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4 Enset in Ethiopia: a poorly characterised but resilient 5 starch staple

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30 Running title: Enset in Ethiopia

1 Abstract

- 2 • **Background** Enset (*Ensete ventricosum*, Musaceae) is an African crop that currently
3 provides the staple food for approximately 20 million Ethiopians. Whilst wild enset
4 grows over much of East and Southern Africa and the genus extends across Asia to
5 China, it has only ever been domesticated in the Ethiopian Highlands. Here, smallholder
6 farmers cultivate hundreds of landraces across diverse climatic and agroecological
7 systems.
- 8 • **Scope** Enset has several important food security traits. It grows over a relatively a wide
9 range of conditions, is somewhat drought tolerant, and can be harvested at any time
10 during the year, over several years. It provides an important dietary starch source, as
11 well as fibres, medicines, animal fodder, roofing and packaging. It stabilises soils and
12 microclimates and has significant cultural importance. In contrast to the other cultivated
13 species in the Musaceae family (banana), enset has received relatively little research
14 attention. Here, we review and critically evaluate existing research, outline available
15 genomic and germplasm resources, aspects of pathology, and explore avenues for crop
16 development.
- 17 • **Conclusion** Enset is an underexploited starch crop with significant potential in Ethiopia
18 and beyond. Research is lacking in several key areas: empirical studies on the efficacy
19 of current agronomic practices, the genetic diversity of landraces, approaches to
20 systematic breeding, characterisation of existing and emerging diseases, adaptability to
21 new ranges and land-use change, the projected impact of climate change, conservation
22 of crop wild relatives (CWRs), by-products or co-products or non-starch uses, and the
23 enset microbiome. We also highlight the limited availability of enset germplasm in
24 living collections and seedbanks, and the lack of knowledge of reproductive and

1 germination biology needed to underpin future breeding. By reviewing the current state
2 of the art in enset research and identifying gaps and opportunities, we hope to catalyse
3 the development and sustainable exploitation of this neglected starch crop.

4 **Keywords:** Biodiversity, biotic and abiotic resistance, climate adaptation, crop wild relatives
5 (CWRs), domestication, *Ensete ventricosum*, false banana, food security, germplasm
6 collections, pests and pathogens, sustainable agriculture, tropical crop ecology.

9 INTRODUCTION

10 Enset (*Ensete ventricosum* (Welw.) Cheesman) is a large perennial monocarpic herbaceous
11 plant, similar in form to the related bananas of the genus *Musa* (Figure 1). The two genera,
12 together with the monotypic *Musella* (Franch.) C.Y. Wu ex H.W. Li, form the family Musaceae
13 within the Monocot order Zingiberales (Figure 2A). Like banana, enset has a pseudostem of
14 overlapping leaf sheaths, large paddle-shaped (oblong-lanceolate) leaves and produces a
15 massive pendulous inflorescence with banana-like fruits. However, unlike sweet and starchy
16 banana (with the latter called plantain in some contexts, although there is no botanical
17 distinction between banana and plantain), which are widely farmed for their fruits, it is instead
18 the swollen pseudostem base, leaf sheaths and underground corm that provide a year-round
19 dietary starch source, typically harvested 4-7 years after planting. Despite a widespread
20 distribution in eastern, central and southern tropical Africa (Baker and Simmonds 1953; Lock
21 1993), enset has only been domesticated in Ethiopia (Brandt *et al.* 1997). Here, hundreds of
22 landraces are found in diverse climatic and agroecological systems (Birmeta *et al.* 2002;
23 Tesfaye and Lüdders 2003; Yemataw *et al.* 2014a) where they provide the staple food source
24 for approximately 20 million rural people (Figure S1 - see Supplementary Information for
25 population estimation methods).

1 Enset has historically been ascribed as a ‘tree against hunger’ (Brandt *et al.* 1997), due to the
2 domesticated plant having important attributes that support the food security of communities
3 that cultivate it. These attributes were evident during the devastating famines of the 1980s,
4 where enset growing communities reported little-to-no food insecurity (Dessaegn 1995). Most
5 significant is the apparent ability of enset to withstand environmental stress, including periods
6 of drought (Quinlan *et al.* 2015). Enset can also be harvested at any time of the year and at any
7 stage over several years (including when it is immature), and enset-derived starch can also be
8 stored for long periods (Birmeta 2004). Enset also supplies fibres, medicines, animal fodder
9 and packaging material (Brandt *et al.* 1997). It stabilises soils and microclimates (Abate *et al.*
10 1996) and is culturally significant (Kanshie 2002; Negash and Niehof 2004; Tewodros and
11 Tesfaye 2014). Enset has a complex management system supported by extensive
12 ethnobotanical knowledge (Borrell *et al.* 2018, *in prep*). In a comparison of starch crops, enset
13 has been reported to produce the highest yield per hectare in Ethiopia (Tsegaye and Struik
14 2001; Kanshie 2002) with relatively low inputs and management requirements. Enset therefore
15 has the ability to support a larger population per unit area than regions relying on growing
16 cereals (Yirgu 2016). As a result of these qualities, enset farming provides a long-term,
17 sustainable food supply capable of buffering not only seasonal and periodic food deficits, with
18 minimum off-farm input, but also demonstrates potential that exceeds its current utilisation in
19 South-West Ethiopia.

20 Despite the current and potential importance of enset, relatively little is known about its biology
21 and ecology. In this review we aim to 1) Summarise the existing knowledge and current
22 research effort both nationally in Ethiopia and internationally; 2) Identify critical knowledge
23 gaps in the ecology, diversity and distribution of enset to direct future research effort; and 3)
24 Catalyse the development of resources needed to enable the sustainable exploitation of enset
25 diversity as a resilient climate-smart crop of the future. Concurrently, we also acknowledge the

1 importance of local ethnobotanic knowledge, management and plant processing; these topics
2 are reviewed in Borrell *et al.* (*in prep*). Finally, we introduce the online resource [www.enset-](http://www.enset-project.org)
3 [project.org](http://www.enset-project.org) to make various tools and data available to researchers both in Ethiopia and
4 internationally.

5

6 **THE GENUS *ENSETE*: EVOLUTION AND SYSTEMATICS**

7 *Ensete* Bruce ex Horan. is a monophyletic genus (Li *et al.* 2010) with seven described species
8 in Africa and Asia (Table 1). Whilst first reported by Bruce (1790) during travels in Ethiopia
9 (Figure 1A and B), and formally described by Horaninow (1862) it was not until almost a
10 century and a half later that Cheesman (1947) elevated the informal ‘giant bananas’ group
11 within *Musa* to re-establish genus *Ensete*. Of the 20 reported synonyms, 65% relate to *Ensete*
12 *ventricosum* (Welw.) Cheesman. The sister genus *Musella* (Li 1978) was originally placed
13 under *Musa* and *Ensete* (Cheesman 1947; Simmonds 1960). Whilst the sole species of this
14 genus, *M. laiocarpa* (the golden lotus banana), occupies a unique geographic distribution,
15 drier and cooler than any other member of the family, there is continuing debate as to whether
16 it should be treated as a member of *Ensete* or as its sister (Liu *et al.* 2003; Li *et al.* 2010).

17 Currently, *Ensete* (7 species) and the sister genera *Musa* (~70 species) and *Musella* (1 species)
18 belong to the Musaceae within the order Zingiberales, together with eight tropical plant
19 families (Figure 2B, Table S1), some including genera known for their medicinal properties
20 and ornamental use. APG IV (Chase *et al.* 2016) has confirmed the position of Zingiberales as
21 a monophyletic order within the monocots, placing it in the commelinoid clade, as sister group
22 to Commelinales, but has not addressed the interfamilial relationships of the other families
23 belonging within the order (Fig. 2B). Understanding the relation and genomic organisation of
24 *Ensete* as sister to *Musa* may provide novel insights into the evolution of the globally important
25 Musaceae family.

1 Like the other Musaceae genera, *Ensete* originated in northern Indo-Burma during the early
2 Eocene, likely followed by a single African colonisation via gradual overland dispersal during
3 a more mesic climate period (Janssens *et al.* 2016). The presence of Eocene *Ensete* fossils in
4 North America (Manchester and Kress 1993) establishes that the genus also reached the New
5 World. *Ensete* differs from bananas in being mainly African in distribution, monocarpic,
6 having large seed size (up to 18mm compared to 10mm) and an apparent adaptation to cooler
7 and drier environments than most *Musa* species (Cheesman 1947; Baker and Simmonds 1953).
8 *Musa* and *Ensete* can be further distinguished by the presence of ‘T’ shaped embryos and
9 granulose papillose pollen grains in *Ensete*, and their absence in *Musa* (Bekele and Shigeta
10 2011). *Ensete* does not normally produce suckers, whereas *Musa* does — although a small
11 number of suckering *E. ventricosum* landraces are known to occur in Ethiopia (provenance
12 unknown). In the field, *Ensete* are perhaps best distinguished from *Musa* by their more rigid
13 and upright leaves (pers. obs.).

14 A further distinction is that *Ensete* is currently only reported to be diploid with $2n=2x=18$
15 (Westphal 1975; Diro *et al.* 2003) and this is consistent with flow cytometry measurements in
16 ten individuals (J.S. Heslop-Harrison and P. Tomaszewska pers. communication and
17 chromosome counts (Figure 3). By contrast, *Musa* has species with $x=7$, 10 and 11 at various
18 ploidy levels; domesticated varieties are commonly sterile, parthenocarpic triploids
19 ($2n=3x=33$) (Bartoš *et al.* 2005). Species in the genus *Ensete* have a relative small DNA
20 content, reported to be about 620Mb per haploid genome for *E. livingstonianum* (measured by
21 flow cytometry, Bartoš *et al.* 2005) and 547Mb for *E. ventricosum* (estimated from whole
22 genome sequencing, Harrison *et al.* 2014). This is similar to the genome size of haploid *Musa*
23 species, ranging from 580-800Mb measured by flow cytometry (Bartoš *et al.* 2005), and the
24 lower estimates from whole genome sequencing of 523Mb for *M. acuminata* (D’hont *et al.*
25 2012). *Ensete* species have $n=9$ chromosomes (Westphal 1975) and the karyotype consists of

1 mainly bi-armed chromosomes of similar size, each slightly bigger than those in banana (Figure
2 3). *Musa* species from the section *Eumusa* which includes the bananas *M. acuminata* and *M.*
3 *balbisiana*, all have n=11. Other *Musa* species outside the section *Eumusa* (in sections
4 *Australimusa* and *Rhodochlamys*) have n=9 and n=10. Molecular cytogenetics of *E.*
5 *ventricosum* localised 5S rDNA sequences at the short arm of a medium pair of chromosomes
6 (Figure 3) adjacent to the secondary constriction harbouring 45S rDNA. In *Musa* species that
7 5S and 45S rDNA are usually adjacent to each other and this has also been observed in *E.*
8 *livingstonianum* (Bartoš *et al.* 2005). The latter has been reported to have additional minor 5S
9 sites, that are either lost in *E. ventricosum*, or more likely varietal differences exist. Whilst
10 phylogenetic relationships within genus *Ensete*, and to other genera within the Zingiberales are
11 poorly known (Figure 2), there does appear to be support for a distinction between African and
12 Asian *Ensete* lineages (Li *et al.* 2010; Janssens *et al.* 2016).

