Received: 30 November 2022 | Revised: 29 January 2023 | Accepted: 31 January 2023

DOI: 10.1002/ppp3.10367

Plants People Planet PPP Open Access

OPINION

Building a feral future: Open questions in crop ferality

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Funding information
National Science Foundation, Grant/Award Numbers: DBI-1547229, DBI-2027654; Botanical Society of America

Societal Impact Statement

Given the rapidly increasing drought and temperature stresses associated with climate change, innovative approaches for food security are imperative. One understudied opportunity is using feral crops—plants that have escaped and persisted without cultivation—as a source of genetic diversity, which could build resilience in domesticated conspecifics. In some cases, however, feral plants vigorously compete with crops as weeds, challenging food security. By bridging historically siloed ecological, agronomic, and evolutionary lines of inquiry into feral crops, there is the opportunity to improve food security and understand this relatively understudied anthropogenic phenomenon.

Summary

The phenomenon of feral crops, that is, free-living populations that have established outside cultivation, is understudied. Some researchers focus on the negative consequences of domestication, whereas others assert that feral populations may serve as useful pools of genetic diversity for future crop improvement. Although research on feral crops and the process of feralization has advanced rapidly in the last two decades, generalizable insights have been limited by a lack of comparative research across crop species and other factors. To improve international coordination of research on this topic, we summarize the current state of feralization research and chart a course for future study by consolidating outstanding questions in the field. These questions, which emerged from the colloquium "Darwins' reversals: What we now know about Feralization and Crop Wild Relatives" at the BOTANY 2021 conference, fall into seven categories that span both basic and applied research:

For affiliations refer to page 10.

(1) definitions and drivers of ferality, (2) genetic architecture and pathway, (3) evolutionary history and biogeography, (4) agronomy and breeding, (5) fundamental and applied ecology, (6) collecting and conservation, and (7) taxonomy and best practices. These questions serve as a basis for ferality researchers to coordinate research in these areas, potentially resulting in major contributions to food security in the face of climate change.

KEYWORDS
crops, cultivation, domestication, feralization, genetic resources, plant breeding, weedy

1 | INTRODUCTION

Feral or de-domesticated plants, that is, free-living populations of domesticated crops that have escaped cultivation, are often considered negative consequences of domestication in that they can pose wide-ranging undesirable challenges to crop production and wild ecosystems (Qiu et al., 2020). Feral rice, for example, is estimated to reduce cultivated rice yield in the United States by up to 5.7 million metric tons annually, a greater impact than either of the two leading rice pathogens (Durand-Morat et al., 2018). Feral crops are also thought to serve as vectors for unintended transgene spread into cultivated and wild relatives, as in the case of turnip rape (*Brassica rapa*) in Japan and Argentina (Hecht et al., 2014; Pandolfo et al., 2018; Saji et al., 2005). However, feral plant populations have also been proposed as a genetic resource to improve crops, as well as unique study systems for understanding general evolutionary processes (Mabry, Turner-Hissong, et al., 2021; Razifard et al., 2020; Wu et al., 2021). For example, feral rice populations have been used to identify potentially useful genetic variation for stress tolerance (Guan et al., 2019; Li et al., 2017; Wang et al., 2019). Despite this potential, feral populations are underrepresented in global germplasm collections and are often misidentified as wild (McAlvay, 2018).

Past and current research on feral plants ranges from uncovering the evolutionary processes involved and the genetic basis of feral traits to the control of invasive and agriculturally problematic feral plants and the ecology of feral populations. For example, advances have been made in understanding the pathways to ferality, with feralization occurring either through introgression from wild relatives (exoferality) or without such introgression (endoferality) (Cronin et al., 2020; Gressel, 2005). Many of our insights into the genetic and phenotypic changes involved in ferality are derived from research on feral rice, which has identified key loci, traits, and evolutionary pathways associated with feralization (Li et al., 2022; Wedger & Olsen, 2018; Zhou et al., 2021). Recently, ferality has also become a topic of interest in the study of domestication, as wild–weedy–domesticated complexes were likely frequent in the early stages of domestication for many plants (Allaby et al., 2021; Purugganan, 2019, 2022).

There have been several calls to examine ferality in a more systematic and comparative manner. Gering et al. (2019) argue for a concerted effort to compare feral plants with their domesticated relatives and wild populations, as well as feral plants across populations or species. Little is known, for example, about how the effects of artificial selection on crops continue to influence descendent feral populations. Mabry, Turner-Hissong, et al. (2021) highlight the power of leveraging genomic resources designed for studying agriculturally important domesticated counterparts. With these resources, we can begin to understand the genomic architecture involved not only in feralization but also in domestication, natural selection, and local adaptation, especially in cases where feralization has occurred in the same domesticated species independently in different parts of the world. To support a more coordinated and systematic approach to feral crops that bridges the work of researchers spanning different disciplinary and organismal foci, we present a series of outstanding questions in the field generated from a colloquium at the 2021 BOTANY conference.

