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1. Abstract

Cultivated plants provide food, fiber, and energy but they can escape, de-domesticate, colonize agroecosystems as weeds, and disrupt natural ecosystems as invasive species. Escape and invasion depend on traits of the species, type and rate of domestication, and cultivation context. Understanding this "de-domestication invasion process" is critical for managing conservation efforts that reduce unintended consequences of cultivated species in novel areas. Cannabis (*Cannabis sativa* L.) is an ideal case study to explore this process because it was one of the earliest plants to co-evolve with humans, has a crop to weed history, and has been introduced and cultivated globally. Moreover, recent liberalization of cannabis cultivation and use policies have raised concerns about invasion risk. Here, we synthesize knowledge on cannabis breeding, cultivation, and processing relevant to invasion risk and outline research and management priorities to help overcome the research deficit on the invasion ecology of the species. Understanding the transition of cannabis through the de-domestication-invasion process will inform policy and minimize agricultural and environmental risks associated with cultivation of domesticated species.

Keywords: crops, hemp, invasion risk, non-native species, weeds

2. Introduction

The advent of agriculture has played a pivotal role in the development of complex human societies by allowing for sedentary settlements and the growth of large civilizations (Purugganan and Fuller, 2009). Agriculture has also had a profound impact on evolutionary and ecological processes of plants by moving species beyond their native ranges and facilitating the evolution of **weeds** and **invasive species** through domestication and cultivation activities (see **Glossary**). In particular, **de-domestication**, or reacquisition of wild-like traits in crops, can have major impacts on agricultural and natural systems by enabling organisms to develop a suite of novel traits and re-colonize as weeds or invasive species (Charbonneau et al., 2018; Ellstrand et al., 2010; Wu et al., 2021). There are multiple mechanistic drivers and pathways that facilitate de-domestication and invasion events. For the purpose of this paper, we refer to this phenomenon as the "**de-domestication invasion process**" (**Box 1**; **Fig. 1).**

New technology and changing interests in agriculture in the past century have initiated and impacted the de-domestication invasion process for many crops, in some instances, increasing the risk of invasion (Petri et al., 2021). For example, increased propagule pressure (e.g., large-scale mass production of seeded crops), advancements in biotechnology leading to rapid breeding advancements (e.g., genetically engineering species to create genetically modified organisms (GMOs) or gene editing with CRISPR technology), and increased movement and importation of novel crops or crop genotypes can all contribute to invasion risk (Østerberg et al., 2017).

An ideal example to explore the threat of changing agricultural interests and practices in shaping invasion potential is *Cannabis sativa* L., s.l. (hereafter **cannabis**). Cannabis has a long cultivation history and a concurrent history of being an agricultural and environmental weed, but uniquely has a haphazard association with modern agriculture. Unlike other major crops, cannabis has seen a latency period in intensive breeding efforts with modern technology. The erratic domestication attempts for cannabis in the past century are due to its cultivation being heavily controlled in most parts of the world because of its use as a psychoactive recreational drug, although there has been substantial clandestine breeding for drug varieties (Russo, 2007). With increasing legalization and interest in the species there is considerable research and development into producing domesticated varieties that have altered secondary metabolites and are adapted for different climatic scenarios (Pattnaik et al., 2022; Wimalasiri et al., 2021). It is not yet clear how new domestication efforts, including those that use weedy germplasm and invasive populations of cannabis, may translate to ecological consequences, especially given the species' history as an agricultural and environmental weed.

In the early twentieth century, there were widespread plantings of cannabis in the Midwest United States for **hemp** fibers and other purposes (USDA and NRCS, 2020). When cannabis prohibition policies put federal restrictions on cannabis (i.e., 1937 Marihuana Tax Act), efforts were made to destroy remaining crops and **naturalized** populations in the following decades. Between 1998 and 2006 the US Drug Enforcement Agency Domestic Cannabis Eradication/Suppression Program claimed to have destroyed more than 1.9 billion **feral** or wild "ditchweed" plants (data were manually summed by accessing final reports from each eradication/suppression program final report from the Source book of Criminal Justice Statistics Online; https://www.ojp.gov/). Despite these major attempts to eradicate cannabis, feral populations are still present today indicating the prolific nature of cannabis. High-volume seed production, frequent establishment in disturbed areas (e.g., roadsides, ditches, and abandoned fields), and the intensive management required to remove populations make eradiation of cannabis exceptionally challenging.

Given renewed global interest in cannabis cultivation, we present a synthesis of the factors that drive cannabis escape, establishment, and invasion, in the context of the de-domestication invasion process. We then highlight research and management priorities aimed to effectively reduce cannabis invasion risk.

Box 1: The de-domestication invasion process

The de-domestication invasion process differs from other invasion processes because of intentional planting and nurturing of large reproductive populations combined with the consequences associated with artificial selection of traits by humans (Petri et al. 2021). Over multiple generations, cultivation activities and trait selection make organisms distinct from **wild-type** genotypes (**Fig. 1**), meaning that they perform and interact with their environment differently (Zeder 2015). Domesticates often have traits that are typically altered (known as the 'domestication syndrome') that distinguish them from their wild progenitors such as larger fruits or grains, reduced seed shattering, as well as physiological changes including altered photoperiod sensitivity and loss of seed dormancy. At this stage the invasion risk is typically low, especially with well-managed food crops (Petri et al. 2021).