13 In *Musa* there are over a thousand landraces with high genetic diversity, indicating multiple
14 origins from different wild *M. acuminata* and its hybrids with *M. balbisiana* (Heslop-Harrison
15 and Schwarzacher 2007). The movement and interactions of various human groups have played
16 an important role in generating this diversity (Perrier *et al.* 2011). Most landraces arise via
17 selection (by farmers) of spontaneously occurring mutants with parthenocarpic fruit
18 production. These are brought under cultivation, multiplied and distributed by vegetative
19 propagation. Extensive hybridisation has occurred, including between diploid wild species or
20 genotypes, involving unreduced gametes, and perhaps residual fertility of triploids (Heslop-
21 Harrison and Schwarzacher 2007). Due to the high levels of domestic diversity indicated in
22 genetic studies (Tobiaw and Bekele 2011; Olango *et al.* 2015) and the overlapping spatial
23 distribution of wild and domesticated enset, it seems likely that there were also multiple
24 domestication events in enset, and/or frequent local introgression from wild populations.
25 However, unlike *Musa*, we hypothesise that all domesticated enset landraces arose from a

1 single species, *E. ventricosum*, as this is the only member of the genus present in Ethiopia or
2 the surrounding region. More detailed diversity studies of wild and domestic enset in Ethiopia
3 are required to elucidate the number of domestication events and population structure.

4 Among communities in Ethiopia, *E. ventricosum* is unusual in that human-enset interactions
5 currently span the entire spectrum of domestication intensity, from wild procurement to full
6 domestication (Hildebrand 2001). As such, there is limited evidence to elucidate the timeline
7 of domestication, not least since the crop has never moved outside its centre of origin and
8 diversity. Nevertheless, whilst wild enset is considered largely inedible, except during periods
9 of severe food insecurity, smallholders report that domesticated landraces are more palatable
10 (Table 2). There is no data about the presence and genetics of secondary products that may be
11 eliminated during domestication. Several authors have suggested that enset was first cultivated
12 by growing wild plants in the terminal Pleistocene or Early Holocene (Brandt 1984; Hildebrand
13 2001). Though there is little evidence for this, it would compete with, or predate, the first
14 evidence of intense *Musa* cultivation (~6500 years before present) in the New Guinea
15 Highlands (Denham *et al.* 2003). Evidence from Uganda and Cameroon dates *Musa* cultivation
16 in Africa to at least 2500 years before present (Mdiba *et al.* 2001; Lejju *et al.* 2006), although
17 these data have not met universal acceptance (Neumann and Hildebrand 2009). There is limited
18 evidence that enset, although not used today, may have been historically consumed in northern
19 Uganda (Thomas 1940; Hamilton *et al.* 2016). It has also been suggested that *Ensete* once
20 formed an '*Ensete* belt' in East Africa from north-east Lake Victoria south-east to the Usambara
21 Mountains, Tanzania (Langhe *et al.* 1994) and was used in times of food scarcity. This is
22 largely consistent with the data presented in Figure 4, and we note that genetic characterisation
23 of these populations would provide crucial insights on their history. Furthermore, among some
24 communities (outside of Ethiopia) enset is reported to maintain a cultural significance
25 (Philippson 1990). It has been suggested that this ancient care of *Ensete* in Africa contributed

1 to the rapid and widespread adoption of the bananas arriving from Asia, with the oldest names
2 relating to banana apparently derived from those in use for *Ensete* (Langhe *et al.* 1994).
3 Elsewhere outside Africa, *Ensete* is reported to have been used as an emergency food source
4 in Vietnam during the Second World War, with the growing point used as a vegetable (Oyen
5 and Lemmens 2002). Similarly, parts of *E. glaucum* are consumed in New Guinea, particularly
6 the ripe fruits which are eaten raw (Kennedy 2009) suggesting additional potential among
7 underexploited wild relatives.

8

9 **THE DISTRIBUTION OF WILD AND DOMESTICATED *ENSETE***

10 *Ensete* consists of three very widespread species (*E. ventricosum* and *E. livingstonianum* in
11 Africa; *E. glaucum* in Asia) and five other localised endemics or near-endemics (Figure 4).
12 Three species have been formally assessed for the IUCN red list of which two (*E. ventricosum*
13 and *E. livingstonianum*) are ‘Least Concern’ and one (*E. perrieri*) is ‘Critically Endangered’.
14 Although not assessed, *E. superbum* would probably meet the criteria for ‘Endangered’, and
15 all other non-cultivated species could be considered ‘Data Deficient’. *Musella lasiocarpa* may
16 be extinct in the wild (Liu *et al.* 2003). *Ensete ventricosum* is the only *Ensete* species in
17 Ethiopia (Brandt *et al.* 1997), occurring in the South and South West (Tsegaye *et al.* 2002)
18 across the Southern Nations, Nationalities and People’s Regional (SNNPR) region, as well as
19 the neighbouring regions of Oromia and parts of Benishangul-Gumuz (Figure 5). In this
20 manuscript hereafter, we refer to *E. ventricosum* as enset and we distinguish wild from
21 domestic landraces. Spelling of regions, zones and other place names follow Davis *et al.*
22 (2018).

23 Wild enset in Ethiopia is considered by some researchers to be range restricted and declining
24 (pers. comm. S. Demissew) although there is a paucity of data to support or refute this. Birmeta

1 *et al.* (2004) report that wild enset occurs mainly around the city of Bonga (SNNPR region;
2 Kaffa zone) and in a smaller area by the Omo river (SNNPR region; Gamo Gofa zone) whilst
3 Garedew *et al.* (2017) report wild enset widely distributed in Sheka forest (SNNPR region;
4 Skeka zone). Herbarium records indicate historical presence in Metekel (Benishangul-Gumuz
5 region), West Wellega (Oromia region), Kefa and Sidama zones (SNNPR region).
6 Observations of wild enset are further complicated by escaped domestic enset occurring on the
7 periphery of villages or in neighbouring forests (e.g. a cluster of 15 enset plants closely
8 resembling domestic varieties in Harena forest, several hundred meters from the nearest
9 habitation; J Borrell pers. obs.).

10 As a forest species, the wild enset distribution will be affected by regional rates of forest loss.
11 Ethiopia currently has less than 4% forest cover, down from a potential climax vegetation
12 maximum of 25-35% (Reusing 1998; Moat *et al.* 2018). It is possible that wild enset has
13 become extinct in some areas, for example, in the Rift Valley area around Hawassa (SNNPR
14 region; Sidama zone), where an estimated 82% of forest has been lost since 1972 (Dessie and
15 Kleman 2007). This area has a strong and diverse enset culture, and is considered by some the
16 origin of enset domestication (Simoons 1965), yet there is no contemporary evidence of wild
17 enset. By comparison, domesticated enset is considerably more widespread in Ethiopia,
18 suggesting substantial niche expansion for the cultivated crop. The distribution of domesticated
19 enset appears to reflect both amenable ecological conditions, population density (Yemataw *et*
20 *al.* 2014b) and the presence of ethnic groups for which it is a staple (Tsegaye and Struik 2002;
21 ethnobotanical aspects also reviewed in Borrell *et al. in prep*). Enset is a highland crop
22 cultivated at altitudes ranging from 1200 to more than 3100 meters a.s.l. (Simoons 1965; Brandt
23 *et al.* 1997; Tsegaye *et al.* 2001, 2002) and is reported to perform best at elevations of 2000-
24 2750 m (Brandt *et al.* 1997). According to Bezuneh and Feleke (1966) the soil type of enset
25 cultivation areas is moderately acidic to slightly basic (pH 5.6-7.3), with 0.10–0.15% total

1 nitrogen and 2–3% organic matter. Similarly, Shank (1994) reported that enset often performs
2 best in acidic, heavy clay soils that retain high levels of organic matter when manured.
3 Preferred climatic conditions are reported to be an average air temperature of 16-20°C and an
4 annual rainfall of 1100-1500mm, evenly distributed throughout the year (Brandt *et al.* 1997).

5 The suitability of environmental conditions for enset cultivation across the domestic
6 distribution clearly differs, as yield, age to maturity and maximum obtainable size vary
7 considerably (Tsegaye *et al.* 2001; J. Borrell and A. Davis, pers. obs.), although this is likely
8 confounded with agriculture practice and landrace selection (Shumbulo *et al.* 2012). At the
9 upper elevation limit, low temperatures and frost has been hypothesised as a constraint; at the
10 lower limit, water availability (Brandt *et al.* 1997). Various authors have defined enset as a
11 drought tolerant (Shumbulo *et al.* 2012; Harrison *et al.* 2014) and it is widely regarded as
12 ‘drought-resistant’ in Ethiopia (Birmeta 2004) although there is a lack of rigorous evidence to
13 demonstrate this.

14 The geographical range of wild enset (in Ethiopia) is more limited, perhaps due to more specific
15 ecological requirements or alternatively loss of habitat (Figure 5). According to several authors
16 it is restricted to 1200–1600 m a.s.l. (Brandt *et al.* 1997). Baker and Simmonds (1953)
17 described enset as a species of swamps, river banks or forest clearings, at middle altitudes,
18 rarely or never in dense shade. Across its regional distribution, they record altitudes ranging
19 from 1300 m to 2300 m. Contemporary wild populations have been reported in humid forest,
20 frequently along river banks, often consisting of 10–200 plants (Birmeta *et al.* 2004). It
21 therefore seems that distribution and environmental tolerance of domesticated enset, relative
22 to its wild progenitor, has been expanded through the domestication process.

1 **COMPARATIVE MORPHOLOGY OF WILD AND DOMESTICATED ENSET**

2 The vegetative morphology of domestic enset is highly variable (Figure 1). Pseudostem colours
3 include red, green, purple, black and many colour combinations (Yemataw *et al.* 2014b).
4 Mature height ranges from 2 m in dwarf variants to more than 10 m for enset plants occurring
5 in the Sidama area. According to farmers, corm size, tissue quality for starch, root structure for
6 harvestability, drought, frost and disease tolerance are all variable among clonal genotypes
7 (Tsegaye and Struik 2001; Bizuayehu T. 2002; Tewodros and Tesfaye 2014). This indicates
8 high phenotypic diversity. By comparison wild enset is predominantly green (also referred to
9 as ‘white’ in Ethiopia). Hildebrand (2001) showed that wild and domesticated enset differ in
10 growth pattern, with the former increasing girth more consistently with age and the latter
11 attaining larger girth earlier in development. This could be evidence of farmer selection for
12 earlier maturing genotypes. Domesticated enset is also characterised by further traits that are
13 not observed in wild enset. Hildebrand (2001) recorded the presence of a wax bloom on the
14 ventral leaf blade and hypothesised that this is a water stress response to hotter conditions and
15 sunlight exposure in farms, as opposed to the conditions found in the forests where wild enset.
16 A general comparison of wild and domestic traits is given in Table 2.

17 18 ***Floral morphology***

19 Poorly known (Figure 6), largely due to the fact that enset is harvested before flowering to
20 maximise starch yield and is exclusively multiplied using vegetative propagation techniques.
21 Despite this, there appears to be variation in inflorescence length, fruit shape and size and some
22 farmers may use fruit morphology to differentiate landraces (pers. Comm. Solomon Tamrat).
23 Whether all cultivated varieties produce viable seed, or indeed whether all varieties flower is
24 currently unknown. Similarly the mode of pollination and seed dispersal has not been studied

1 extensively, with various authors suggesting self-pollination (Tabogie 1999), nectar seeking
2 insects (Shigeta 1990), bats (Fleming *et al.* 2009) or monkeys (Hildebrand 2001) as vectors.

