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Article Title: Weeds are plants of human-modified environments, not plants out of place

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Short Running Title: What makes a plant a weed?

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Abstract

The question “What makes a plant a weed?” has persisted in both the agricultural sciences and plant ecology and evolution for well over a hundred years. Various authors—agriculturists focused on crop yield, ecologists examining community assembly, and plant biologists interested in adaptation—have each defined the term weed. However, these definitions, developed from unique vantage points, have led to siloed studies and thus constraints on our understanding of weedy plant evolution. Here we briefly review how weeds have been defined historically and argue that weeds are best defined by the environment they occupy: plants that are found, uncultivated and reproducing, in human-modified environments. We then ask whether weeds are human commensals, populations that depend on human-provided resources and have diverged from non-commensal ancestors, treating human dependence as a gradient to be measured. We highlight critical gaps in our understanding of weedy plant occurrence across agricultural, suburban, and urban environments, and propose a database approach leading to testable hypotheses for studying weed presence and persistence. Important outcomes of our reframing include a bridge between agricultural and (sub)urban research disciplines and a shared, data-driven basis for comparing species across the human-modified environments they occupy, illuminating the forces that underlie the weedy lifestyle.

Introduction

The concept of a ‘weed’ is one which most people, biologist or not, are intuitively familiar with. Weeds are everywhere humans are, both part of nature and hellishly difficult to remove from our lawns, gardens, and old sidewalks. The term ‘weed’ has been applied across many organisms—plants and animals alike (Doubleday & Connell, 2018; Simberloff, 2022)—but the notion of ‘weediness’ and its evolutionary and ecological underpinnings have the longest history of investigation in the plant sciences. Both agricultural scientists and plant biologists have attempted to name and define what a weed is, and while these two fields have been largely separate (a history that is interesting in its own right, see (Neve *et al.*, 2009; Menalled *et al.*, 2016; Baucom, 2019)), the long-standing colloquial definition of a weed is *a plant that is out of place or a plant that does not belong*.



Fig 1. Top 10 worst agricultural weeds (WSSA, 2023), shown here in city and suburban landscapes. Despite >3,000 species classified as weeds in agriculture, comparable urban and suburban data are lacking, leaving the extent of overlap between agricultural, suburban, and urban weed communities unknown. Top row (L–R): *Convolvulus arvensis* (field bindweed), *Conyza canadensis* (horseweed), *Amaranthus retroflexus* (redroot pigweed), *Chenopodium album* (lamb’s quarters), *Taraxacum officinale* (dandelion). Bottom row (L–R): *Ipomoea hederacea* (ivy-leaf morning glory), *Ambrosia artemisiifolia* (common ragweed), *Amaranthus tuberculatus* (waterhemp), *Cyperus esculentus* (yellow nutsedge), *Cirsium arvense* (Canada thistle). Photographers, licenses, and source links for images are listed in S1 Table.

This definition, however, tells us as much about the person making the observation of the weed as the plant itself. More specifically, the designation of a plant as a weed is a value judgment made by an individual about a particular plant, in a particular place, and at a particular time—contingent on shifting human preferences and on the context in which the human and plant are found. Defining a weed as simply *a plant out of place* is unnecessarily limiting, both conceptually and scientifically. Who is the appropriate designator? Should there be a timeframe associated with such designations? Do we focus our designation of a weed on those plants that cause economic damage, rather than the species that are ever-present and underfoot but are not necessarily a nuisance? These questions expose the subjectivity built into the term; removing

that subjectivity opens up a broader range of scientific questions—for example, why do some species become a nuisance across many human-created environments (Fig. 1), while others are problematic only in certain contexts?

In this perspective, we argue that weeds are best defined by the environment they occupy: plants that are found, uncultivated and reproducing, in human-modified environments that differ in the type and frequency of disturbance and in the resources they provide. This definition builds on prior disturbance-based definitions but focuses on the context: the plant is in a human-modified environment, where disturbance becomes a measurable variable. We then ask whether weeds are human commensals (Fawthrop et al., 2025), that is, populations that depend on human-provided resources and have diverged from non-commensal ancestors, and we treat dependence as a measurable continuous variable. We review how weeds have been defined, show where the commensalism framework applies to agricultural and urban weeds, and identify gaps in our understanding of weedy plant occurrence across agricultural, suburban, and urban environments, which impose both shared and distinct selection pressures. We then propose a database of weedy plants and the hypotheses it makes testable. The result is a shared basis for connecting the largely siloed study of weeds in agricultural and (sub)urban contexts, and a structured framework for future empirical work designed to understand the evolutionary forces that lead to “weediness”.