2 | THE STATE OF FERALIZATION RESEARCH

To better understand the landscape of feral research, we performed a bibliometric analysis to visualize the citation relationships between individual articles on feral plants and the institutions where the authors of these articles were based (Methods S1). We found that cross-citation, and therefore likely scholarly communication, appears to be limited based on focal species (Figure 1) and terminology (e.g., "weedy," "volunteer," and "feral"). Among the factors that may play a role in this isolation are the distinct emphases on applied research such as weed control studied by agronomists and on fundamental evolutionary research by evolutionary biologists. Alternatively, or additionally, this pattern may be driven by a tendency to use single-species model systems for specific research questions rather than multispecies comparative studies. For example, the genetic mechanisms underpinning ferality in rice have been extensively studied but rarely addressed in other species (Gering et al., 2019; Qiu et al., 2020). Similarly, feral *Brassica napus* has been the target of numerous studies investigating the potential for transgene spread (Pandolfo et al., 2016) but less thoroughly addressed in most other feral organisms.

This lack of communication has likely hampered the full potential for progress on a cohesive, multidisciplinary global effort to address

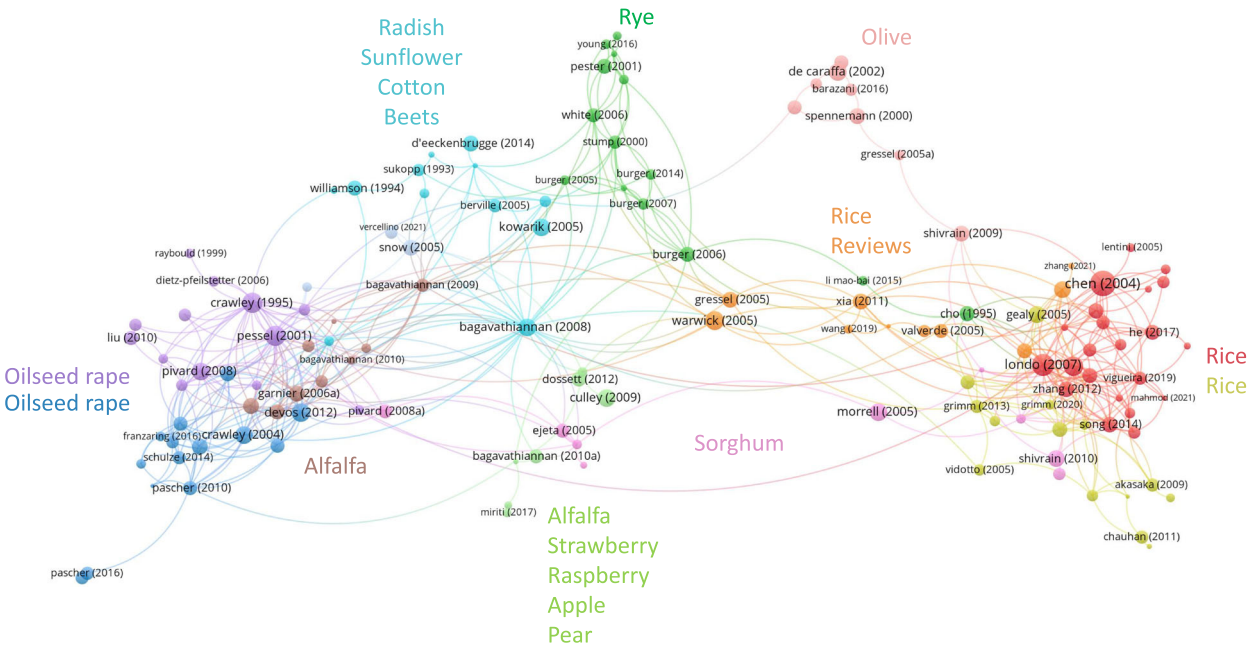

FIGURE 1 Citation network analysis of research articles focused on feral crops. Each circle represents a separate publication. The size of the circle is proportional to the number of connections it has to other publications. Circle colors correspond to the topic species. Importantly, this does not include all possible publications on feralization, just those available on Web of Science retrieved with the search terms used.

fundamental questions about feral plants and feralization. Despite being internally connected, in several cases, clusters of articles focused on individual species are not closely associated with other species in the same family, for example, radish (*Raphanus*) and *Brassica* are both members of the Brassicaceae, but their clusters are not closely associated, nor are rye (*Secale*) and *Sorghum* (Poaceae). There is a lack of research that leverages the potential power of comparisons among feral cereals like wheat, rye, rice, sorghum, and maize and of feral Brassicaceae crops like field mustard (*B. rapa*), oilseed rape (*B. napus*), and radish. There is also untapped potential to compare similar types of crops across families, for example, comparing feral oilseed crops like oilseed rape and sunflower. Although clusters of articles that focus on particular species are to be expected to some degree, the limited citations of studies on other species that are shared between species-focused publications indicate that there may be limited integration at a generalizable and theoretical level.