3

4 ***Seed morphology and germination***

5 As with other Musaceae, seed germination is generally poor and inconsistent, with a thorough
6 understanding of germination requirements not yet achieved. Desiccated seeds have
7 successfully been used in germination tests (Tesfaye, 1992), suggesting that storage behaviour
8 is orthodox (Ellis and Roberts, 1980). According to Priestley (1986), *E. ventricosum* seeds can
9 be maintained for 1-2 years in commercial storage. The thick testa with a cutinous inner
10 integument (Graven *et al.*, 1996) provides considerable protection, and has led people to
11 consider enset as being physically dormant requiring scarification (Tesfaye, 1992); however it
12 seems that enset seeds are able to imbibe water without mechanical intervention to equilibrium
13 in four days (Bezuneh, 1971, Karlsson *et al.*, 2013). Furthermore, whilst soaking can improve
14 imbibition, it is not essential and numerous chemical treatments have been applied to enset
15 seeds with little success (Tesfaye, 1992, Karlsson *et al.*, 2013). Enset embryos do not extend
16 within the seed (Karlsson *et al.*, 2013), so they are not therefore morphologically dormant.
17 Eco-physiological germination tests have so far been inconclusive, and an area of exploration
18 could be the role of alternating temperatures, as this is important for *Musa* seed germination
19 (Chin, 1996, Stotzky and Cox, 1962, Ellis *et al.*, 1985), but has given inconclusive results for
20 enset (Bezuneh, 1971, Tesfaye, 1992).

21 Like *Musa* (Cox *et al.*, 1960, Asif *et al.*, 2001), *in vitro* germination of excised embryos has
22 been used as an alternative technique to provide access to enset plant regeneration and the
23 development of new genotypes (Negash *et al.*, 2000, Diro *et al.* 2003, 2004). Progress on this,

1 and other in vitro techniques (shoot tip culture, callus culture and somatic embryogenesis) has
2 been reviewed by Diro et al. (2004).

3 In a comparison of wild and domesticated enset, it is important to note that wild enset, to the
4 best of our knowledge, engages exclusively in sexual reproduction, whilst in a farm setting
5 domestic enset is exclusively clonally propagated by farmers (see Borrell et al. *in review*).
6 When permitted to flower (enset are normally harvested before flowering) seed production and
7 fertility appears further diminished in domesticated plants (Hildebrand 2001), which may pose
8 challenges for germplasm conservation. Dissection of a small number (n=4) of wild,
9 naturalised and domestic enset showed a marked difference in well-formed, viable seeds per
10 fruit and per infructescence. Wild enset tend to have thousands of seeds, whilst domestic enset
11 have few fruits with full-sized seeds, and low numbers of viable seeds in each fruit, possibly
12 due to the absence of suitable pollinators in the domestic environment, or reduced fitness
13 resulting from a domestication bottleneck.

14

15 **DIVERSITY OF WILD AND DOMESTICATED ENSET**

16 Whilst Enset has only been domesticated in a comparatively small region of the species' wild
17 distribution, the reported phenotypic diversity of cultivated enset landraces is exceptionally
18 high (Shank 1994; Brandt *et al.* 1997; Tsegaye and Struik 2002; Bizuayehu 2008). Farmers
19 claim to maintain diverse enset varieties for several reasons, including; different qualities that
20 suit different food products, alternative uses such as fibre, fodder or medicine and different
21 climatic and pest tolerance (Olango *et al.* 2014; Yemataw *et al.* 2014a).The Areka Agricultural
22 Research Centre (Wolayta Zone, Ethiopia), for example, reports that it maintains 623 distinct
23 enset landraces from 12 major enset growing areas of Ethiopia (Yemataw *et al.* 2017). In our
24 own literature survey, we recorded 1270 unique vernacular names for wild and domestic enset

1 varieties from 28 publications (Table S2). After clustering similar sounding names, we still
2 recovered 475 phonetic groups (Figure 7). Furthermore, there was remarkably low
3 commonality between studies with the vast majority of enset landraces being referenced in the
4 literature only once.

6 ***Indigenous knowledge***

7 Farmers use vernacular names for identification of enset clones, with up to 26 landrace names
8 being recorded from a single farm (Yemataw *et al.* 2014a). Whilst vernacular names are known
9 to vary considerably based on region, language and ethnic group, it is difficult to know if this
10 represents distinct diversity or vernacular duplication. Indeed the true number of landraces may
11 be considerably less or more than we report: as in many other crops, the same genotype may
12 be given multiple names (synonyms), or different genotypes given the same name (homonyms;
13 see for apple (*Malus*) Liang *et al.* 2015).

14

15 ***Phenotypes***

16 Whilst the majority of studies rely on indigenous knowledge for identification of differing
17 landraces (Olango *et al.* 2014; Yemataw *et al.* 2016), several authors have also attempted to
18 document and analyse enset landraces using phenotypic characters (morphology). Initially,
19 Zippel and Kefale (1995) developed a field survey technique for the rapid identification of
20 enset clones based on morphological characters, principally colour. In subsequent research
21 Tabogie (1997) reported significant variation among 79 enset accessions collected from
22 different parts of Ethiopia and attempted to associate yield with different traits. Bekele *et al.*
23 (2013) undertook a similar study and categorized 120 distinct enset landraces into 11 clusters.
24 The most important morphological descriptors included pseudostem circumference, corm

1 weight and fibre yield, with maturity period and number of leaves also contributing useful
2 information. This suggests that there is indeed high diversity in desirable crop traits. Other
3 authors report similar morphological diversity in field surveys (Yemataw *et al.* 2012, 2014a,
4 2017). However due to the vast number of landraces and considerable variability between
5 individuals, the degree of precision and consistency in morphological studies is unclear.

6

7 ***Genotypes***

8 In comparison with other important food crops, there are few studies employing molecular
9 markers for germplasm characterization and evaluation of genetic diversity in Enset (Table 3).
10 In the first studies of their kind, RAPD (Random Amplified Polymorphic DNA) was used to
11 measure the genetic diversity and relatedness of 111 cultivated enset clones collected from nine
12 enset growing regions (Birmeta *et al.* 2002) and 146 cultivated enset clones collected from four
13 regions, in Ethiopia (Negash *et al.* 2002). The authors reported high level of genetic variability
14 among the tested germplasm as well as considerable duplication of vernacular names (for
15 landraces) among the collection and suggested that full identity between two clones can only
16 be determined by more extensive genome comparison. In a later study, domesticated enset was
17 then compared to five wild enset populations by Birmeta *et al.* (2004), with the two groups
18 found to cluster separately in an UPGMA analysis based on RAPD markers.

19 Subsequently, 71 cultivated enset clones collected from two different areas of south-western
20 Ethiopia (Keffa and Dawro zones, SNNPR region) were evaluated with ISSR (Inter simple
21 sequence repeats) markers to estimate genetic variation (Tobiaw and Bekele 2011). Two ISSR
22 markers produced 26 clear scoreable bands and clustered all the 71 cultivated enset landraces
23 in to two major groups, which aligned with their collection regions. Olango *et al.* (2015)
24 developed the first set of genomic microsatellite markers from pyrosequencing of an enriched

1 genomic library of *E. ventricosum* and examined their cross-genus transferability to related
2 taxa, using them to estimate genetic diversity, as well as relationships between wild and
3 domesticated enset accessions. Analysis demonstrated the intra-population allelic variation
4 contributed more to genetic diversity than inter-population variations. Phylogenetic data
5 combined with PCA results revealed that wild enset clustered together and were distinct from
6 domesticated enset landraces sampled across the region (Olango *et al.* 2015).

7 More recently there has been an effort to enable enhanced enset research through the
8 publication of the *E. ventricosum* draft genome sequence (Harrison *et al.* 2014), with an
9 approximate size of 547 Mb (GenBank accession number AMZH02). Whilst the original
10 ‘JungleSeeds’ assembly has unknown provenance and is only distantly related to Ethiopian
11 plants, the subsequent assemblies of the Ethiopian landraces ‘Onjamo’, ‘Bedadeti’ and ‘Derea’
12 are likely to be of more use to researchers. A further 17 *E. ventricosum* accessions have
13 subsequently been re-sequenced using Illumina HiSeq and MiSeq platforms and raw reads
14 aligned against the published *E. ventricosum* ‘Bedadeti’ reference genome sequence (Yemataw
15 *et al.* 2018). Available genome sequences are reported in Table 4.

16

17 ***Crop Wild Relatives (CWRs).***

18 Of the studies reporting vernacular, phenotypic and genetic diversity of enset, almost all
19 exclusively address domesticated enset landraces. Only two studies, by Birmeta *et al.* (2004)
20 and Olango *et al.* (2015) included formal analysis of wild enset accessions in Ethiopia.
21 Therefore, whilst wild and domesticated enset are distinct, the relationship between
22 domesticated landraces and their wild crop progenitors, as well as their value in breeding
23 programmes is unclear.

24 ***Spatial patterns of diversity.***

1 Without a clear understanding of enset diversity (and how it is partitioned across vernacular
2 taxonomies, phenotypic and genetic components, and wild vs. domestic), it is difficult to draw
3 conclusions on the geographic distribution of diversity in Ethiopia. Negash *et al.* (2002)
4 documented 146 clones from four enset growing zones; Kefa-Sheka (western SNNPR region),
5 Sidama (eastern SNNPR region), Hadiya and Wolayta (both in central SNNPR region) in
6 Ethiopia. While Birmeta (2004) recorded 111 clones from nine enset growing areas. Emerging
7 from these studies are a first indication of regional patterns of diversity; for example (Yemataw
8 *et al.* 2014a) found Hadiya (within the Gurage-Wolayta enset area; Figure 5) to have the highest
9 landrace richness, as well as the greatest number of unique landraces, whilst Sidama had the
10 lowest (Fig. 5). In Sidama, Tesfaye and Lüdders (2003) found enset diversity to be correlated
11 with elevation, whilst in the Gamo Highlands Samberg *et al.* (2010) found enset diversity
12 peaked at 2500-2800m with an average of 15 landraces per farm, and only six or seven per
13 farm below 2000m and above 3000m respectively, thus hinting at important biogeographical
14 patterns. Despite the above studies, a national assessment of areas of enset diversity is lacking.

15

16 **NEAR-TERM THREATS: ENSET PESTS AND PATHOGENS**

17 Pests and diseases affecting enset growth and yield represent the most serious short-term threat
18 to enset production. The most important disease is *Xanthomonas* wilt of enset (XWE;
19 *Xanthomonas campestris* pv. *musacearum*), whilst enset root mealy bug (*Cataenococcus*
20 *ensete*) (Figure 6). Additional pests (nematodes, mole rat, porcupine, termites) and diseases
21 (bacterial, fungal and viral) currently cause moderate to limited damage.