A number of mechanistic drivers and pathways can lead to de-domestication and ultimately independent reproducing **feral** populations that have greater invasive potential. Wu et al. (2021) outlines how the reacquisition of wild-like characteristics that enable establishment beyond cultivation can occur via one of three pathways: from an endoferal origin where there is spontaneous mutations in genes underlying key traits, [e.g., Weedy rice (Qiu et al, 2017), Tibetan semiwild wheat (Guo et al. 2020), feral apple (Cronin et al. 2020) and feral olive (Mekuria et al. 2002)]; an exo-endoferal origin from natural hybridization between domesticate-derived forms with divergent genotypes (e.g., feral Callery pear (Culley and Hardiman 2009)), or lastly, an exoferal origin from introgression between weedy or wild relatives [e.g., California wild radish (Hegde et al. 2006), johnsongrass (Paterson et al. 1995), weed beet (Fénart et al. 2008)]; (Ellstrand et al. 2010, Kanapeckas et al. 2016, Wu et al. 2021).

The classification of de-domesticated populations depends on their impacts and where they colonise (Wu et al. 2021). If feral crops colonize managed environments, such as agroecosystems and gardens, they are typically deemed to be a **weed**. In some instances feral populations are intentionally brought back into these managed environments as crops or ornamental plants. Feral crops that colonize natural areas but are inconsequential are **semiwild**, but those that have observable impacts and spread at considerable rates can be considered **invasive.** (**Fig. 1**).

3. The de-domestication invasion process for cannabis

3.1. *Origin and taxonomy*

Cannabis (family: **Cannabaceae)** is an annual herbaceous plant that is one of the earliest plants (~10,000 ya) to experience domestication, which has greatly influenced the taxonomy of the species (Kudo et al., 2009). Cannabis is now generally accepted to be a monotypic genus with genetic differences at the rank of subspecies *C. sativa* subsp. *sativa* and *C. sativa* subsp. *indica,* although the systematics and nomenclature of the plant is highly debated (Barcaccia et al., 2020; Long et al., 2017; McPartland, 2018; McPartland and Small, 2020; Rull, 2022; Sawler et al., 2015; Serrano-Serrano Martha et al., 2021). A recent whole-genome resequencing study by Ren et al. (2021) identified well-separated genetic clusters which can be separated into four groups: basal cannabis (feral plants collected from China and the US [likely originating from Chinese landraces]), hemp-type (distributed globally), drug-type (distributed globally), and drug-type feral (collected in China, India, Pakistan). Within genetic clusters there are formal subtaxa (e.g., varieties, modern commercial cultivars, locally adapted traditional landraces) but also innumerous informal designations from the breeding of 'strains' (McPartland and Small, 2020). SeedFinder, a crowd-sourced database of Cannabis strains lists over 20,000 strains, most of which are marijuana or drug-type variants from clandestine parentage (en.seedfinder.eu; Accessed: 24th May 2022).

Clandestine breeding, widespread dispersal and propensity of cultivated plants to become feral and hybridize has meant that "wild" populations of cannabis no longer exist, making it difficult to confidently circumscribe a native range. Although, basal-feral accessions from China sequenced by Ren et al. (2021) may be the closest genotypes to truly wild cannabis and indicate an ancestral gene pool and single origin in East Asia where cannabis was likely first domesticated. Despite this, Cannabis populations may be considered non-native to East Asia as they are a separate genetic entity from the now extinct wild-type plants, and subsequently, can be **invasive** if impacts occur (Essl et al., 2018).

3.2. *Extensive use and dissemination by humans*

Fossil records indicate that cannabis populations closely mirrored peregrinations of early humans in Eurasia, suggesting it was regionally spread through a trans-Eurasian exchange/migration network (Long et al., 2017; Vavilov, 1926) (**Fig. 2a**). Cannabis was later moved around the world via intercontinental trade routes (**Fig. 2b**) for both drug and fiber crops, and in the last century for the purpose of recreational drugs (**Fig. 2c**) (Vavilov 1926, Russo 2007). Today, there are occurrence records in over 135 countries and territories, with cannabis reported as invasive in 50 of those (GBIF.org (14 February 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.j87ygp; **Fig. 2d**)). However, the distribution and production of cannabis is likely underreported - it is estimated that there is some level of cultivation happening in 172 countries, most of which is illegal production of **marijuana** drug-types, with an annual prevalence of 147 million people consuming cannabis or 2.5% of the world population (United Nations Office on Drugs and Crime (UNODC), 2009; World Health Organization (WHO), 2020). As such, cannabis is one of the most widely introduced and naturalized plants, globally (**Fig. 2**).

3.3. *High rates of hybridization*

Historical movement of cannabis, intentional or not, increased opportunities for hybridisation and likely contributing to the immense variety of subtaxa seen today by enabling isolated populations to overcome biogeographic barriers. Hybridization is extremely common in cannabis from cross-fertilization of windborne pollen. Further, hybridization can happen across considerable distances, in some instances up to 100 km, although pollen viability declines with distance (Cabezudo et al., 1997; Campbell et al., 2019; Rahn et al., 2016).