3 | CHARTING A COURSE FOR THE FUTURE FERALIZATION RESEARCH

In an attempt to build more bridges across clusters of researchers focused on feral crops, a colloquium on crop feralization was organized at the 2021 Botanical Society of America Conference (BOTANY 2021). Presenters and attendees were brought together in discussion to develop a list of open questions in feralization research (Methods S2). These questions were then combined with results from a survey that was sent to additional researchers in the field and organized into seven categories, which are discussed below.

3.1 | Definitions and drivers of ferality

The first set of questions highlight the need for research to understand how feral populations form and persist (or do not persist) over time. Asking these questions, especially across multiple crop species, would enable researchers to better define ferality and provide insights into their use to further crop improvement.

1. How do we define ferality?
2. How do we differentiate between domestic, feral, and invasive plants?
3. How frequently does feralization occur, both within and across species?
4. How common are endoferality, crop-to-crop exoferality, and crop-to-wild exoferality?
5. Are there climatic conditions associated with a greater frequency of feralization?
6. Are there plant traits that make feralization more liable to happen?
7. Are any taxonomic groups more prone to giving rise to feral plants?
8. How does the degree of domestication affect the likelihood of becoming feral?
9. What determines the short- or long-term persistence of feralized populations?

A baseline need in feralization research is a more comprehensive understanding of how many species feralization has occurred in. To date, feral populations have been identified across several species and

TABLE 1 Suspected and confirmed feral agricultural/horticultural crops. Crops with unconfirmed feral populations are indicated by a question mark (?) next to the common name. Cells with dashes indicate unknown information.

Crop relative	Feral name	Family	Feral type	Life history	Crop use	Feral location(s)	Recent citations
Alfalfa (*Medicago sativa*)	-	Fabaceae	-	Perennial	Forage and grain	Canada; USA	(Bagavathiannan et al., 2010)
Apple (*Malus domestica*)	-	Rosaceae	Endoferal	Deciduous	Fruit	Canada, Europe	(Cronin et al., 2020; Kišek et al., 2021)
Apricot (*Prunus armeniaca*)	-	Rosaceae	-	Deciduous	Fruit	Dagestan	(Asadulaev et al., 2014)
Artichoke (*Cynara cardunclus*)	-	Asteraceae	Exoferal/ endoferal?	Perennial	Vegetable	Iberian Peninsula	(Leak-Garcia et al., 2013; Pavan et al., 2018)
Barley (*Hordeum vulgare*)	*Hordeum spontaneum*	Poaceae	Exo-endoferal	Annual	Grain	Tibet	(Civáň et al., 2021; Zeng et al., 2018)
Bitter vetch (*Vicia ervilia*)	-	Fabaceae	-	Annual	Grain	SW Asia and Greece	(Zohary et al., 2013)
Blackberry (*Rubus* spp.)	-	Rosaceae	-	Perennial	Fruit	Romania; Chile	(Strik et al., 2007)
Black raspberry (*Rubus occidentalis*)	-	Rosaceae	-	Perennial	Fruit	NE United States	(Dossett et al., 2012)
Callery pear (*Pyrus calleryana*)	-	Rosaceae	Exo-endoferal	Deciduous	Ornamental	USA	(Culley & Hardiman, 2009)
Cannabis/Hemp (*Cannabis sativa*)	-	Cannabaceae	-	Annual	Fiber and oil	USA: Minnesota and Nebraska	(Busta et al., 2022; Wenger et al., 2020)
Chestnut (*Castanea sativa*)	-	Fagaceae	-	Deciduous	Tree nut	N Mediterranean, N Turkey, Caucasus	(Zohary et al., 2013)
Cole crops (*Brassica oleracea*)	-	Brassicaceae	-	Annual/ biennial	Vegetable	Coastal ranges of Ireland, UK, The Netherlands, Germany, Denmark, France, Spain, Portugal, Chile, New Zealand, and USA: California	(Mabry, Rowan, et al., 2021; Maggioni et al., 2020; Mittell et al., 2020) https://maps.biodiversityireland.ie/Species/28500 https://www.verspreidingsatlas.nl/5481
Common vetch (*Vicia sativa*)	-	Fabaceae	-	Annual	Forage	Mediterranean basin	(Zohary et al., 2013)
Corn (*Zea mays*)	-	Poaceae	-	Annual	Grain and vegetable	Mexico; Central Europe	(Pascher, 2016; Raybould et al., 2012)
Cotton (*Gossypium hirsutum*)	-	Malvaceae	-	Annual/ perennial	Fiber	Mexico	(Alavez et al., 2021)
Cucumber (*Cucumis sativus*)	-	Cucurbitaceae	-	Annual	Vegetable	SW China	(Bo et al., 2015)
Date Palm (*Phoenix dactylifera*)	-	Arecaceae	Endoferal/exoferal	Perennial	Fruit	SW Asia, NE Sahara, N Arabia; Egypt, Spain	(Gros-Balthazard et al., 2016; Obón et al., 2018; Zohary et al., 2013)