22

23 *Xanthomonas wilt of enset (XWE)*

1 Caused by the pathogen *Xanthomonas campestris* pv. *Musacearum*, XWE was first observed
2 on enset in Ethiopia in the 1930s (Castellani 1939), but only identified as *X. campestris* pv.
3 *musacearum* on enset in 1968 (Yirgou and Bradbury 1968) and subsequently on banana in
4 1974 (Yirgou and Bradbury 1974). Various symptoms characterize the disease: leaf yellowing,
5 distortion and wilting/collapse, and pockets of yellow or cream-colored slimy ooze are visible
6 in cut vascular tissues in leaf sheaths, leaf midribs and real stem (Blomme *et al.* 2017). Vascular
7 bundles often become discolored, although this symptom is not as conspicuous as the internal
8 discoloration observed in banana. Total yield loss is expected once the disease takes hold,
9 although plant recovery has been observed in tolerant landraces (e.g. the landraces ‘Mazia’,
10 ‘Badadeti’, ‘Astara’, J Borrell pers. obs.; Hunduma *et al.* 2015).

11 The main mode of spread of XWE is through cultivation tools and contaminated planting
12 material. However porcupines, warthogs and mole rats often eat rhizomes, and in the process,
13 can transmit XWE (Brandt *et al.* 1997). Insect-vector transmission via flowers does not occur
14 in cultivated enset as plants are harvested before or at flower emergence. The incidence of
15 XWE in wild enset is not known. More broadly, the pathogen arrived in Uganda and the Eastern
16 Democratic Republic of Congo in 2001 and has since spread across most of the highland
17 banana production zones of east and central Africa, most likely from the disease reservoir in
18 enset (Blomme *et al.* 2017). Control measures that could prevent, reduce or eliminate the spread
19 of XWE include the disinfection of tools between use on different plants, preventing animals
20 from browsing infected plants, fencing infected sites and the rigorous removal of infected
21 plants (Quimio and Tessera 1996). We also note concurrent genomic research on the *X.*
22 *campestris* pv. *Musacearum* which has identified evidence of two distinct sublineages,
23 suggesting more than one introductory event, and candidate virulence factors that may facilitate
24 host infection (Nakato *et al.* 2018).

25 ***Pests affecting enset growth and yield***

1 The enset root mealy bug (*Cataenococcus ensete*) is a major pest of enset in southern Ethiopia,
2 having been first reported at Wonago (Tsedeke 1988; Addis *et al.* 2008). Enset root mealybugs
3 have an elongate-oval body covered with bright white wax secretions on the dorsal and lateral
4 sides. Although the insect has been present in various parts of the enset growing region, it has
5 only become a serious threat to enset production in recent years (Addis *et al.* 2008). The insect
6 attacks enset of all ages, but particularly young plants, with symptoms including retarded
7 growth, dried out outer leaves (but with a green central shoot) and eventual plant death,
8 especially under moisture stress. Enset plants attacked by root mealybugs have a significantly
9 lower number of roots as compared to healthy plants. As a result, mealy bug-damaged enset
10 plants are more easily uprooted. Mealy bugs are mainly spread through infested planting
11 materials (Bizuayehu 2002; Addis *et al.* 2008), thus production of mealy bug-free planting
12 materials is a key control measure.

13 Although symptoms are often not clearly visible, root necrosis due to nematodes poses an
14 increasing constraint to enset production (Addis *et al.* 2006). Bogalel *et al.* (2004) carried out
15 a nematode survey at 25 enset cultivation sites, representative of seven agro-ecological zones.
16 The predominant nematode species found was *Pratylenchus goodeyi* (5640 per 100 g fresh root
17 weight), followed by *Aphelenchoides ensete* and *Meloidogyne* spp. The nematode
18 *Aphelenchoides ensete* was also isolated from leaves that showed severe streak-like symptoms
19 on young enset plants. In a subsequent study, 294 enset plants across the enset growing region
20 were assessed for root damage and sampled for nematode identification. Twelve plant parasitic
21 nematode taxa were identified: *P. goodeyi* was the most common species, present in about
22 ~90% of samples, with *Ektaphelenchoides* spp. and *Meloidogyne* spp. also observed (Addis *et*
23 *al.* 2006).

24 ***Minor diseases caused by bacterial, fungal and viral pathogens***

1 The fungal disease *Sclerotium root and corm rot of Enset* is characterized by a gradual rotting
2 of roots and leaf sheaths at soil level and stunted plant growth (Quimio and Tessera 1996). The
3 causal agent was identified as a *Sclerotium* sp. which can gain entry to enset plants through
4 damaged roots and corms. The pathogen survives in disintegrating root and corm tissue present
5 in the soil (Quimio and Tessera 1996). A second fungal disease, *Cephalosporium inflorescence*
6 *spot of enset* causes extensive necrosis of flower bracts and necrotic spots on leaf sheaths of
7 mature plants (Tessera and Quimio 1994). Finally, *Enset streak* is believed to be caused by a
8 badnavirus (Tessera *et al.* 1996) and chlorotic and yellow mosaics, streaks and stripes are
9 characteristic leaf symptoms of the disease. Severely affected plants have also narrow distorted
10 leaves and become stunted. Early infection results in a significant reduction in yield. The major
11 means of dissemination of the disease is through infected corms or suckers arising from an
12 infected corm. A complete overview of enset bacterial, fungal and viral diseases is described
13 in Jones (2000).

14

15 **LONG-TERM THREATS: CLIMATE CHANGE AND DECLINING**

16 **DIVERSITY**

17 In the longer term, shifting environmental conditions due to climate change and declining farm
18 diversity of landraces are likely to be increasingly important threats to enset agriculture
19 (Adhikari *et al.* 2015). Social changes through urbanization, mobility and labour are all threats,
20 too, to traditional farming practices. Threats to germplasm diversity are compounded by a lack
21 of nationally and internationally secure germplasm collections, including both *in vivo* and long-
22 term storage as seeds or through cryopreservation, with the strong restrictions on germplasm
23 movement and confidentiality considerations limiting opportunities outside Ethiopia and
24 public availability of knowledge. Climate change is projected to substantially impact all

1 agricultural systems in East Africa, resulting in declining and more variable yields, with
2 subsequently adaptation and transitions to new growing areas becoming necessary (Challinor
3 *et al.* 2014; Adhikari *et al.* 2015; Rippke *et al.* 2016). Despite this, the projected impact on
4 enset cultivation has not been assessed. Concurrently, several authors have suggested an overall
5 decline in the diversity of enset landraces on farms in Ethiopia (Negash et al 2002; Birmeta *et*
6 *al.* 2004; Zengele 2017), however there have been no systematically repeated surveys or clear
7 empirical data to support this.

8

9 ***Enset susceptibility to climate change***

10 Ethiopia's mean annual temperature increased by 1.3°C between 1960 and 2006 at an average
11 rate of 0.28°C per decade (McSweeney *et al.* 2010). Nationally, mean annual temperature is
12 projected to increase by 1.3 to 3.1°C by the 2060s and 1.5 to 5.1°C by the 2090s (McSweeney
13 *et al.* 2010). Historic precipitation patterns are less clear due to strong inter-annual and inter-
14 decadal variation, but appear to have declined slightly overall (Jury and Funk 2013; Mekasha
15 *et al.* 2014). Future projections indicate increasing annual precipitation but are highly variable
16 (McSweeney *et al.* 2010; Mekasha *et al.* 2014).

17 Despite these past and future climatic changes, there have been no studies assessing the
18 projected impact on enset. In studies on *Coffea arabica*, for which there is substantial
19 environmental niche overlap with enset, Moat *et al.* (2017) showed that 39–59% of current
20 growing area could experience climate changes large enough to render them unsuitable for
21 coffee farming, and Davis *et al.* (2012) report a 38–90% reduction in climatically suitable areas
22 for wild populations. Coffee requires the correct environmental conditions at specific times of
23 the growing cycle for successful flowering and fruiting (Moat *et al.* 2017). By contrast, enset
24 is less susceptible to short term temperature or precipitation variation which can detrimentally

1 impact coffee crops, and is not reliant on a sexual reproduction cycle for food production
2 (DaMatta and Cochicho Ramalho 2006).

3

4 *Enset germplasm collections*

5 Whilst empirical evidence of declining enset diversity is lacking, systematic collection and
6 maintenance of diverse crop germplasm is important to maximise use and availability in
7 sustainable agricultural development, and guard against the erosion of genetic diversity.
8 Bioversity International (a CGIAR Research Centre) is currently committed to the long-term
9 preservation of the entire banana genepool. This has been achieved through the collection and
10 maintenance of 4928 *Musa* germplasm accessions, encompassing numerous crop wild
11 relatives, including a handful of *Ensete* spp. (Ruas *et al.* 2017). Collected accessions are
12 preserved as living collections across numerous partner organisations, as well as *in vitro* under
13 slow growth conditions and using cryopreservation. To facilitate this, the Musa Germplasm
14 Information System (MGIS) was developed ([URL:https://www.crop-diversity.org/mgis/](https://www.crop-diversity.org/mgis/))
15 which has served to accelerate *Musa* research
16 (for example, MusaNet 2016. Virus free *Musa* germplasm is now freely available for
17 international distribution upon request through the MGIS website; between 1985 and 2014 the
18 Bioversity International *Musa* Germplasm Transit Centre distributed over 17,000 samples
19 among 109 countries worldwide. However, to date only six *Ensete* accessions are available
20 through the MGIS database (Table 5), of which only two are *E. ventricosum*. Of these two, one
21 is termed the ‘red mutant’ which is most likely a commonly available horticultural cultivar
22 named ‘Maurelii’, the other – arguably the most important accession – is of unknown
23 provenance, but reported to be wild. Therefore, it is possible that despite 5000 Musaceae

1 accessions, domesticated landraces of this important tropical crop are not conserved
2 internationally.

3 Comparatively two very large living collections of domesticated enset exist at field sites in
4 Ethiopia. The first, Areka field station (part of the Southern Agricultural Research Institute),
5 reports to maintain a collection of approximately 600 landraces (Harrison *et al.* 2014) from
6 several regions of Ethiopia, with four clonal replicates of each. Second, is a newer collection
7 at the University of Wolkite (Figure 1C), which maintains approximately 110 landraces from
8 the Gurage region with up to 15 replicates of each. Information on these collections, such as
9 the landraces they contain, is not publicly available. Finally, Guzzon and Muller (2016)
10 conducted a review of the availability of stored and fresh seeds of *E. ventricosum*, *E. homblei*
11 and *E. livingstoninum*. Of the 27 African genebanks, 42 botanic gardens and 4 researchers
12 contacted, only one collection was available: one accession of *E. ventricosum* collected in
13 Tanzania maintained at the Millennium Seed Bank, RBG Kew, UK, stored in orthodox
14 conditions (15%RH, -20°C).

15

16 **FUTURE RESEARCH PRIORITIES**

17 Global food demand is increasing, and is likely to continue increasing into the second half of
18 this century (Godfray *et al.* 2010). By 2050, a projected 100-110% increase in global crop
19 demand, relative to 2005 levels will be required (Tilman *et al.* 2011). In the latter half of the
20 twentieth century this has been largely met, not through substantial growth in cropland, but by
21 improvements in crop productivity often dubbed the ‘Green Revolution’ (Evenson and Gollin
22 2003). In this article we have shown that despite unique and valuable crop attributes, as well
23 as the dependency of 20 million Ethiopians, enset has been overlooked by modern crop
24 improvement research. This therefore represents an opportunity for sustainable exploitation to

1 support livelihoods and improve food security in the region. Here, building on the literature
2 examined in this review, we identify our **ten priority areas for research** (summarised in
3 Figure 8) and make recommendations for short- and long-term development of enset as a key
4 food security crop.