Baker and Harlan & deWet were both right

The generic *plant out of place* definition of a weed may be the default because as Baker (1965) observed, “definitions of a weed are almost as numerous as the authors of papers dealing with them.” In *Some Thoughts About Weeds*, Harlan and deWet (1965) organized the many existing definitions into three categories based on the community that developed them. “Professional weed men” described weeds as *obnoxious*, *nuisance*, *plants with harmful or objectionable habits*, *unwanted*, or *does not belong* (Table 1), whereas the “ecologically minded” placed emphasis on weeds being *pioneers of secondary succession* in the *weedy arable field*, or *artifacts* or *camp followers* (Table 1). Both categories of definition have limits. Human judgment alone offers no insight into why or where weeds exist, how they interact with other species and with crops, or how to manage them (Radosevich et al., 2008). Ecological context alone fails to capture how a species may behave differently in other contexts: is a plant a weed in one setting but not another? Finally, definitions made by “enthusiastic amateurs”—namely, Ralph Waldo Emerson’s weed as *a plant whose virtues have not yet been discovered* (Blatchley, 1912)—

highlights why weeds should not be defined *via* value judgment. Human values shift through time or vary according to social construct; a *nuisance* or *obnoxious* plant in one context may be a valuable source of food or forage in another.

In Table 1, we present a summary of definitions of the term *weed* and rank them according to whether they lend themselves to testable hypotheses. For example, the definition from the Weed Science Society of America (WSSA) allows for greater evaluation than prior definitions as it positions a weed as “A plant that causes economic losses or ecological damage, creates health problems for humans or animals, or is undesirable where it is growing” (WSSA, 2016). Economic loss or ecological damage can be quantified, as can the potential to create health problems in humans or other animals; however, this view still leans into the human value of undesirable.

Even more neutral—and thus more easily testable—definitions of a weed come from Harlan and deWet (1965) and Baker (1965). Harlan and deWet define weeds as plants that display “An adaptive syndrome which permits a species or variety to thrive and become abundant and difficult to eradicate within areas of human disturbance,” whereas Baker’s definition notes that “A plant is a “weed” if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without being deliberately cultivated).” In the same period, Baker proposed a set of traits that characterized the “ideal weed,” and later argued that successful weeds often possess a “general-purpose genotype”—a genotype conferring wide environmental tolerance and the ability to grow across a multitude of climates and edaphic situations (1965, 1974). We expand on this aspect of Baker’s contribution in Box 1. While distinct from his formal definition of a weed, these concepts established the groundwork for later examinations of weediness traits and the importance of plasticity for the weedy plant lifestyle.

In both of these definitions, a plant is a weed if it can take advantage of human-based disturbance—the disturbance humans create is relevant, human opinion about the plants that exploit it is not. Baker’s definition includes no constraint on population size or abundance, allowing it to capture presence in its own right, rather than requiring a species to reach some threshold of abundance before it qualifies as weedy. Leaning into Baker’s human-disturbance based definition aligns with a key question in ecology and evolution: how humans, as the

world's greatest evolutionary force (Palumbi, 2001), may alter the evolutionary trajectories of the species around them.

In that light, we propose a more encompassing definition of a weed, as *uncultivated plants that are able to take advantage of, or tolerate, the environments humans create or manipulate, and that are able to reproduce in such environments, whether through adaptation or plasticity* (Table 1). This definition builds on Baker's (1965) and Harlan and deWet's (1965) emphasis on human disturbance, but centers the human-modified environment, rather than exposure to human-mediated disturbance. We make this shift for two reasons. First, human-modified environments differ in disturbance type and frequency, so disturbance is better included as a measured variable than as a prerequisite for inclusion. Second, humans modify environments in ways that are not disturbance (e.g., supplying water, nutrients and shelter), and these changes may matter as much as disturbance for the plants that persist there. The reframing was inspired by the view of humans as an evolutionary force and by the human commensalism framework (Fawthrop et al., 2025), which recognizes that some species depend on the resources humans provide and are adapted to, and found in, human-modified environments. This shift also follows a broader move in ecology and evolution to treat agricultural, suburban, and urban landscapes as human-modified systems, each with shared and unique pressures (Foley et al., 2005; Ellis & Ramankutty, 2008; Johnson & Munshi-South, 2017). Centering the environmental context lets us ask whether weeds are also commensal, that is, dependent on those environments. We next explain the human commensalism framework and how it informs the definition.