TABLE 1 (Continued)

Crop relative	Feral name	Family	Feral type	Life history	Crop use	Feral location(s)	Recent citations
Eggplant (*Solanum melongena*)	-	Solanaceae	Exoferal	Perennial	Vegetable	India	(Page et al., 2019)
Fig (*Ficus carica*)	-	Moraceae	Exoferal	Perennial	Fruit	Mediterranean basin	(Zohary et al., 2013)
Finger millet (*Eleusine coracana*)	-	Poaceae	-	Annual	Grain	Africa	(de Wet et al., 1984)
Mango (*Mangifera indica*)	-	Anacardiaceae	-	Perennial	Fruit	Borneo; Indonesia	(Bompard, 2009)
Mulberry (*Morus* spp.)	-	Moraceae	-	Perennial	Fruit	Japan	(Yoshinori et al., 2022)
Musk strawberry (*Fragaria moschata*)	-	Rosaceae	-	Perennial	Fruit	Germany	(Buschmann et al., 2021)
Oat (*Avena sativa*)	-	Poaceae	-	Annual	Grain	-	(Rösler, 1969)
Oilseed rape (*Brassica napus*)	-	Brassicaceae	-	Annual/ biennial	Vegetable and oil	Argentina	(Pandolfo et al., 2016; Schlink, 1994)
Okra (*Abelmoschus esculentus*)	-	Malvaceae	-	Annual/ perennial	Vegetable	USA: Texas	Personal observation by MB
Olive (*Olea europaea*)	-	Oleaceae	Endoferal/exoferal	Perennial	Fruit and oil	Australia; Sicily and Balearic Islands	(Angiolillo et al., 1999; de Caraffa et al., 2002; Mekuria et al., 2002; Spennemann & Allen, 2000)
Parsnip (*Pastinaca sativa*)	-	Apiaceae	-	Biennial/ perennial	Vegetable	-	(Zohary et al., 2013)
Peach (*Prunus persica*)	-	Rosaceae	-	Perennial	Fruit	USA	(Chen & Okie, 2021)
Pear (*Pyrus communis*)	-	Rosaceae	Exoferal	Perennial	Fruit	Europe and W Asia	(Thorpe & Kaye, 2007; Zohary et al., 2013)
Pecan (*Carya illinoinensis*)	-	Juglandaceae	-	Perennial	Tree nut	S United States	(Wood & Marquard, 1992)
Radish (*Raphanus sativus*)	-	Brassicaceae	Exoferal/endoferal	Annual/ biennial	Vegetable	USA, Argentina	(Ellstrand et al., 2010; Ridley et al., 2008)
Rice (*Oryza sativa*)	Weedy Rice; *Oryza* spp.	Poaceae	Endoferal/ exoferal/ exo-endoferal	Annual	Grain	Worldwide	(He et al., 2017; Li et al., 2017, 2022; Qiu et al., 2014; Qiu et al., 2017; Qiu et al., 2020; Sun et al., 2019; Thurber et al., 2010)
Rye (*Secale cereale*)	-	Poaceae	Endoferal	Annual	Grain	USA: California	(Burger & Ellstrand, 2014)
Sorghum (*Sorghum bicolor*)	Shattercane	Poaceae	Endoferal/exoferal	Annual	Grain	North America, East Africa	(Morrell et al., 2005; Ohadi et al., 2018)
Soybean (*Glycine max*)	-	Fabaceae	-	Annual	Oil	-	(Lu, 2005)
Sunflower (*Helianthus annuus*)	-	Asteraceae	Endoferal	Annual	Oil	Europe	(Casquero et al., 2013; Gutierrez et al., 2010)

(Continues)

TABLE 1 (Continued)

Crop relative	Feral name	Family	Feral type	Life history	Crop use	Feral location(s)	Recent citations
Sugar beet (*Beta vulgaris*)	-	Amaranthaceae	Exoferal/ endoferal	Annual/ biennial	Vegetable	-	(Sukopp et al., 2005)
Squash (*Cucurbita* spp.)	*Cucurbita foetidissima*	Cucurbitaceae	-	Annual/ perennial	Vegetable	North America	(Bemis et al., 1978; Provvidenti et al., 1978)
Sweet Cherry (*Prunus avium*)	-	Rosaceae	-	Perennial	Fruit	Temperate Europe, N Turkey, Caucasus, Transcaucasus	(Zohary et al., 2013)
Tea (*Camellia sinensis*)	-	Theaceae	-	Perennial	Oil and leaves	Japan	(Yoshinori et al., 2022)
Tomato (*Solanum lycopersicum*)	-	Solanaceae	Endoferal	Annual	Vegetable	South America, Mesoamerica, USA	(Barnett et al., 2022; Razifard et al., 2020)
Turnip (*Brassica rapa*)	*Brassica rapa ssp. sylvestris*	Brassicaceae	-	Annual/ biennial	Vegetable and oil	-	(McAlvay et al., 2021)
Grape (*Vitis vinifera*)	-	Vitaceae	Exoferal	Perennial	Fruit	Europe and Western Asia	(Zohary et al., 2013)
Wheat (*Triticum aestivum*)	-	Poaceae	Endoferal	Annual	Grain	Tibet	(Guo et al., 2020)