5

6 [Copy-editor and typesetter: Please keep numbers in the following
7 section as they relate to the ten priority areas of Fig. 8]

8

9 **1. Coordination of research and methods**

10 Whilst enset has only been domesticated in Ethiopia, enset research encompasses researchers
11 from at least 40 institutions in 11 countries. Currently, despite positive national and
12 international collaborations (for example, Brandt *et al.* 1997; Yemataw *et al.* 2018), enset
13 research is still disconnected with many interesting and important research programmes
14 running in isolation. Partly, the aim of this review is to draw together many disparate aspects
15 of enset research to facilitate discoverability and collaboration by researchers.

16 In addition, we relate the experience of the Global Musa Genomics Consortium
17 (<http://www.musagenomics.org>) which sought to bring together expertise and enable close
18 collaboration, the sharing of materials, resources, data and technology to accelerate *Musa*
19 breeding efforts (Roux *et al.* 2011). It is our view that enset research and food security in
20 Ethiopia could benefit from such an approach, with equitable and appropriate access and
21 benefit sharing agreements in place. Here, we present and make available the resource
22 www.enset-project.org which will act as an open repository for data emerging from our current
23 research programme.

24

2. Experimental evaluation of enset agronomic practices

There are numerous cultural practices employed in enset cultivation that are reported to significantly influence growth and yield, however few of these have been empirically evaluated in robust, replicated and controlled experiments (reviewed in Borrell *et al. in prep.*). A key practice, for instance, involves systematic transplanting of enset at specific ages, which appears to have a dramatic impact on the resulting pseudostem and corm size (Yemataw *et al.* 2016), perhaps by delaying maturity. In a study by Tsegaye (2007) transplanting treatments significantly affected height, pseudostem circumference and dry matter yield, and increased partitioning of dry matter to harvestable parts. To our knowledge a similar practice has not been reported in any other crop. Other practices include aeration of the soil, mulching with discarded plant material, companion plants, the use of fertilizer, various rhizome preparation practices for vegetative multiplication, as well as treatments for pests and diseases. However, the efficacy of these practices is largely unknown and represent an important first step in optimising enset agriculture.

3. Disease characterisation and development of disease free tissue culture protocols

Whilst several pests and pathogens are known to affect enset cultivation in Ethiopia, their impact on regional yields is yet to be quantified. Similarly, geographic patterns in disease incidence are not yet available. In the medium-term, it is likely that different degrees of disease tolerance may be identified across enset landraces and crop wild relatives. This genetic diversity will provide the long-term basis for crop breeding to generate disease resistant genotypes. The generation of disease free tissue culture protocols (for example; Tripathi *et al.* 2015) is also likely to play an important role. Concurrently, ongoing surveillance to identify newly emerging pathogens, or the potential for transmission from related species (e.g. the widely cultivated *Musa*), is an important safeguard for enset sustainability.

4. Remote sensing

Estimates of the land area under enset cultivation (e.g. Shank 1994 and Central Statistical Agency, CSA, Government of Ethiopia 2004), and associated yields (Pijls *et al.* 1995; Tsegaye and Struik 2001; Sahle *et al.* 2018) are highly variable and have been historically hampered by difficult access to remote areas. The long-term nature of enset cultivation, local differences in cultivated landraces, plant growth rates, agronomic practice and dependency on co-staple crop productivity in any given period, makes estimating enset production difficult (Cochrane and Adam 2017). Therefore, standardised empirical analyses of the land area under enset cultivation, yield components and inter-annual trends is lacking.

Advances in the resolution and availability of satellite data (e.g. MODIS, Sentinel 2) are increasingly being applied to vegetation and crop surveys (Hütt *et al.* 2016; Immitzer *et al.* 2016; Moat *et al.* 2017). Thus in the near-term there may be the potential to use freely available satellite data to directly monitor annual enset production. Furthermore, this approach could be applied to mapping bacterial wilt outbreaks. Concurrently, improved regional bioclimatic datasets (e.g. Worldclim2) and an enhanced network of climate stations and data loggers across the enset growing region will allow better characterisation of the enset environmental niche and stress conditions. The impact of climate change under a range of future scenarios is yet to be quantified for enset and will form an important part of any future development strategy, as undertaken for coffee in Ethiopia (Moat *et al.* 2017; Davis *et al.* 2018).

5. Diversity and local adaptation

High enset genetic diversity distributed over a wide range of environmental conditions suggests that the domestication process may have facilitated adaptation of landraces to local conditions,

1 and indeed to a wider range of conditions than its wild progenitor. Because enset is clonally
2 reproduced and distributed plant, this represents a powerful system to investigate the genomic
3 basis of adaptive traits. Key steps to achieve this would be the characterisation of existing enset
4 genetic diversity using high resolution genomic markers, standardised methods to measure
5 fitness and yield as well as robust monitoring of environmental conditions. Concurrently,
6 assessing the risk of erosion to enset genetic diversity through the loss or decline of landraces
7 should be a priority for future enset monitoring strategies. In the medium-term this could
8 similarly be extended to monitoring of crop wild relative diversity. In the long-term, with the
9 prerequisite knowledge of germination biology, novel sexual breeding utilising mapping
10 populations and pan-genomic sequencing may enable the development of improved landraces,
11 tolerant of disease, better adapted to current and future climates, or with desirable yield or by-
12 product attributes (Tester and Langridge 2010).

13 **6. Investigation of crop wild relatives**

14 During the process of domestication, crops typically experience a genetic bottleneck resulting
15 in reduced variation when compared to wild progenitors. CWRs are therefore an important
16 source of genetic diversity for crop improvement (Jarvis *et al.* 2008), and may possess desirable
17 traits that have been lost in domesticated landraces. The susceptibility of wild enset to
18 pathogens such as XWE, for example, is currently unknown they may harbour important
19 genetic diversity for disease tolerance or resistance (see for example in wheat, Ali *et al.* 2016;
20 Rasheed *et al.* 2018). Wild enset is also reported to have a higher seed set and germination rate
21 compared to domesticated enset, therefore understanding the reasons why this is diminished
22 the latter will be important in developing seed-based germplasm collections for breeding.

23 Whilst CWRs have been used extensively for breeding in other species (Tester and Langridge
24 2010), such as improving drought tolerance in wheat (Faroq and Azam, 2001), their use is

1 anticipated to further increase due to advances in molecular technology (Hajjar and Hodgkin,
2 2007). Therefore, long-term conservation of wild diversity is a key foundation for the
3 sustainable exploitation of enset. A similar approach has already been undertaken in Ethiopia
4 through the formation of biosphere reserves for wild populations of Arabica coffee (*Coffea*
5 *arabica*) (Davis *et al.* 2012; Aerts *et al.* 2016).

6 **7. Exploring alternative uses**

7 In addition to being a major dietary starch source, enset also has the potential to produce other
8 valuable by products. Fibre can be extracted from the pseudostem and leaves, and has been
9 found comparable with other natural fibres such as flax, sisal and hemp (Teli and Terega 2017).
10 High value wax is currently extracted from closely related banana species (Yanagida *et al.*
11 2003) and several authors have identified the importance of enset as animal fodder (Fekadu
12 and Ledin 1997; Mohammed *et al.* 2013). Enset is also widely considered as an important
13 medicinal plant in Ethiopia, and particularly used to treat fractured or broken bones, as well as
14 for placental discharge in humans and livestock (Tsehaye and Kebebew 2006; Assefa and
15 Fitamo 2016). The chemical basis of these uses has not been explored.

16 **8. Microbiome and endogenous yeast cultures**

17 The plant microbiome is likely in the order of tens of thousands of species, and its relevance to
18 plant health and yield is only beginning to be understood (Berendsen *et al.* 2012). Importantly,
19 there are indications that the microbiome may have a role in suppression of plant diseases.
20 Therefore, in the long-term, characterisation of the enset microbiome across different
21 agroecological environments, combined with whole genome and population genomic studies
22 may provide novel pathways to crop improvement. Concurrently, a significant component of
23 enset agriculture is fermentation of the pseudostem and corm tissue using endogenous yeasts.
24 This practice is currently performed by farmers and is thus highly variable. Development of

1 improved fermentation cultures may result in rapidly improved product quality, as well as an
2 opportunity to improve micro-nutritional content.

3 **9. Systematic germplasm banking and development of genetic resources**

4 Considering their economic and food security value, *Ensete* species, and particularly
5 domesticated enset landraces, are currently severely underrepresented in global *ex situ*
6 germplasm collections. This chronically limits the potential for plant breeding and crop
7 improvement. In the long-term, under scenarios of habitat loss, agricultural intensification,
8 disease spread, climate change and introduction of high yielding genotypes, both wild and
9 domestic enset are at risk of losing genetic diversity, and with it potentially important adaptive
10 traits.

11 Whilst a large number of landraces are present in two collections in Ethiopia, germplasm
12 management of vegetatively propagated plants species such as enset, is costly, time-
13 consuming, vulnerable to poor documentation and requires a large land surface area for proper
14 maintenance. Therefore, a key research goal should be further exploration of the potential for
15 germplasm banking as seeds, together with a strategy to collect germplasm from a wide range
16 of spatial and ecological conditions. Conventional breeding and *ex situ* conservation by seed
17 also requires an understanding of seed desiccation tolerance, longevity in storage, and
18 essentially, germination requirements. As with *Musa*, much of this is not well understood.

19 Similarly, access to domestic enset germplasm outside of Ethiopia is challenging and
20 historically limited. If (with appropriate access and benefit sharing agreements) additional
21 domesticated germplasm could be admitted in to the ITC genebank (Leuven, Belgium) it will
22 not only be more readily accessible to the scientific community (benefiting research and
23 sustainable exploitation), but would also safeguard a critically important tropical crop.

24 **10. Exploring the potential for enset cultivation in Ethiopia and Africa**

1 Within Ethiopia, domesticated enset appears to occupy a range of conditions distinct and
2 somewhat broader than wild enset. Similarly, the wild distribution outside Ethiopia of *E.*
3 *ventricosum* extends as far as South Africa, encompassing a range of environmental conditions
4 not found in Ethiopia. Therefore, it seems likely that the climatic envelope of this already
5 tolerant crop could be further enlarged and potentially introduced to new areas.

6 In Ethiopia, a current research programme has collected four landraces from Dilla (Gedio zone;
7 SNNPR region) and introduced these to a novel enset cultivation area in the vicinity of Ankober
8 (North Shewa; Amhara region), north of Addis Ababa, to investigate performance. An equally
9 important component is the concurrent introduction of enset harvesting and processing cultural
10 knowledge (see Borrell *et al.*, *in prep*). Further afield, a second project is exploring the potential
11 introduction of enset to Zambia in an effort to combat hidden hunger (Cardenas *et al.* 2018).
12 Future research effort should focus on characterising the environmental requirements of enset
13 to predict habitat suitability and assess the feasibility of introduction to novel areas.

14

15 **SUPPLEMENTARY DATA**

16 Supplementary data are available online at <https://academic.oup.com/aob> and consist of the
17 following. **Table S1.** Species and associated GenBank accession numbers for ITS sequences
18 included in the phylogenetic analysis (Figures 2 and Supplementary Figure, S2). **Table S2.**
19 Landrace names for domesticated varieties of *Ensete ventricosum*, identified in the review of
20 available literature. **Figure S1.** Estimated population size of the major enset growing regions.
21 **Figure S2.** Phylogenetic relationships of *Ensete spp.* species within the Zingerberales.
22 **Supplementary Information:** Detailed information on methods used to prepare Figures 2,3
23 and 7 and Supplementary Figures S1 and S2.

