally controlled by multiple genes of individually small effects, the progress in understanding achieved through such studies has been limited [26]. In recent years, new statistical approaches that synthesise genomic associations and whole genome data with phenotypes and 'home environments' have been developed that provide a way forward for more effective interpretation (I) [27]. Though still in their infancy for application to trees, such approaches promise to be especially relevant for the limited number of species that already have multilocational field trials of at least some 'wild tree' provenances. This is especially true for cases in which thorough passport (provenance) data exist and where environmental fitness-related data has been collected, rather than just measurements of production-related traits. Application of such methods will enable deployment of tree genetic diversity in landscapes that more effectively deals with novel growth conditions caused by anthropogenic climate change (D) [15], in support of more efficient climate adaption and mitigation responses (O).

Manipulation of orthologs of processability-related genes to bridge biotechnology and markets

As important components of product quality, **processability traits** are key determinants of market demand; and yet such traits have been relatively understudied for trees compared with annual crops, limiting improvement progress (B). Biotechnology provides new opportunities to improve tree product processability through the manipulation of orthologs of processability-related genes from model plants (I). An example could be the manipulation of triacylglycerol (TAG) lipase class III family genes that share a function in releasing fatty acids from triacylglycerols in both the tomato clade [28] and the African oil palm (*Elaeis guineensis*), among other plants [29]. Allelic variation in the relevant gene (*EgLIP1*) in oil palm influences the quality of commercially-extracted palm oil; and its targeted manipulation, perhaps through 'knockout' gene editing [30], could allow more marginal farmers to grow the crop by extending the time permissible between harvesting and oil extraction under circumstances of poor processing infrastructure [29]. Beyond food uses, processability encompasses such things as the ability to profitably extract wood pulp and biofuel, critical industrial traits that depend on the manipulation of known genes involved in lignin biosynthesis [31]. Orthologs, whose manipulation has significant impact on lignin composition, have been identified across nonmodel as well as model plants, including trees [32]. The result of application of such approaches will be the more effective deployment of tree genetic diversity in landscapes for market-determined traits (D), in support of production system diversification and resilience via a broader range of options for quality plant products (O).

Advances in production system modelling to bridge markets and participation

When the growers of tree products are independent small producers with little influence on markets, the profitability of their engagement in market-based production has in the past often been neglected, leading to marginal and often highly variable incomes (B). Especially in low-income nations where production systems remain relatively unmechanised, a key objective for improving the profits for these growers is to reduce the manual labour costs of production [18]. To achieve this will require new cooperative modes of participation between commercial companies, tree breeders, and growers, such as in the application of innovative production system modelling frameworks (e.g., [33]), to understand the costs of production and identify candidate approaches that better match specific tree genotypes (e.g., with specific architectures and phenologies) to particular production niches (I). This approach to identify 'what varieties to grow where' within production systems, designed to maximise labour investments and thereby increase profitability, could be especially useful where women growers are currently excluded from participation in tree product markets because they are particularly time-poor due to their multiple demanding household roles [34]. The result will be the more effective deployment of tree genetic diversity in specific production landscape niches (D), in support of production system diversification especially for women growers (O).

Manipulation of orthologs of architecture- and phenology-related genes to bridge participation and biotechnology

Some constraints to grower profitability identified via cooperative engagement between companies, breeders, and growers (B) will likely present challenges to tree breeding that, as for processability-related traits, may be addressed through new opportunities to manipulate the orthologs of relevant genes identified in model plants (I). Key traits that relate to the return on investment from labour inputs include tree architecture (determining ease of harvest), the years taken from tree planting to production maturity (determining the first returns on labour investments), and within-season phenology (determining conflicts or synergies with labour needs for growers' other activities, such as harvesting annual crops). Phenology is not only important from a labour perspective but, for fruit trees, adjusting the time in the year of fruiting can help address poor growers' 'hunger gaps' [35]. Genes involved in controlling all of these traits are well characterised in several model organisms; and orthologs have been identified in a broad range of plants, including trees [18]. A good example is the *TERMINAL FLOWER1* gene, discovered in *Arabidopsis thaliana*, that has been shown to participate in the control of juvenility in many plants [36], with transgenic lines of apple flowering earlier where the ortholog (*MdTFL1*) has been 'knocked out' [37]. As in the previous example (markets and participation), the result of application of such approaches, coupled with testing by growers, will be the more effective deployment of tree genetic diversity in production landscape niches (D), thereby supporting diversification and additionally helping fill hunger gaps (O).