3.4. *Intermediate or semi-domestication*

Domestication can both increase or decrease invasion potential in plants; food crops domesticated for high intensity management have low invasion risk, whereas biomass-producing crops bred for high productivity under low management intensity have a high risk of becoming invasive (Petri et al., 2021). In the case of cannabis both scenarios occur, and many more, depending on the intended usage. Additionally, cannabis subtaxa have varying levels of retention of wild traits, or the degree to which they are domesticated, making the probability of ferality different among genetic groups (**Fig. 1**; (Haney and Bazzaz, 1970; Small et al., 2003). For example, many modern fiber and grain varieties of cannabis are more closely related to wild or feral types than to those with “improved” or “stable” genetics (Sawler et al., 2015; Zhang et al., 2018) (See **Glossary**). In just 50 generations, cultivated varieties were observed to lose their domesticated seed phenotypes in crops that became wild-growing following cannabis prohibition in Canada (Small, 1975). Atavistic traits (i.e., wild or ancestral characteristics) have also been observed in cultivated cannabis in the absence of hybridization, which includes early maturation, lax floral clusters and freely shattering achenes (one-seeded fruit) that contribute to its feral nature (Clarke and Merlin, 2013). In general, semi-domesticated taxa that retain wild or feral characteristics have a higher likelihood of possessing invasive qualities. Warwick and Steward (2005) posited that **intermediate domestication** of a species is likely to result in a greater ability to transition between wild, cultivated, feral, and invasive forms (**Fig. 1**). A good example of this is Asian wild rice which is classified as a hybrid swarm with extensive gene flow from domesticated, feral, and weedy forms that readily escape cultivation (Qiu et al., 2017; Wang et al., 2017).

3.5. *Preference for human-disturbed habitats*

Non-cultivated populations can be found on the periphery of human-managed areas with nutrient-rich soils and disturbed open habitats, including agricultural fields, abandoned lands, areas adjacent to infrastructure and along riverbanks (Campbell et al., 2019). As such, cannabis can be described as a **synanthropic** species because it often grows near or benefits from a close association with humans (**Fig. 3**). This means there is often an interface between where feral and cultivated cannabis plants grow, allowing for admixture of genotypes that may help maintain an intermediate state of domestication in cultivated populations.

3.6. *Competitive traits and impacts*

Cannabis has traits that are associated with greater competitive ability, including annual life-span, rapid growth, and high photosynthetic rates (Guo et al. 2018). Dense thickets in naturalized populations can have impacts on non-native communities by reducing light availability to other plants and emerging seedlings (McPartland, 1997; Small et al., 2003). It is not clear how long cannabis can maintain dominance before being shaded out by larger or perennial species. Minor allelopathic properties have also been reported (McPartland, 1997; Pudełko et al., 2014). Yet, despite the prevalence of escaped cannabis around the world, there have been few dedicated studies on impacts, and no formal ecological studies have quantified impacts of invasive hemp on native communities.

3.7. *Dispersal traits*

The seeds, more precisely achenes, of cannabis can escape and spread beyond cultivation by two main dispersal mechanisms: water via floating down waterways and alluvial sites, and endozoochory. When cannabis seeds were compared to 93 other invasive species, they were found to be more buoyant than 78% of other species tested (Moravcová et al., 2010). On average, it took 52 hours for 100 seeds to sink (Moravcová et al., 2010). For this reason, infestations are often found alongside banks of waterways, or in previously flooded areas where seeds can reach by floating (**Fig 3b**). The seeds are also palatable to animals, and do not accumulate cannabinoids (Campbell 2019). Seeds can retain viability in the feces of mammals, including dogs and humans (McPartland and Naraine, 2018), and anecdotally observed in cattle and birds (Ridley, 1930). The use of cannabis seeds in bird seed is a known vector for transporting new populations. In Minnesota, United States, hemp seeds were imported for caged bird feed, resulting in volunteer plants emerging from the refuse from cleaning bird cages (Johnson, 1898). Similarly in Europe, jackdaws (*Coloeus monedula)* have been observed to distribute seeds from feeding points to areas below where they nest (Hohla et al., 2015). Darwin (1859) reported diploendozoochory, or ingestion spanning two trophic levels, where hemp seeds germinated in England following excretion from different birds of prey that had fed on carrier pigeons (*Columba livia domestica*) from France. Epizoochory, transport of seeds externally on animals, is less common as seeds lack mechanisms for latching. However, fire bugs (*Pyrrhocoris apterus*) have been observed to carry seeds over long-distances (Janischevsky, 1924). It should be noted that like many other domesticates, seed size varies considerably in cannabis - feral and wild-type populations are smaller than those that are cultivated, although how this affects seed dispersal is unknown (Vavilov, 1926).

3.8. *Environmental tolerance*

Cannabis has a broad environmental tolerance attested by the global records indicating naturalization of feral populations on every habitable continent. Although different types of cannabis have varying environmental preferences, commercial cultivation has yet to advance in the tropics at the scale of temperate zones indicative of global climate and geopolitics. This tolerance breadth may be influenced by early distribution of the species by humans, clandestine breeding and propensity of cultivated plants to become feral and hybridize across large geographic ranges.

4. Changes to cultivation activities of cannabis related to invasion risk

4.1. *Pathway changes*

Recent changes in regulation of cannabis in many countries around the world have driven increased investment in cannabis for a multitude of uses, including medicine, food, textiles, construction materials and bioenergy (Chandra et al., 2019; Salentijn et al., 2015) (**Fig. 1**). The greatest concern is in areas where there are new pathways for its introduction, or where the extent of plantings has dramatically increased propagule pressure due to new breeding efforts that select for weedy traits, including environmental tolerance and grain yield.