24

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9

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18 [Typesetter: TEXT BOX with Figure 9; please place at the end of the
19 article]

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21 **In memoriam: Mark Goodwin**

22 We are deeply saddened to write that our co-author, colleague and friend, Mark Goodwin
23 (Figure 9), passed away suddenly in his University office on 25th August 2018, aged just 58.
24 During the day, he had held many discussions related to Enset, including ways to connect
25 researchers and build collaborations. Mark’s particular expertise was in the delivery of

1 impact from research projects, linking with pedagogy and the importance of advanced
2 training. After finishing his PhD, Mark worked for the UK Government's Overseas
3 Development Administration and The Open University, before joining the University of
4 Leicester in 2006. Within the Department of Genetics and Genome Biology, he was a leader
5 in the Centre for Excellence in Teaching and Learning (CETL), lead the Virtual Genetics
6 Education Centre project, managed the Leicester-Gondar PhD programme and he was an
7 Academic Partner for British Council programmes in Afghanistan and Bangladesh. Mark was
8 a co-investigator for the GCRF Foundation project on Enset leading to the work presented in
9 this publication. Mark was taken from us much too soon, and we will greatly miss his input to
10 the delivery of impact from research programmes.

11

Table 1. Accepted species of the genus *Ensete*, with conservation and domestication.

Accepted species ¹	Common names and synonyms	Conservation status ² and distribution	Domestication status	Uses	Notes
Africa					
<i>Ensete homblei</i>	None	DD; Possibly restricted range	Crop wild relative	Unknown	The majority of locality information for this species, are from historic herbarium collections. Reported to die down to the corm in the dry season (Timberlake and Martins 2010).
<i>Ensete ventricosum</i>	Abyssinian banana, False banana, <i>E. edule</i>	LC; Widely distributed	Domesticated & Crop wild relative	Human food; animal fodder; Fibre; packaging; medicine; ornamental	Due to the practice of harvesting domestic enset before the flowers mature, there is likely limited gene flow between wild and cultivated populations (Birmeta <i>et al.</i> 2004).
<i>Ensete livingstonianum</i>	<i>E. gilettii</i>	LC; Widely distributed.	Crop wild relative	Unknown	Reported to die down to the corm in the dry season (pers. Obs).
<i>Ensete perrieri</i>	Madagascar banana, <i>Musa perrieri</i>	CR; Endemic to Madagascar; Only three known mature individuals.	Crop wild relative	Unknown	Reported to die down to the corm in the dry season (Schatz and Phillipson 2011). Possibly present in the ornamental trade, but genetic confirmation of identity required.
Asia					
<i>Ensete superbum</i>	Cliff banana	EN; Endemic to India	Crop wild relative	Human food; packaging; medicine; ornamental	Overharvesting from the wild of leaves, seeds and young plants has been reported (Bhise <i>et al.</i> 2015).
<i>Ensete glaucum</i>	Snow banana	LC; Widely distributed. (<i>E. glaucum</i> var. <i>wilsonii</i> listed as DD)	Evidence of utilisation	Animal fodder; cultural; ornamental	Denham and Donohue (2009). There is some doubt as to whether <i>E. glaucum</i> var. <i>wilsonii</i> (Tucher) Häkkinen is distinct from <i>E. glaucum</i> . The two species are largely sympatric, with <i>E. glaucum</i> var. <i>wilsonii</i> being a smaller, higher elevation species endemic to Yunnan (Wu and Kress 2000). Possibly present in the ornamental trade, but could be <i>E. glaucum</i> .
<i>Ensete lecongkietii</i>	Orphan banana	NE (Not Evaluated); Endemic to Vietnam	Crop wild relative	Unknown	The most recently described <i>Ensete</i> species (Luu <i>et al.</i> 2012).
Close relatives					
<i>Musella lasiocarpa</i>	Golden lotus banana <i>E. lasiocarpa</i> , <i>Musella lasiocarpum</i>	DD; Essentially unknown in the wild, but common in agricultural areas.	Semi-cultivated	Medicinal use; human food; animal fodder; fiber; alleviation of soil erosion; ornamental.	There is some degree of conflict in the literature over whether genus <i>Musella</i> is truly distinct from genus Enset (Liu <i>et al.</i> 2003; Li <i>et al.</i> 2010). We follow recent evidence from (Janssens <i>et al.</i> 2016).

¹Sources: All species reported here are considered accepted species by POWO (WCSP, 2018). ²IUCN Red List conservation status classifications - NE, Not Evaluated; DD, Data Deficient; LC, Least Concern; EN, Endangered; CR, Critically Endangere

1 **Table 2.** Wild and domesticated traits in *E. ventricosum*

Character	Wild enset	Domesticated enset
Morphology		
Leaf colour	Green / glaucous	Green, red, yellow, purple
Midrib colour	Green	Green, red, yellow, purple, black
Petiole colour	Green	Green, red, yellow, purple, black
Pseudostem colour	Green	Green, red, yellow, purple, black
Pseudostem shape	Conical	Conical, basal enlargement possible in some varieties
Corm size	Small	Enlarged
Corm colour	Dark (reported sometimes black)	Cream to white.
Wax	Not present	Present on ventral leaf blade
Discolouration of tissue after cutting	Present	Uncommon
Palatability		
Pseudostem edibility	Bitter	Edible
Corm edibility	Bitter, largely inedible	Variable, generally sweet. Edible
Genetics		
Genetic diversity	High	High
Chromosomes number	n=9	n=9
Ploidy	Diploid	Diploid
Reproduction		
Reproduction method	Sexual	Asexual (sexual also possible)
Sucker production	No	In some varieties
Seed dormancy	Unknown	Unknown
Other uses		
Medicinal use	None reported	Yes
Fibre	None reported	Yes
Disease susceptibility		
Bacterial wilt	Unknown	Highly susceptible (though some are tolerant)
Mealybug	Unknown	Highly susceptible
Frost	Unknown, suspected intolerant	Tolerant

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1 **Table 3.** Previous genetic and genomic studies of wild and domestic *E. ventricosum* in Ethiopia.

Marker	Aims	No. of markers	No. of genotypes	Origin	Reference
AFLP	Genetic diversity and identity of cultivated enset clones	180 loci	146 domesticated clones	Domesticated	Negash <i>et al.</i> (2002)
RAPD	Genetic diversity among Ethiopian Enset clones	97 loci	111 domesticated clones	Domesticated	Birmeta <i>et al.</i> (2002)
RAPD	Comparison of wild and cultivated gene pools in Ethiopia	72 loci	5 wild populations (48 plants), 9 domesticated clones	Wild and domesticated	Birmeta <i>et al.</i> (2004)
ISSR	Genetic diversity of cultivated enset clones	26 loci	71 domesticated clones	Domesticated	Tobiaw and Bekele (2011)
SNP	Genome sequence	-	1 domesticated clone	Domesticated	Harrison <i>et al.</i> (2014)
SSR	Cross-taxa transferability of markers, Genetic diversity and phylogenetic relationship with <i>Musa</i> spp.	34 markers	6 wild and 64 domesticated clones	Wild and domesticated	Olango <i>et al.</i> (2015)
SNP	Genome assemblies, phylogenetics and SNP datasets	20,000	17 domesticated clones	Domesticated	Yemataw <i>et al.</i> (2018)

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1 **Table 4.** Comparison of available *E. ventricosum* genome sequences and assemblies, with related *Musa* species.

Landrace	<i>E. ventricosum</i> "Bedadeti"	<i>E. ventricosum</i> "JungleSeeds"	<i>E. ventricosum</i> "Onjamo"	<i>E. ventricosum</i> "Derea"	<i>M. acuminata</i> subsp. <i>malaccensis</i>	<i>M. itinerans</i>	<i>M. balbisiana</i>
BioSample	SAMN02854351	SAMN01797775	SAMN05751581	SAMN05729394	SAMEA2272344	SAMN04505257	SAMN02333823
Genbank Assembly	GCA_000818735.2	GCA_000331365.2	GCA_001884845.1	GCA_001884805.1	GCA_000313855.2	GCA_001649415.1	- *)
Coverage	30	40	21	18.4	20.5	92	41.4
Scaffold count	45,745	52,692	51,525	-	7,512	28,415	-
Scaffold N-50	21,097	13,866	16,208	-	1,311,088	195,772	-
Contig count	46,254	71,088	54,038	60,129	29,249	55,966	180,175
Contig N-50	20,943	11,721	15,546	12,314	28,326	35,438	7,884
Size (Mb)	451.3	437.3	444.8	429.5	472.2	455.0	402.5
Total gap length	10,455	286,734	46,732	0	81,753,624	39,952,266	61,115,757

2 *) Assembly is available at: <http://banana-genome-hub.southgreen.fr/organism/Musa/balbisiana> [18 October 2018]

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1 **Table 5.** Internationally available *Ensete* germplasm accessions.

Species	Landrace	Accession number	Institute code	Field collection	In vitro	Lyophilized Leaves	Cryopreserved	Available for distribution	Origin	Origin
<i>E. gillettii</i> (<i>livingstonianum</i>)	-	ITC1389	BEL084 (ITC)	No	Yes	No	Yes	No	Wild	NGA_Jos, Plateau State, Nigeria
<i>E. glaucum</i>	Pisang Pidak	IFRI-001	IDN150 (ICHORD)	Yes	No	No	No	No	Wild	Indonesia
<i>E. glaucum</i> subsp. <i>glaucum</i>	Vudu Vudu	ITC0775	BEL084 (ITC)	No	Yes	Yes	Yes	Yes	Wild	Papua New Guinea
<i>E. ventricosum</i> subsp. <i>ventricosum</i>	-	ITC1387	BEL084 (ITC)	No	Yes	Yes	No	Yes	Wild	Unknown
<i>E. ventricosum</i> subsp. <i>ventricosum</i>	red mutant	ITC1388	BEL084 (ITC)	No	Yes	Yes	No	Yes	Wild	Unknown
<i>E. unknown</i>	Chuoi Nguon	VNIO60	VNM007 (FAVRI)	Yes	No	No	No	No	Landrace	Vietnam

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Figure legends

Figure 1. Domesticated *Enset ventricosum* in Ethiopia. A-B) Original plates of ‘*Ensete*’ from Bruce (1790). C) Large enset plants (landrace ‘Medasho’) grown by small scale farmers in Teticha (Sidama Zone, SNNPR region). D) A typical enset home garden near Butajira (Gurage Zone, SNNPR region). E) An enset germplasm collection at Yerefezy research station, University of Wolkite, (Gurage Zone, SNNPR region). Clear differences in morphology can be observed, with substantial differences in growth rate under local environmental conditions.

Figure 2. Evolutionary relationships of genus *Ensete*. A) The genus *Ensete* is included in the Musaceae, one of eight families of the monocot order Zingiberales which together with the Commelinales is a sister to the Poales that contain the cereal crops including wheat, maize and rice. B) Evolutionary relationships of genus *Ensete* within the Zingiberales base on ITS sequences, including collapsed sister genera within Musaceae and outgroups representing the eight families (see Figure S2 for expanded tree and Supplementary Information for method details). Provenance of the two *E. ventricosum* accessions are Hamburg Botanic Garden (HBG) and Costa Rica (CR; Introduced).