Novel methods to explore relationships between genetics, product quality, and production system design to bridge environment and markets

Progress in the development of a broader range of context-specific tree production options has been constrained by a lack of genetic-level work on minimising the trade-offs, and maximising any synergies, between markets (emphasis on businesses' profitability) and the environment (emphasis on ecosystem services provisioning). Often, greater market profitability is associated with increasingly negative environmental impacts (B). New attempts at progress involve comparing the product qualities (and thus market values) of different varieties or breeding lines when they are grown in production systems of varying environmental value (I). The work is relevant for tree breeding and variety choice because it is known that tree product quality can exhibit significant genotype-by-environment-by-management interactions (GxExM), in the sense that tree genotypes can interact strongly not only with the environment *per se* (E) but also with different production system configurations (M). For example, in perennial coffee (*Coffea* species), certain varieties only produce high quality beans when they are grown in shade systems, which happen to also be biodiversity friendly [38]. Systematic research committed to understanding the extent of the relationships between genetics, product quality, and production system designs should allow for more effective deployment of tree genetic diversity within species-rich contexts that are both profitable and environmentally friendly (D), in support of broader production system diversification and sustainability goals (O).

Concluding remarks

We have here proposed tree diversity breeding as a case study for a coherent, systems-oriented approach to more effectively maintain and amplify biodiversity in production systems to address global challenges [39]. The approach, based on the deliberate advancement of novel and creative linkages capable of breaking down barriers between existing trend-responsive breeding methods, embraces multiple values and seeks to guide effective action in creating landscapes that sustainably support people and the environment [40]. We have illustrated the approach for trees by outlining the motivations and conditions for a coordinated application of a wide range of methods, including: (i) citizen science; (ii) new genome- and production system-level statistics and modelling; (iii) the manipulation of known gene orthologs; and (iv) exploration of the

Outstanding questions

How do we monitor the relative progress of different breeding initiatives to consider broad impacts on people and the environment? Productivity and profitability are not sufficient measures, as a holistic approach also considers aspects including wider human wellbeing and environmental health. Developing and understanding how to implement appropriate metrics represent important areas for future research.

How do we best breed to maximise positive interactions among the components of complex production systems, including tree species? Starting points are to consider annual crop-to-crop-based intercrop development approaches, and what we know already about genetic–level interactions between trees and other species. More work is however required to explore relevant interactions. These extend to the interactions between trees and zoonotic disease vectors at forest-to-agriculture interfaces.

relationships between genetics, product quality, and production systems. The underlying principles encompass a broad set of values that, in an increasingly complex world, also must be addressed in annual crop breeding, whether embracing new and 'orphan' crops that support diversification or working to enhance the sustainability of production of existing major crops [18].

Looking to the future, we suggest that further progress in a systems approach to plant breeding requires work on a broader set of measures to define breeding success. These metrics should extend beyond traditional measures of productivity and company profitability to embrace resilience, sustainability, human nutritional security, cultural values, and species- and genetic-conservation benefits [41]. The informed placement of trees in working landscapes also requires that attention be given to breeding methods that explicitly consider interactions among trees and other system components [42]. Connected with this, we suggest that tree diversity breeding could, with appropriate research investment, play a role in supporting forest–agriculture interfaces that through their structure and specific compositions minimise zoonotic disease leakage from forests, a crucial consideration currently [2]. More understanding however of the features of successful structures and compositions, and how tree diversity breeding could support these, is required. We outline these points in Outstanding questions.

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Declaration of interests

No interests to declare.

Resources

[i] www.worldagroforestry.org/products/switchboard/

[ii] www.cbd.int/abs/

[iii] www.bonnchallenge.org/

[iv] www.worldagroforestry.org/project/provision-adequate-tree-seed-portfolio-ethiopia

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