4.2. *Trait selection*

Because trait selection has shifted over time, historic types (e.g., landraces) and modern bred types (e.g., cultivars) of cannabis might vary in their invasion risk. Hemp breeding for fiber nearly ceased after the market for hemp declined due to emergence of synthetic fibers, whereas modern breeding efforts are focused on selection of cannabinoids, specifically inebriating Δ^9-THC and non-inebriating cannabidiol (CBD) (Salentijn et al., 2015). In samples of marijuana confiscated across the United States and Europe, mean THC concentration increased from 8.9% to 17.1% between 2009 and 2017 (Chandra et al., 2019). It is unknown how cannabinoid levels might alter ecological impacts, as few studies have explored the effects of escape by varieties with high cannabinoids. Presence of glandular hairs and specialized metabolites such as cannabinoids might serve as a defense against herbivores (Rodziewicz et al., 2019). Extracts of cannabis have been used as repellents and insecticides (McPartland, 1997). Insect activity can vary by cannabis type (Rothschild and Fairbairn, 1980), for example, the hemp cultivar ‘Futura 75’ had much higher levels of herbivory by Japanese beetles (*Popillia japonica*) than other cultivated cannabis varieties in field trials in Kentucky (Pearce, 2019).

Furthermore, invasion risk of future commercial cultivars of cannabis will be influenced by parental stock if competitive or weedy forms are selected for breeding. Undesirable seed traits may be derived from feral germplasm, for example, feral hemp seeds can remain dormant for months while seeds from cultivated varieties are expected to sprout within days (Vavilov, 1926). Some programs already source feral seeds for breeding programs to increase environmental resilience of hemp.

4.3. *Cultivation activity*

Cannabis invasion risk is also expected to vary with how and where it is cultivated. Highly contained (and often secured) environments, such as greenhouses and growth chambers, that are used to grow recreational and medicinal varieties with high cannabinoid levels tend to control or eliminate seed production, reduce cross-pollination, and thereby lower the risk of escape and invasion. In contrast, grain and fiber production is characterized by large amounts of planted seeds (i.e., higher propagule pressure) and greater potential for seed escape (e.g., via waterways, predation by animals, or seed transfers by outdoor machinery), which could enhance invasion risk. Lastly, illegal production could be either low risk (e.g., contained rooms with controlled lighting and heating) or high risk (e.g., plants grown illicitly in natural areas and areas that are difficult to detect and access).

5. Research priorities for cannabis

The illegal status of cannabis in most countries (i.e., 293 countries for recreational use and cultivation) has been a significant barrier for scientists attempting to study cannabis, especially notable in the medical field but this has also been true for ecologists, blocking the production of valid peer-reviewed observations and experiments (Nutt, 2015; Stith and Vigil, 2016). Therefore, it is important to disentangle an assumption that the lack of peer-reviewed literature on impacts and invasions indicate a low invasion risk of cannabis, but rather indicate a deficit in research on the invasion ecology of cannabis and its impacts on biodiversity. This scenario can be compared to novel bioenergy crops where information needed to inform risk assessment and screening protocols is data-limited (Flory et al., 2012). Flory et al. (2012) suggests that in this situation an experimental approach can mediate some of these information gaps by generating data to inform predictive models. Given the growing liberalization of policy surround cannabis allows for commercial cultivation, this may provide some of the first opportunities in decades for ecologists to establish research projects and monitoring programs that specifically test and predict invasion risk. Research should include both small-scale local experiments on specific habitats, cultivation practices, and cannabis types (e.g., different landraces, cultivars, feral populations), and larger experimental introductions across geographic networks that cover the range of climates where cultivation might occur (Flory et al., 2012). Based on literature discussed here, we suggest the following topics and questions should be prioritized for experimental research:

(1) *Local establishment, spread, and impact:* To what extent do populations escape from managed or disturbed areas to invade natural areas?
(2) *Geographic context*: How does invasion risk vary across geographic ranges (i.e., climates), habitats, and cultivation regimes?
(3) *Genetic diversity:* How does invasion risk vary among cannabis types?

Local establishment, spread, and impact: A greater understanding of the fundamental biology and ecology of cannabis is needed to predict local establishment and spread, but also the conservation implications to native species. Firstly, we know cannabis is a synanthropic species where factors such as high disturbance and soil nutrients of disturbed habitats are important factors for establishment, but it is unclear to what extent populations are constrained to such environments and if they can move into natural areas. Making use of small-scale experiments, such as those on reproductive traits, including flowering phenology, seed production and dispersal, existence of a soil seed bank, and seed germination across varying habitats, can reveal areas at risk from spreading populations (Negussie et al., 2013). Secondly, even if the probability is low for cannabis to establish in less than optimum areas (such as where there is greater competition from resident species or low resource availability), high propagule pressure might overcome these barriers (Von Holle and Simberloff, 2005). Experiments should be prioritized that quantify the number and frequency of seeds or propagules required for escaped plants to result in an established population under different scenarios. One introduction event may result in establishment, but often repeated introductions of propagules are required for invasion success (Von Holle and Simberloff, 2005). With crop production, seeds are introduced repeatedly in large amounts, which can lead to human-induced seed swamping and greater likelihood of establishment. Multiple introduction events of different crop cultivars and landraces can also provide greater genetic diversity and reduce bottleneck effects (Gepts and Papa, 2003). Lastly, in situations where populations have escaped, efforts should be made to quantify any ecological or economic impacts associated with feral populations. Documenting impacts, either through experimental or observational methods, is imperative for guiding future management decisions and conservation efforts.