families (Table 1). Additional species likely have feral populations, but genetic and/or phenotypic research has not been conducted to distinguish them from wild relatives. Additionally, there is still a lack of consistency and consensus on the definition of ferality, possibly due to researchers approaching feral crops from different fields. Some authors define feral organisms as populations derived from crops that have at least one wild type or "weedy" trait not typically present in crop forms, which allow the line to exist outside of cultivation on a multiyear basis (Gressel, 2005). Others define feral organisms more broadly as populations that have persisted outside of human propagation, regardless of trait changes (Gering et al., 2019). Wu et al. (2021) suggest that when diagnosing ferality, the ecological role should be considered in addition to the genetic donor (domesticate or wild relative) and origin (endoferal, exoferal, or exo-endoferal). Definitions of ferality are further complicated by ambiguity surrounding terminology. For example, "weedy" can be applied to plants adapted to disturbance and/or growing in undesirable areas in competition with cultivated plants. Finally, several of the questions highlight the need to investigate characteristics of crop species that make them more susceptible to ferality. For example, diploid crops may be more likely to become feral than polyploid crops (Wu et al., 2021), but it is not clear whether certain families, traits, life history, or environmental conditions predispose crops to become feral.

3.2 | Genetic architecture and pathway

The second set of questions deal with the process of ferality at a genetic level. Several recent studies have determined that feralization is not exclusively the "undoing" of domestication, where genes are being returned to an original undomesticated state, but may involve changes that occur at loci unrelated to domestication (Gering et al., 2019; Qiu et al., 2020; Wu et al., 2021). Additional research is needed to further understand the genomic signature of each case of feralization.

1. Are there unifying genetic mechanisms underlying crop ferality?
2. Does adaptation to the natural environment after cultivation occur through fixation of standing variation or through newly emerged mutations during feralization?
3. Is feralization achieved primarily through few changes of large effect or small effect changes across many loci?
4. Can feralization accompany adaptation in the form of increased plasticity?
5. What are the roles of potentially adaptive genomic features in genetic compatibility/incompatibility between crops and wild relatives?
6. What is the relationship between when a crop was domesticated and the tendency toward feralization?
7. Are certain domestication traits more reversible than others?
8. Do feral crops tend to have more or less genetic diversity than their cultivated relatives?

Most of our understanding of feralization genetics comes from work in rice (*Oryza* spp.). Researchers found adaptation to the natural environment after cultivation can occur through mutations in pre-existing alleles, or as found in *O. sativa* ssp. *indica* and *O. sativa* ssp. *japonica* feral rice, some of the selected alleles were derived from new mutations (Li et al., 2022; Scossa & Fernie, 2021). Also in rice, researchers have found that, in some cases, independently evolving feral populations have several shared "de-domestication" genomic blocks (Qiu et al., 2020). These blocks include genes with known functions related to protecting seeds against pathogens (Guo et al., 2013), indicating that there are at least some shared genomic targets of selection in parallel feralization events in rice (Qiu et al., 2020). Yet, other research has found that although most de-domesticated rice accessions carry the domesticated allele at the *sh4* gene (which determines delayed shattering in a domesticated background), these plants still effectively disperse their seeds at maturity (Thurber et al., 2010). The shattering phenotype in these feral accessions was thus fixed through different mutations at other loci. Therefore, weediness adaptation appears to be occurring largely through different genetic mechanisms in some feral rice populations (Li et al., 2017; Qi et al., 2015). Beyond rice, recent research on sunflowers has found that a feral population exhibited rapid adaptation of increased seed dormancy, but not increased competitive ability or herbicide resistance (Hernández et al., 2022). In general, it is the assumption that genome-wide nucleotide diversity will be lower in feral populations than in their respective inferred crop wild relatives but higher than that of cultivated populations (Hernández et al., 2022; Qiu et al., 2020). However, research that compares wild, feral, and domesticated populations has yet to determine if this is true across all crop complexes, especially when comparing exo- and endoferals.

3.3 | Evolutionary history and biogeography

The third set of questions relates to the evolutionary origins and biogeography of feral crops. Feralization likely has a history that is as long as domestication. Humans have long altered wild plants through cultivation and selection (unintentional or intentional); similarly, domesticated plants escape cultivation and evolve further through selection and hybridization. The process of feralization can proceed in a variety of different ways (Gressel, 2005). Below we discuss a few questions concerning the evolutionary history of feralization:

1. How often are feral lineages in a single species polyphyletic?
2. What is the role of human and non-human transportation of plants in ferality?
3. How does ancient feralization differ from recent or contemporary feralization events?
4. Is there introgression between wild-feral-domesticated forms from the beginning of most domestication processes?
5. What type of insights can feral populations provide in understanding the history of domestication?
6. How does the direction of introgression relate to phenotype (e.g., are feral crops that have wild traits introgressed different from wild individuals that have crop traits introgressed)?
7. How much gene flow from feral crops to conspecifics occurs (for both incipient feral plants and those that evolved further)?
8. What is the role of landraces versus breeders' varieties in feralization? How does gene flow from feral crops impact landraces and breeders' varieties differently?