Figure 3. Metaphase chromosomes of *Ensete ventricosum* ‘Maurelli’ $2n=18$. Chromosomes appear blue with the DNA stain DAPI and show two distinct 5SrDNA loci (red) at the ends of a medium sized chromosome pair (A). The simple sequence repeat AAC (green) is distributed along all chromosome arms (B). Sequences were mapped by fluorescent *in situ* hybridization (FISH) using the method by Schwarzacher and Heslop-Harrison (2001, for details see supplementary information. Bar = 5 μ m; ‘x’ denotes unspecified soil/contamination in image.

Figure 4. Three species of *Ensete* occur in mainland Africa, *Ensete homblei*, *E. livingstonianum* and *E. ventricosum*, with a fourth, *E. perrieri*, restricted to Madagascar. *E. ventricosum* is likely to be the most widespread species within the Musaceae, occurring over

much of central, south east and east Africa. Whilst the contemporary distribution reaches as far North as the Ethiopian Highlands, it has been suggested that enset was historically known to the Egyptians (Simoons 1965). By comparison, distribution records for *E. homblei*, *E. livingstonianum* and their numerous synonyms are sparse. *E. livingstonianum* appears to be a species of drier habitats and is reported to die back in the dry season. It has a more westerly distribution than *E. ventricosum*, although they are likely to be sympatric over at least a portion of their range (Baker and Simmonds 1953). Comparatively, *E. homblei* is recorded from only a handful of locations in the south eastern Congo, and neighbouring northern Zambia. This could represent low sampling effort, rarity, or both. Finally, *E. perrieri* is known from only three mature individuals, and is likely to be the most endangered crop wild relative of enset. Due to difficulty in distinguishing species with varying morphology, of different ages, and sometimes only from seed samples, it is possible that some geographically disjunct records represent misidentification, particularly for *E. livingstonianum* and *E. ventricosum*. Records presented here are collated from the literature (Cheesman 1947; Baker and Simmonds 1953), online databases (GBIF, 2018), herbaria (AAU, K) and personal observations.

Figure 5. Distribution of major domesticated enset growing regions (shaded polygons) and wild enset records (red points) in Ethiopia. Whilst domestic enset is occasionally encountered in the wider area, these four enset farming areas represent the major centers of cultivation, where enset is frequently the most important starch staple. The Sidama zone (SNNPR region) is predominantly high elevation, with enset sometimes grown together with crops such as coffee under sparse shade trees. At the highest elevations, enset is subject to frost damage. Gurage-Wolayta cultivation area (from north to south) encompasses adjacent zones (Gurage, Hadiya, Kambata and Wolayta) in the SNNPR region. The northern part of Gurage is markedly drier than many other areas of enset cultivation. Here enset is predominantly grown in dense stands with few other crops and no shade trees. Gamo (Gamo zone) and Ari (South Omo zone)

are relatively poorly known areas of enset cultivation, with high spatial variation in enset importance. Sheka and Dawro (SNNPR region) and adjacent areas in Oromia (Oromia region) are also relatively poorly researched. Here domestic enset occurs in close proximity to wild enset.

Figure 6. Floral morphology and diseases of enset. A) A young inflorescence (landrace: ‘Dima’). B) A mature inflorescence (landrace: Touzoma). C) Ripe enset fruits (landrace: ‘Lemat’). D) A mealybug infested corm. E) A young enset plant showing symptoms of bacterial wilt (XWE). F) An enset plant recently killed by bacterial wilt.

Figure 7. Frequency of enset landrace vernacular names in the literature. By comparison to the high number of domesticated enset vernacular names, only four names were reported for wild enset (*E. ventricosum*) in our survey.

Figure 8. Roadmap for the sustainable development and exploitation of the Ethiopian starch crop enset for food security and to support livelihoods.

Figure 9. [to be placed in the text box]

Mark Anthony John Goodwin: 9th August 1960 – 25th August 2018 (left) and in Hawassa, Ethiopia with enset in May2012 (right, Images Pat Heslop-Harrison)