Geographic context: Local experiments will need to be scaled-up to consider invasion risk across the broad biogeographic ranges where cannabis is currently distributed and in regions proposed for cultivation (**Fig. 2**). Factors such as resident competitors, predators, pests, pathogens, and edaphic condition (soil type, nutrient availability) will vary considerably and could have mixed effects on invasion potential. Habitat suitability models can be used to identify areas where establishment might occur (e.g., Wimalasiri et al. 2021); Wengert et al. (2021)). One challenge for conducting such models with species that have a long cultivation history, such as cannabis, is that early wild distribution is not clear. This knowledge gap can be alleviated through greenhouse/lab experiments that identify species phenotypic plasticity, genetic/epigenetic diversity, and the main factors that drive establishment in different geographic ranges (e.g., temperate to tropical), habitats (e.g., open landscapes to closed canopy forests), and across varying management regimes (e.g., intensive cultivation to abandonment).

Genetic diversity: Invasion research on cannabis has additional challenges due to the genetic diversity of subtaxa. Although, this is not unique to cannabis and is a flagged issue with assessing many crop and ornamental varieties of domesticates. Phenotypic traits of domesticated species can vary considerably as they have been altered from the "wild-type" parent species to include distinct landraces and cultivars. (Petri et al., 2021). We suggest experiments that delineate the differences in genetic clusters (e.g., feral, drug-type, hemp-type, etc.), and how they translate to performance outside of cultivation (Petri et al., 2021). Information on these differences is imperative for risk assessment tools and regulatory frameworks which usually focus on the species-level, but for cannabis assessments should be done at the subtaxa level to identify high-risk landraces and cultivars. For example, cannabis types cultivated for fiber are associated with greater yields and environmental resilience (e.g., resistance to disease and pests) whereas those selected for medicinal and drug purposes focus on alterations to cannabinoids or secondary metabolites of plants (Salentijn et al., 2015).

Development of corollary types or substitutes that are of lower risk but can still offer similar economic returns should be encouraged in breeding and cultivation. It would also be interesting to explore any physiological trade-off between increased CBD production and associated reductions in herbivory and whether high-cannabinoid plantings of female clones or fiber crops are reliably managed and terminated prior to seed production. If a trade-off exists in physiology and management, are there consequences for growth rates, reproduction, and inter-specific competitiveness that might define invasiveness? The plasticity of particular traits and likelihood of reversion to wild types should also be established if a landrace or cultivar is to be considered as lower risk (Datta et al., 2020).

6. Management recommendations

When a novel crop is evaluated and found to be high risk for escape and invasion, socio-political and economic considerations can override environmental and conservation concerns. In this case, provisions should be taken to minimize potential for escape through cultivation practices, similar to extirpation programs developed for illegal cultivation efforts. We suggest that recommendations, as outlined by Barney et al. (2014) for biofuel invasions can be applied to other novel crop introductions, including cannabis. These best management practices to limit escape from cultivation broadly include:

(1) *Site selection:* choosing cultivation sites that are not adjacent to ecologically sensitive habitats and to natural corridors or transport networks;
(2) *Buffer area:* maintaining a specified buffer around perimeter of planting area, especially near riparian areas;
(3) *Regular monitoring:* develop programs or protocols to detect escape around production fields and processing facilities;
(4) *Removal plans:* instigate immediate removal of volunteer plants that establish in buffer area as detected by monitoring protocols;
(5) *Permitting:* additional permitting for new planting areas;
(6) *Transport provisions:* postharvest transportation of material, especially seed, should be conducted in a manner that prevents or minimizes escape;
(7) *On-site provisions:* clean all planting, maintenance, machinery and harvesting equipment thoroughly to prevent spread of material outside of cultivation areas;
(8) *Informed personnel:* provide training to farmers and/or people involved with production;
(9) *Long-term indemnity:* implement surety bonds, or equivalent, to financially guarantee that growers have resources to offset impacts or facilitate wider landscape scale management if invasions occur.

Management protocols should vary depending on the location and configuration of planting. For example, open-field production for grain may require netting structures to prevent consumption and dispersal of ingested seed by birds to nearby landscapes, but this method would not be applicable for indoor hydroponic production of CBD types. Secondary pathways or vectors may also present risks and should be managed, such as avoiding cannabis seeds in bird feed, in particular non-devitalized and freely dispensed seeds in natural areas (Oseland et al., 2020). Selection of feral types of germplasm for breeding novel cultivars may present additional risks, as well as scenarios that enable cross-pollination among cultivated and feral populations. If breeding populations are selected from or interact with feral populations, they may have a higher ability to establish outside cultivation compared to plants that have been more specialized in their trait selection (Petri et al., 2021). However, a critical limitation to obtaining records on breeding and selection for management purposes is unwillingness of commercial breeders to share proprietary information on trait selection and plant performance.

Management protocols need to be implemented at the breeding stage, in the field, and across the production and supply chain, as seed may escape throughout the process. In an experimental open field trial in South Florida, 25-40% of live hemp seeds (adjusted by expected emergence from germination trials) emerged after planting, suggesting that 60-75% of seeds remained in the soil or were predated (Brym et al., 2019). Registered hemp varieties can have achenes shattering rates as high 40% but, in general, trait selection for non-shattering in crops has declined over time (Meyer et al., 2012). Achenes are also lost during mechanical harvesting and transportation to processing facilities. Typically, spilt seeds are not managed, and the producer would be responsible for scouting their fields for volunteers. In some instances, spilled seeds can be used for animal feed, which could be an additional dispersal pathway if not managed (Bailoni et al., 2021; Small and Marcus, 2002; Wimalasiri et al., 2021).