Recent studies on *Brassica oleracea* (Mabry, Rowan, et al., 2021), *B. rapa* (McAlvay et al., 2021), and rice (Londo & Schaal, 2007) have found evidence for multiple independent feralization events at varying timescales and paths to ferality (exoferal or endoferal). Feral and cultivated plants often coexist with the potential for extensive backcrossing. This complicates the interpretation of the phylogeny, especially when trying to clarify the biogeographic patterns of feral plants transported across different regions, especially when subsequent backcrossing homogenizes their genomic background with local cultivars. One study on rice revealed that extensive gene flow from domesticated to wild populations has eroded or replaced a substantial portion of the genetic diversity of wild rice (Wang et al., 2017). Recent work suggests that domestication evolved as a landscape process in which disconnected populations of plants were sustained by human contact and gene flow (Allaby et al., 2022; Spengler, 2020). Although not specifically stated that some of these coexisting populations could be feral, descriptions of these plants—wild populations with low levels of domestication syndrome alleles—certainly fit the description, indicating that feral crops may have always played a role in domestication. We know that feral populations have been of interest to researchers for over 100 years. In 1850, at least four different "weedy" rice types were documented (Craigmiles, 1978). Two decades later, Charles Darwin (Darwin, 1868) also described the process of feralization.

> In our turnip and carrot beds a few plants often "break" — that is, flower too soon; and their roots are generally found to be hard and stringy, as in the parent species. By the aid of a little selection, carried on during a few generations, most of our cultivated plants could probably be brought back, without any great change in their conditions of life, to a wild or nearly wild condition.

3.4 | Agronomy and breeding

Feral crop populations can serve as important germplasm resources for improving crops with a range of agronomic traits, including adaptation to biotic and abiotic stress factors. However, gene flow involving feral crop populations in agricultural landscapes may have negative consequences for maintaining crop genetic uniformity and achieving novel trait confinement. Here, the following questions highlight

the beneficial and detrimental impacts of feral crops, as well as potential management avenues to thwart the establishment of feral populations.

1. Can feral crops be used as genetic resources for crop improvement to make cultivated crops more locally adapted or provide useful traits already embedded in a more favorable genetic background? What specific traits from feral crops could be of value? Are there opportunities to introgress genes from feral plants to endow tolerance to biotic and abiotic stress factors?
2. Is there an opportunity to redomesticate feral crops using classical breeding or genome editing?
3. Do sympatric feral populations unintentionally impart adaptive variation into crops via gene flow?
4. Can we intentionally conduct breeding that produces crops with less ferality potential?
5. How does the use of certified weed-free seed help prevent the dispersal of feral plants?
6. What agronomic management practices influence the formation of feral crop populations and how can they be modified to prevent their establishment?
7. Do feral crops act as refuges for pollinators or pests?
8. Are there any ecosystem services offered by feral populations in agricultural landscapes?
9. Can feral populations serve as a component of a metapopulation for specific plant species in agricultural landscapes?

Recently, Pisias et al. (2022) reviewed the possibility of utilizing feral crops, which have a more similar genomic background to crops than their wild relatives, for crop improvement using de novo domestication, especially through genome-editing techniques (Curtin et al., 2022; Fernie & Yan, 2019; Lemmon et al., 2018; Shan et al., 2020; Wu et al., 2021; Zsögön et al., 2018). Depending on the species, this process could still require extensive baseline research to establish transformation and tissue culture regeneration systems. However, feral populations could be integrated into crop improvement methods using traditional breeding techniques, such as marker-assisted backcrossing, as well. Because feral populations likely harbor genes related to tolerance to biotic and abiotic stress, these plants could play important roles in creating locally adapted crops (Bohra et al., 2022; Burgarella et al., 2019; Gutaker et al., 2022; Van Tassel et al., 2020; Zsögön et al., 2022). Additionally, it has been suggested that feral crops could be redomesticated into completely new crops. Although few documented examples have been confirmed genetically in crops, such as *B. rapa*, (McAlvay, 2018), there are potential candidates, such as cultivated red rice, which might have been redomesticated from feral red rice in some places (Wu et al., 2021). However, a large majority of research to date on feral crops has been centered around the negative effects of competition with crops, or transgene spread (Al-Ahmad et al., 2006; Gressel, 2015; Gressel & Al-Ahmad, 2005). Understanding the landscape genetics of feral plants and their crop conspecifics at multiple scales as has been done with some feral animals (Delgado-Acevedo, 2010) could provide insights into the microevolutionary forces involved in wild–feral–crop and feral–crop complexes, which could, in turn, shed insight on management, domestication, and other topics.