Figure 1



Figure 2

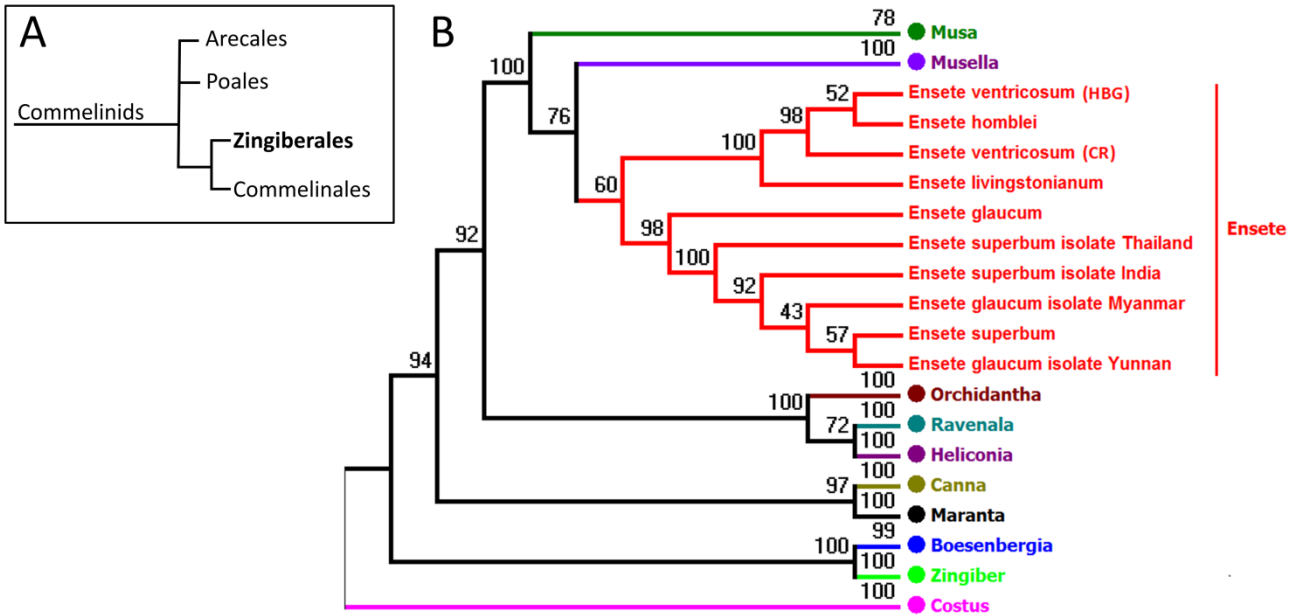


Figure 3

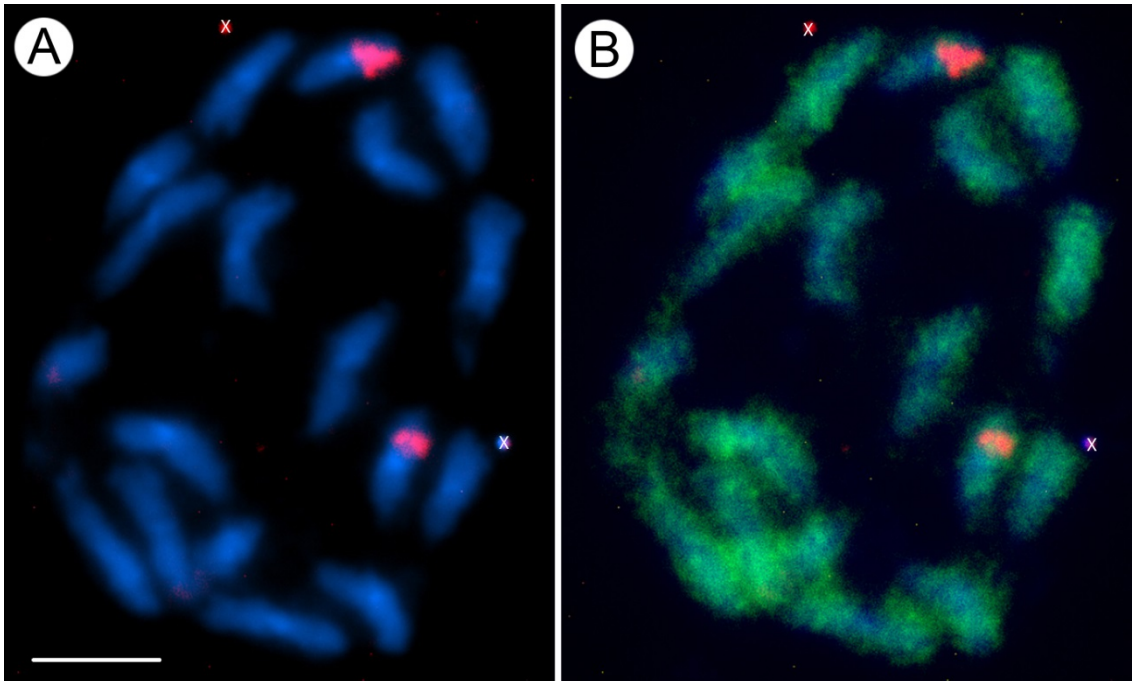


Figure 4

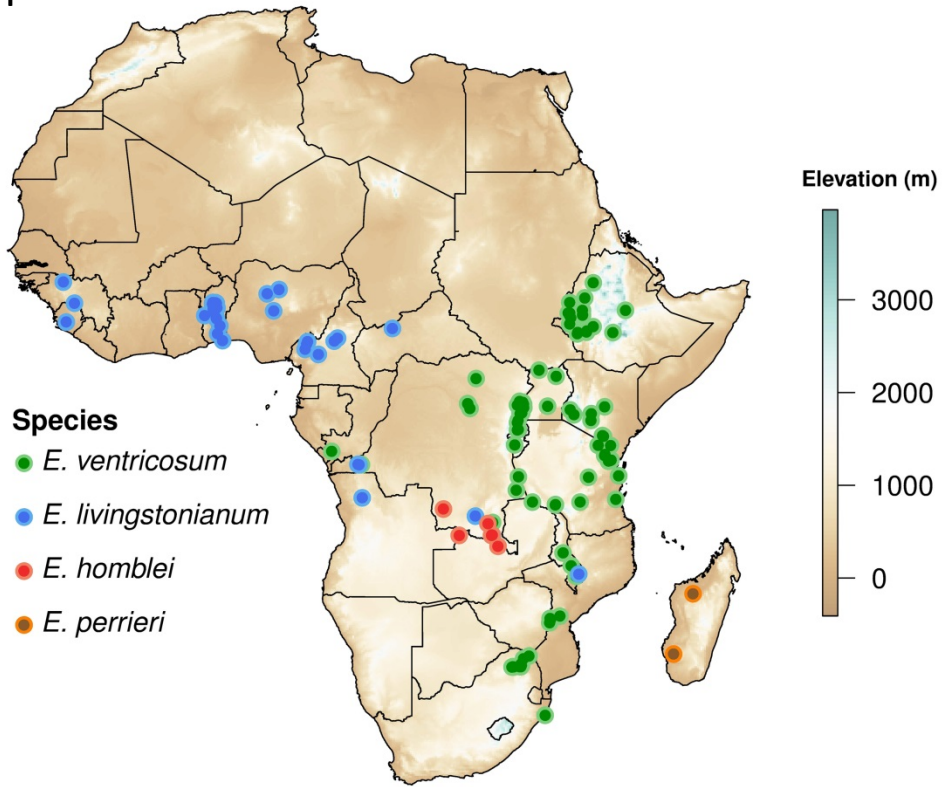


Figure 5

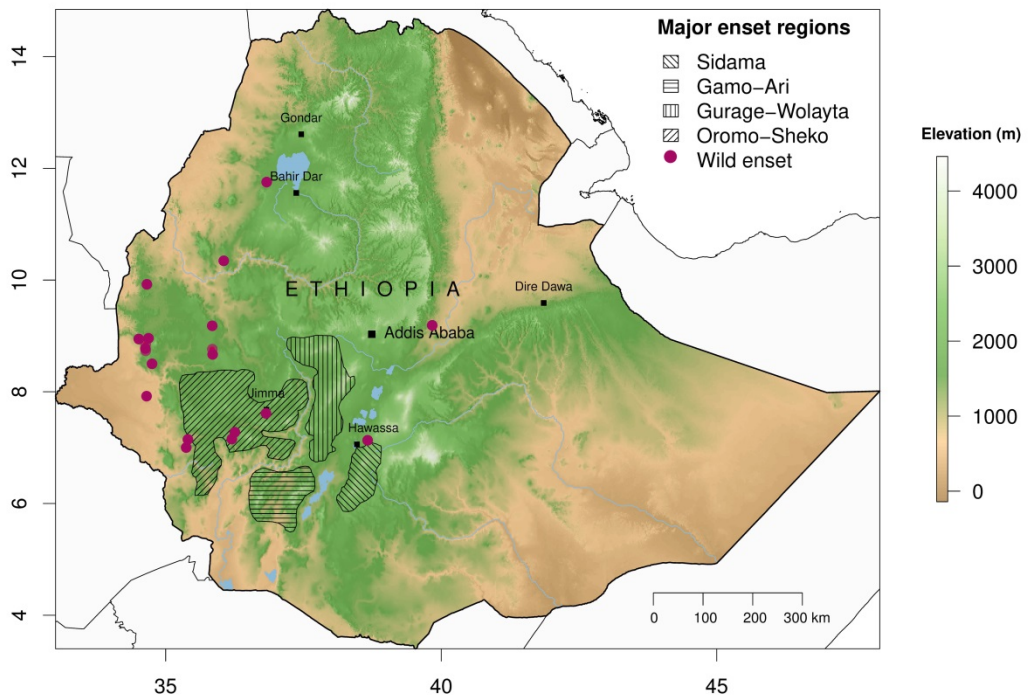


Figure 6

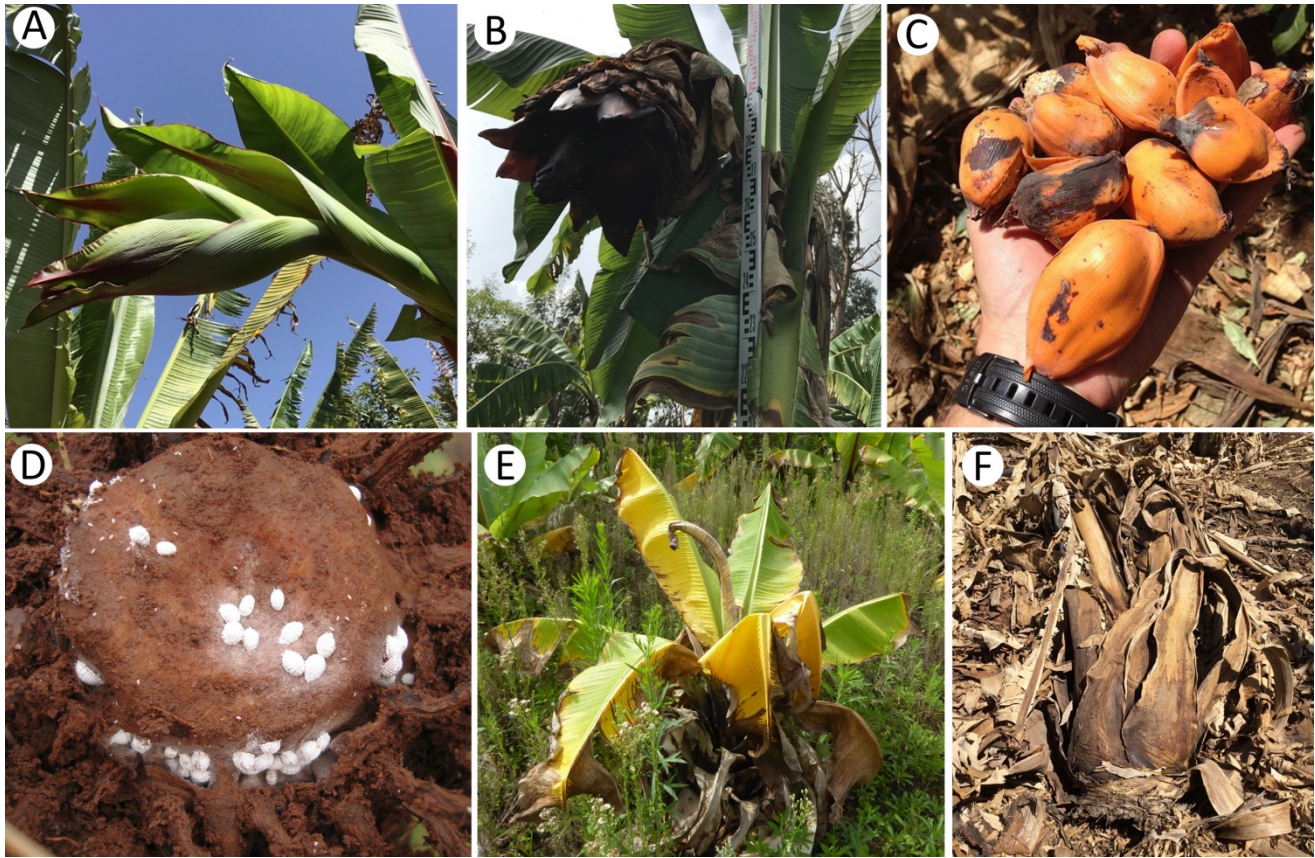


Figure 7

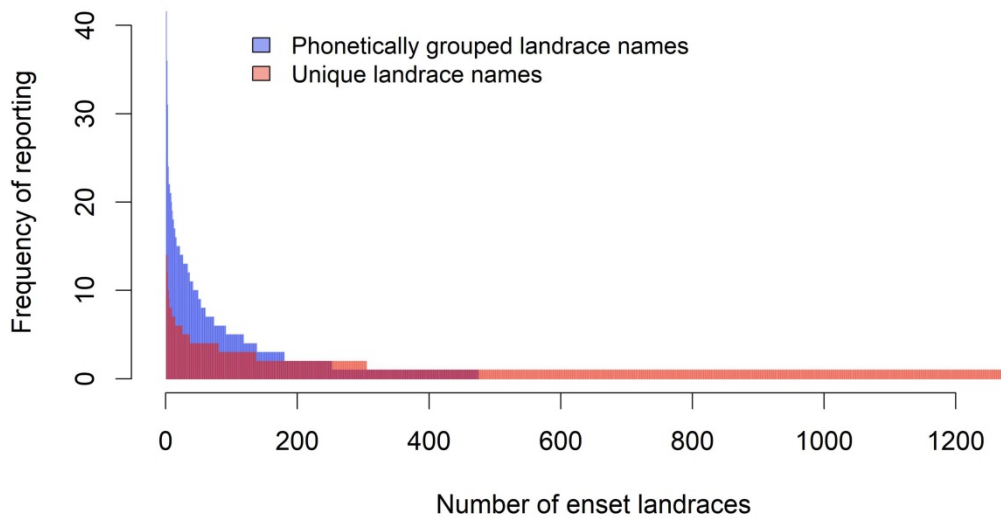


Figure 8

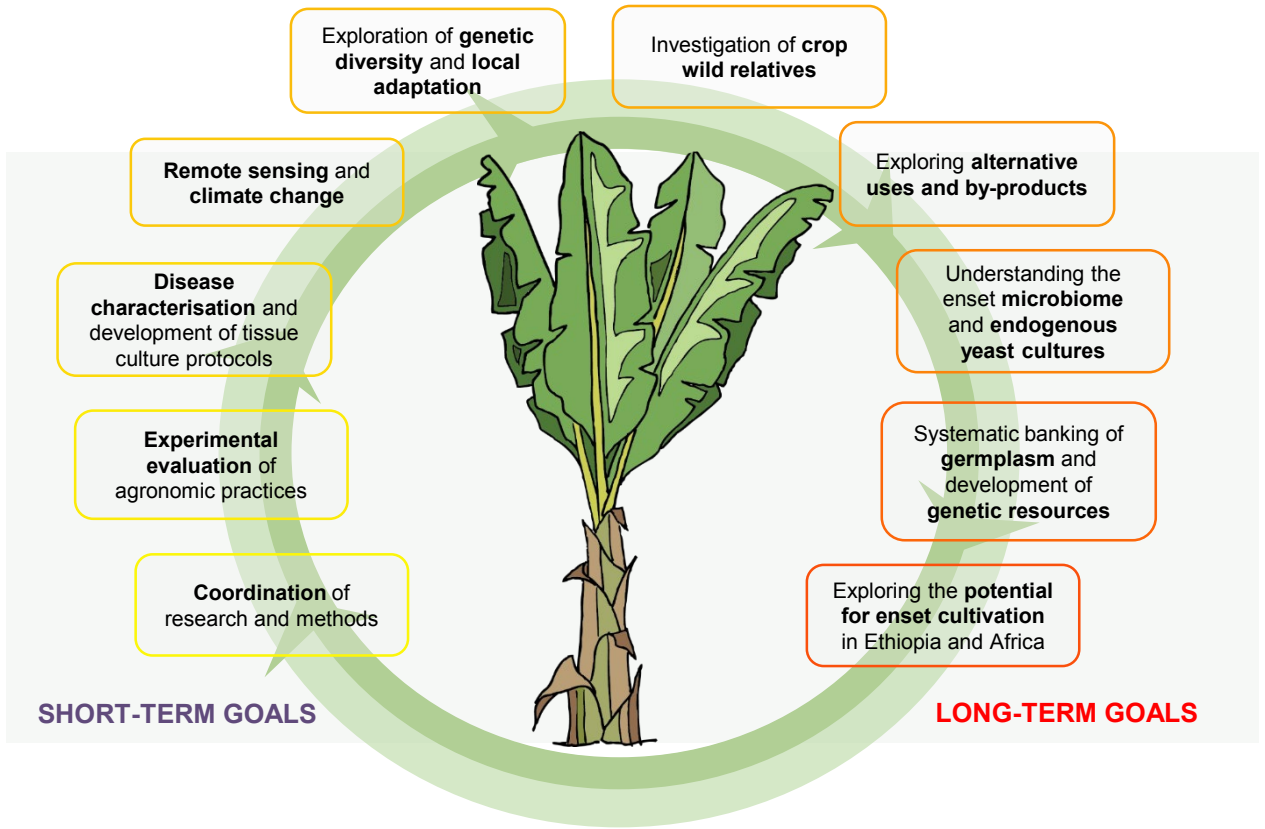


Figure 9