Protocols should be put in place for monitoring and surveillance of volunteer plants for early target eradication. However, currently, if volunteer plants are identified there are limited management methods beyond hand-pulling for small infestations and repeat herbicide applications. In an experiment by Dochev et al. (2016), multiple chemical applications at particular times of year were required to extirpate 'wild hemp' from crop fields (Reisinger et al., 2005). In a preliminary cannabis trial in Florida, United States, a post-cultivation protocol approved by USDA rules to reduce volunteer cannabis plants that included disking and tilling failed to prevent volunteer hemp from emerging after one cultivation event (Z. Brym personal observation; U.S. Domestic Hemp Production Program (2021)). Volunteer cannabis plants are unlikely to be an anomaly in future outdoor plantings but rather commonplace. Therefore, to prevent cannabis weediness and invasion in natural areas, more effective early detection and rapid response protocols are needed.

7. Conclusion

A reoccurring challenge in invasion ecology is how to accurately evaluate and distinguish subtaxa of species with a long-domestication history and to assess the impacts they have on native species and ecosystems. The plant cannabis is an exemplar case of this challenge due its illegal status in many parts of the world making it perhaps one of the most understudied economic plants with regards to invasions and impacts, but also a taxonomically complex species. It has become pressing to understand the ecological consequences of escaped cannabis due to increased liberalization of policy promoting industrial-scale cultivation. Here, we reviewed the invasion risk of cannabis in the context of the de-domestication invasion process and found that transitions from cultivated to feral forms are common and likely influenced by the immense genetic diversity of the species, its semi-domesticated nature and the variety of reasons it is cultivated. Similar to other novel crops or social-drug plants, ecological research has been absent or insufficient, therefore, experimental research is imminently needed to minimize conservation implications from a new era of cannabis cultivation. Given the interdisciplinary interest for cannabis, collaboration among researchers in agronomy, weed ecology, and invasion ecology will be pivotal to understanding and managing all stages of the de-domestication invasion process.

Glossary of terms

Cannabis: Overarching term to refer to all infraspecific derivatives or subtaxa of the species *Cannabis sativa* L. s.l.

Cultivar: An assemblage of plants that have been selected by humans for a particular attribute or combination of attributes and that is clearly distinct, uniform, and stable in these characteristics that when propagated by appropriate means retains those characteristics (Brickell et al., 2002).

De-domestication: The reacquisition of wild traits in domesticated plants and animals.

Domestication: The alteration of a species over multiple generations through intentional, and sometimes unintentional, human activity.

Feral: A decedent of a domesticated species that exists beyond direct human influence and is wild-growing.

Hemp: Cannabis sativa types with low levels of Δ^9-THC (Tetrahydrocannabinol), the principal psychoactive constituent of cannabis, typically lower than 0.3% depending on regional regulations. Hemp is grown for its derived products such as fiber, grain, oil, textiles etc.

Intermediate domestication: Species that have been subject to some degree of selection and alteration by human activity but where a functioning level of wild characteristics are still retained.

Invasive alien species: Species that are introduced to a region by human activity that produce reproductive offspring, often in very large numbers, are able to disperse considerable distances from parent populations, and thus have the potential to spread over a large area (Richardson et al., 2000) and to produce negative impacts on biodiversity (CBD/IUCN).

Landrace: Cultivated varieties that have evolved and may continue evolving, using conventional or modern breeding techniques, in traditional or new agricultural environments within a defined ecogeographical area and under the influence of the local human culture (Casañas et al., (2017).

Marijuana: Plants or plant derivatives from *Cannabis sativa* primarily used as a psychoactive drug; high-THC.

Naturalized species: Non-native species that sustain populations over many life cycles without direct intervention by humans (Pyšek et al., 2004; Richardson et al., 2000).

Semiwild: a subspecies or population shows not only traits similar to those of a corresponding cultivated population, but also some wild-like traits (Wu et al., 2021).

Synanthropic species: Species that benefit from an association with humans and have adapted to live near human modified habitats, but have not been intentionally domesticated.

Weeds/weedy species: A plant that is considered to be problematic or cause impacts in an ecological, economic or social capacity. Unlike invasive species, weeds can be either native or non-native (or translocated within a country) in the range or habitat or land-use they are perceived to cause problems in.

Wild-type: The phenotype of the typical form of a species as it occurs in nature without human influence.