3.5 | Fundamental and applied ecology

Feral plants offer a useful test system with which to address key ecological and eco-evolutionary questions due to their relationship with conspecific crops that have carefully studied genomes and evolutionary histories. On the other hand, feral plants also tend to have certain tendencies that distinguish them from many wild plants, such as an affinity for disturbed anthropogenic areas (Garnier et al., 2008; Warwick & Stewart, 2005), persistent genetic/evolutionary characteristics retained from domestication, such as differences in life history trade-offs (Gering et al., 2019; Meyer & Purugganan, 2013), and sometimes complex genealogies deriving from populations brought together artificially by humans. Addressing the questions below would not only contribute to the fundamental understanding of plant ecology but also the control of invasive or otherwise problematic feral plants.

1. How do feral crops fit into the larger ecological and evolutionary footprint of humans in the Anthropocene?
2. How do feral plants adapt to novel environments? How does this differ from local adaptation in non-feral plants? Does the genetic heritage of feral plants facilitate their adaptation to a changing climate?
3. What can feral plants teach us about invasion ecology?
4. What determines the success of feral crops in novel environments? Why is it rare to find feral crops in mature forests?
5. What makes some feral crops such effective competitors in agricultural fields?
6. What ecological characteristics are typical of feral plants at the scales of individual traits, integrated phenotypes, and biotic interactions?
7. How often does a necessity for crop mimicry play a role in ferality?

Anthropogenic ecological impacts over the last several tens of thousands of years have gained renewed attention recently (Ellis & Ramankutty, 2008; Otto, 2018), but a better understanding of the role of ferals in anthropogenic biomes or "anthromes" sensu (Ellis, 2015) could help move us toward a more comprehensive understanding of how humans have sculpted ecosystems throughout time. Studies of local adaptation in model or near-model organisms have been an important source of insights in the past (Leinonen et al., 2009), as have feral species (Franks et al., 2007), but there are abundant opportunities for more work in this area, especially in the genomic era (Saastamoinen et al., 2018). Feral organisms also present an opportunity to investigate invasion ecology, including eco-evolutionary questions, as many feral organisms are also invasive (Ellstrand et al., 2010). This work might include predictive models to anticipate future invasion and habitat suitability and characterization of the features that tend to make feral

plants such effective competitors in certain environments. Finally, a detailed investigation into functional ecological traits as has been proposed for domestication (Meyer et al., 2012; Milla et al., 2015) would shed further light on the ecological dimensions of feralization.

3.6 | Collecting and conservation

Conservation was a common concern among participants both in the sense of conserving wild crop relatives and conserving native ecosystems. Resolving these unknowns would facilitate the management of ecosystems invaded by feral populations and the preservation of valuable crop wild relative diversity.

1. What are the impacts of feral populations on native diversity?
2. To what extent have the genomes of closely related wild relatives of crops been eroded or replaced by feral crops?
3. How do feral plants become invasive?
4. What is the frequency of feral ornamentals?
5. How prevalent are transgenes in feral populations? How often do they serve as a bridge to spread them to other populations?
6. How will climate change affect ferality?
7. Might feral populations act as "bridgeheads" for herbivores or pathogens that attack wild relatives?
8. Are certain feral populations a relevant target for genetic conservation, assuming they acquire novel genetic variation?

Comprehensive reviews have not yet been undertaken to gauge the relative ecological impact of feral crops compared to non-feral species on native biodiversity. Likewise, research that assesses the presence and/or impact of gene flow and introgression with wild conspecifics/congenerics is needed (Ellstrand et al., 2013; Gering et al., 2019). Insights gleaned from the fast-growing field of invasion biology, which encompasses studies of rapid evolution, invasibility, and eco-evolutionary dynamics could be potentially translatable to feral models. Although feral crops account for up to 14% of invasive species in the United States, feral ornamental plants account for up to half of invasive species in the United States but are even less well-studied than feral crops (Culley & Hardiman, 2009; Li et al., 2004; Reichard & Campbell, 1996). Understanding pathways to domestication and feralization in ornamentals could provide a useful parallel study system to crops. Both feral crops and ornamentals could be useful systems for studying "drivers versus passengers," an understudied hypothesis (Wilson & Pinno, 2013) asking if invasive drive community change or if they are passengers following environmental change such as disturbance. This is an unresolved area, but one, which may be very relevant to feral species due to their origin in disturbed cropping systems. Despite questions about transgene spread mediated by feral populations being the driver of one of the initial waves of interest in feral plant research (Allainguillaume et al., 2006; FitzJohn et al., 2007; Warwick et al., 2008), there are still outstanding questions about the frequency of its occurrence. Although range expansion and rapid evolution of many species are anticipated with climate change and other environmental shifts (Franks et al., 2014), it is not clear whether feral plants will be impacted differently due to their unique evolutionary histories and preadaptations to anthropogenic ecosystems. Despite their widespread occurrence, feral crops are under investigated compared to truly wild relatives, despite their potential to harbor useful alleles. Including feral populations in germplasm collection and conservation may provide a resource for adapting crops in the future.