Figures

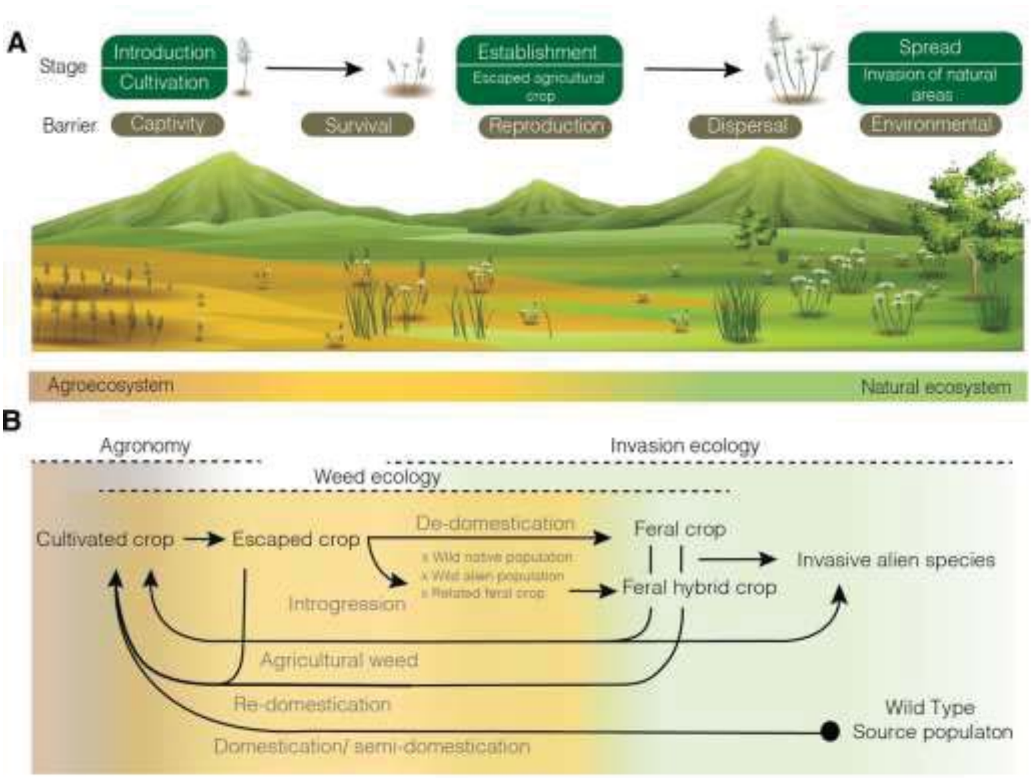

Figure 1. The de-domestication invasion process. **(A)** A generalized framework of multiple pathways where a domesticated organism (in this case a plant) can move beyond cultivation through an agroecosystem to a natural ecosystem. **(B)** Studying the entire process requires a multi-disciplinary approach, including (for crop plants) agronomy, weed ecology, and invasion ecology. The initial stage begins with domestication and is a major focus of agronomy. Domestication occurs when plants are selected from a 'wildtype source population' in a natural ecosystem and are typically cultivated and moved into a human-transformed landscape suited for agriculture. Here, plants become 'cultivated crops' but they can escape the agroecosystem boundary, and either perish or persist. If escaped plants persist and produce self-sustaining populations beyond human influence, de-domestication can occur leading to 'feral crops'. Mutations, introgression with wild, native or related plants and crops, and adaption to new environmental constraints can all contribute to the de-domestication process. Although feral crops exist in natural ecosystems, they are not the same as the original wild-type population. At any point during the de-domestication invasion process escaped or feral crops can feed-back into agroecosystems as agricultural weeds or be re-domesticated. Alternatively, escaped crops can move into natural ecosystems

as invasive species. During this process, feral crops are of interest to agronomists, weed ecologists, and invasion ecologists, depending on what part of the process they move into.

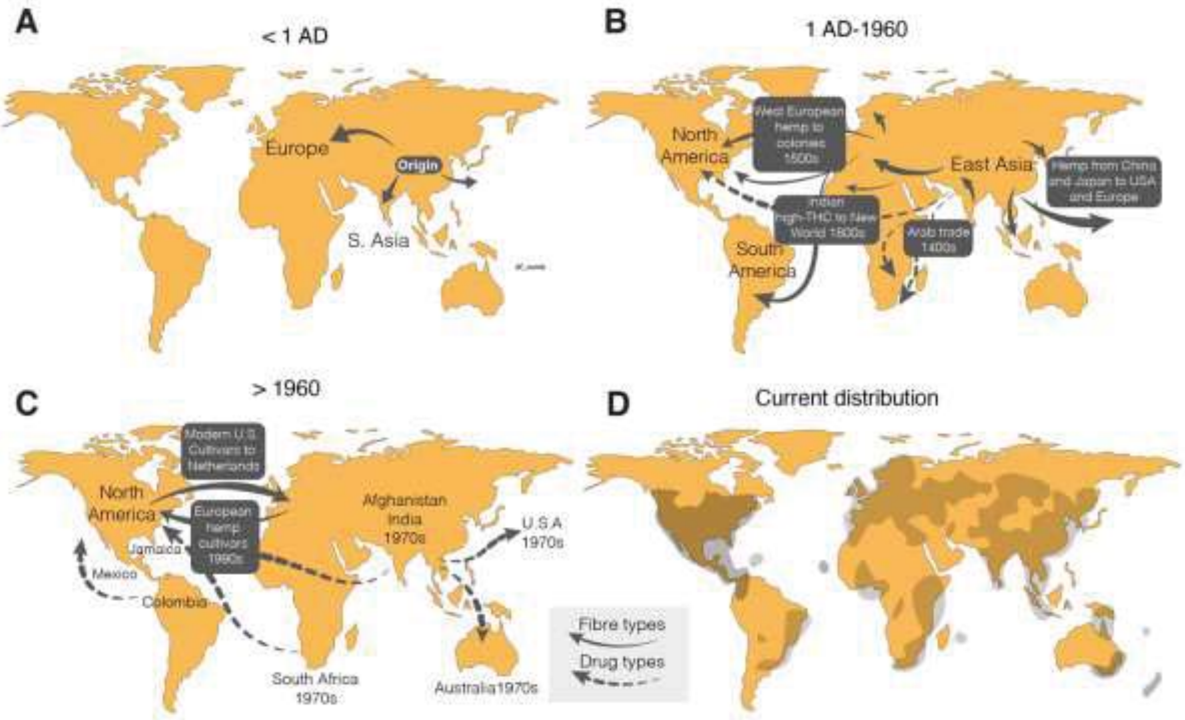

Figure 2. Movement of cannabis (A) from its putative native range in East Asia to areas throughout Asia and Europe during early domestication, (B) worldwide via early trade routes for both drug and fiber crops, and (C) in the past century, mostly for the purpose of recreational drugs. Current distribution (D) of cannabis spans all continents, where plants occur in cultivation, as a feral crop, and as an invasive species. Figures (A) through (C) redrawn and updated from Clark and Merlin (2013). (D) Estimated distribution is based on occurrence records accessed via GBIF.org (14 February 2022) (GBIF Occurrence Download https://doi.org/10.15468/dl.j87ygp).