3.7 | Taxonomy and best practices

To address the questions above and others, the authors also discussed methods and best practices for moving forward collaboratively in this field:

1. Is it possible to develop a standardized terminology around feral crops to facilitate communication between researchers?
2. What are the best methods for understanding feralization?
3. Can we do experimental feralization?
4. How can herbarium specimens (or specimens in general) be used to understand feralization?
5. How can we standardize our methods for compatibility across studies?
6. What are the best practices for naming feral populations?
7. How can we address the issue of wild relatives being feral in seed banks?
8. Can we increase the exchange of information with researchers studying feralization in animals to inspire questions and methods for plants?

The first question relates to the importance of the wording we use to describe feral crops. Researchers from across fields use the terms weedy, feral, and domestication in different ways, which can hamper communication (Ammann et al., 2005). As mentioned above, the term "weedy" can refer to ecological strategy or competition with desirable plants, and definitions of ferality can include or exclude trait change as a criterion. Because feral populations are often confused with wild populations, they are minimally sampled or left out of studies. Taxonomic confusion has also hampered research. For example, feral *B. rapa* has been alternatively called *Brassica rapa* ssp. *sylvestris*, *Brassica rapa* ssp. *campestris*, or simply *B. campestris*–each also referring to truly wild *B. rapa* despite separate evolutionary histories (McAlvay et al., 2017). One option would be to give these feral populations a new infraspecific taxonomic rank as has been done in rice (*Oryza sativa* forma *spontanea*), but this is not widely agreed upon (Roma-Burgos et al., 2021). By clarifying taxonomy, researchers can then address challenges in seed banks where wild accessions are actually feral populations. Finally, researchers should reach out beyond plants to collaborators studying feralization in animals and other organisms to find ways in which we can work synergically, possibly to identify any shared patterns in becoming feral across plants and animals.

4 | CONCLUSIONS

Although above we highlight a wide range of open research questions in feralization research, we recognize that there are an even greater number of questions not addressed, that will be spurred by continued research and conversation. As hopefully demonstrated here, understanding feralization is interdisciplinary in nature, as it has already—and will need to continue to—span disciplines that include both basic and applied research. As the questions suggest, the field of ferality research is well-positioned to enter a new phase. Rice has been established as an evolutionary and genomic model for ferality, laying the foundation for large-scale comparative work across species that could build theory and generalizable knowledge. Other emerging directions include the use of feral populations in breeding programs, reexamining domestication in light of the role of feralization, and rapid adaptation of feral populations. Working as a global community and using shared terminology and methods will allow for more efficient and concerted work in this field, with potentially important implications for food security, conservation, plant breeding, and understanding of evolutionary processes.

AUTHOR CONTRIBUTIONS

Makenzie E. Mabry and Alex C. McAlvay organized the colloquium at the BOTANY 2021 conference; Makenzie E. Mabry, Muthukumar V. Bagavathiannan, James M. Bullock, Hongru Wang, Ana L. Caicedo, Clemon J. Dabney, Emily B.M. Drummond, Emma Frawley, Jonathan Gressel, Brian Husband, Amy Lawton-Rauh, Lorenzo Maggioni, Kenneth M. Olsen, Claudio Pandolfo, J. Chris Pires, Michael T. Pisias, Hamid Razifard, Douglas E. Soltis, Pamela S. Soltis, Sofía Tillería, Soledad Ureta, Emily Warschefsky, and Alex C. McAlvay contributed questions; Alex C. McAlvay conducted citation network analyses; Makenzie E. Mabry, James M. Bullock, Muthukumar V. Bagavathiannan, Hongru Wang, and Alex C. McAlvay drafted section summaries; all authors edited the manuscript.

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ACKNOWLEDGMENTS

We thank iDigBio (NSF DBI-1547229; DBI-2027654) for funding and the Economic Botany section of the Botanical Society of America for their support of the colloquium at the BOTANY 2021 conference. We also thank two anonymous reviewers for their suggestions, which helped to improve the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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How to cite this article: Mabry, M. E., Bagavathiannan, M. V., Bullock, J. M., Wang, H., Caicedo, A. L., Dabney, C. J., Drummond, E. B. M., Frawley, E., Gressel, J., Husband, B. C., Lawton-Rauh, A., Maggioni, L., Olsen, K. M., Pandolfo, C., Pires, J. C., Pisias, M. T., Razifard, H., Soltis, D. E., Soltis, P. S., … McAlvay, A. C. (2023). Building a feral future: Open questions in crop ferality. *Plants, People, Planet*, 1–15. https://doi.org/10.1002/ppp3.10367