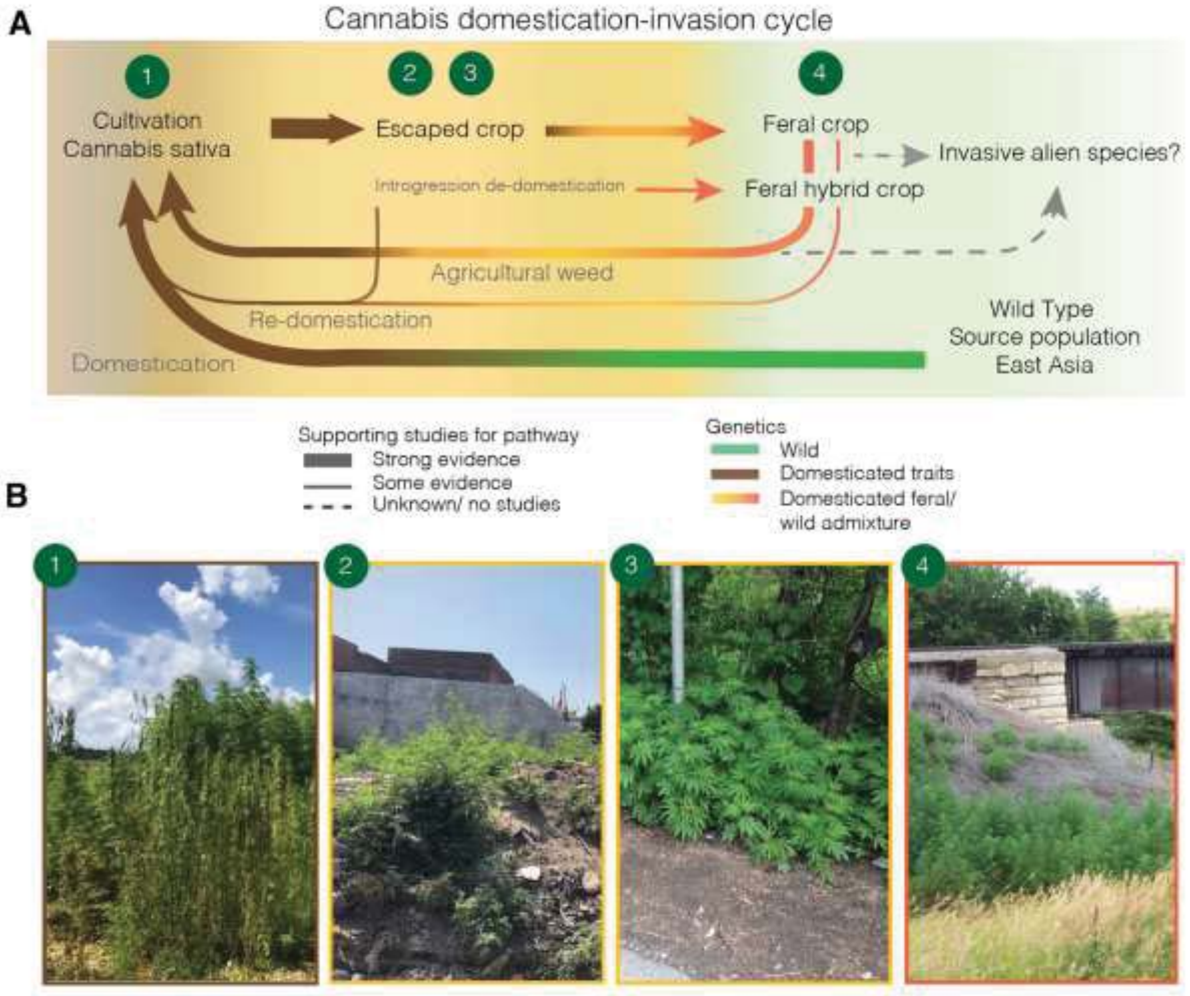

Figure 3. (**A**) Cannabis has transitioned through the de-domestication invasion process (as indicated with thick arrows) from domestication, to escape and cultivation, and back into agroecosystems as a weed. There is evidence for re-domestication and hybridization of feral cannabis crops, although fewer studies have focused on this portion of the process (thin arrows). The ability of feral cannabis populations to move beyond disturbed environments into natural ecosystems and the consequences of such invasions are not, as yet, well understood. **(B)** Cannabis thrives in a wide variety of human-influenced landscapes as (1) a crop and agricultural weed in Florida, United States(photo: William Wadlington); (2) and (3) feral plants in urban environments in India and Kazakhstan (photos: Ajay Sharma, Dennis Keen), (4) an invasive plant in semi-natural areas in the Midwest United States (photo: Luke Howell).

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