Type	Definition	Source	Testability
Anthropomorphic / Judgment-Based	A plant out of place / Any plant which grows where it is not wanted	(Blatchley, 1912); (Georgia, 1916) (Muenscher, 1946); (Isely, 1960); (Salisbury, 1961); (Klingman, 1961); (Wodehouse, 1963)	Low; depends entirely on an unspecified observer's intent
	Any plant that interferes with man's plan of conquering the earth	(Pieper, 1930)	Low; rhetorical framing
	Higher plants which are a nuisance / Obnoxious plants / Unsightly	(Harper, 1960); (Robbins <i>et al.</i> , 1952); (Thomas, 1959)	Low; purely evaluative language
	A plant that causes economic losses or ecological damage, creates health problems for humans or animals, or is undesirable where it is growing	(WSSA, 2016)	Moderate; economic, ecological, and health clauses are measurable, but the disjunctive 'or undesirable' clause allows subjective classification
Ecological / Trait-Based	Predominant and pernicious / A plant that grows so luxuriantly or plentifully that it chokes all other plants that possess more valuable properties	(Gray, 1879); (Brenchley, 1920)	Low; no measurable threshold given for "predominant", and "valuable properties" reintroduces a value judgment
	Pioneers of secondary succession, specifically of arable fields / Artifacts, camp followers	(Bunting, 1960); (Anderson, 1952)	Moderate; successional stage is observable, but scope is narrowly agricultural
	A plant species that can thrive in disturbed habitats (whether altered by natural or anthropogenic forces) due to increased plant fitness through functional and adaptive traits	(Sharma <i>et al.</i> , 2021)	High; fitness and traits are directly measurable, though "disturbed" still needs defining
Association with Human Disturbance	A plant is a "weed" if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without being deliberately cultivated)	(Baker, 1965)	High; disturbance and cultivation status are both observable in the field
	An adaptive syndrome which permits a species or variety to thrive and become abundant and difficult to eradicate within areas of human disturbance	(Harlan & deWet, 1965)	Moderate–High; "adaptive syndrome" implies measurable traits, but "difficult to eradicate" is harder to quantify consistently
Association with Human-Modified Environments	Uncultivated plants able to take advantage of, or tolerate, the environments humans create or manipulate, and likewise able to reproduce in such environments, whether through adaptation or plasticity	<i>Baucom & Josephs</i>	High; persistence and reproduction in human-modified habitats are directly observable and quantifiable

Table 1. Example definitions of the term 'weed' through time, grouped by four themes. Anthropomorphic or judgment-based definitions emphasize human opinion. Ecological or trait-based definitions focus on ecological context or life-history traits. Association-with-human-disturbance definitions define weeds as plants found in human-disturbed areas. We propose a definition of weeds based on association-with-human-modified-environments as a fourth category. We note that groupings overlap and should not be interpreted strictly. We rank each definition according to whether its criteria can be measured directly (e.g., population density, presence in disturbed habitats) or if it relies on human judgment (e.g., nuisance, undesirable).

Box 1

Baker's "ideal weed" traits and the general-purpose genotype

Herbert Baker, a plant biologist and "genecologist" from California, developed a list of traits describing the "ideal weed" by contrasting weedy plants to non-weedy close relatives (Baker 1965 and references therein). The list, first published in *The Genetics of Colonizing Species*, includes the following:

1. Has no special environmental requirements for germination.
2. Has discontinuous germination (self-controlled) and great longevity of seed.
3. Shows rapid seedling growth.
4. Spends only a short period of time in the vegetative condition before beginning to flower.
5. Maintains a continuous seed production for as long as growing conditions permit.
6. Is self-compatible, but not obligatorily self-pollinated or apomictic.
7. When cross-pollinated, this can be achieved by a nonspecialized flower visitor or by wind.
8. Has very high seed output in favorable environmental circumstances.
9. Can produce some seed in a very wide range of environmental circumstances. Has high tolerance of (and often plasticity in face of) climatic and edaphic variation.
10. Has special adaptations for both long-distance and short-distance dispersal.
11. If a perennial, has vigorous vegetative reproduction.
12. If a perennial, has brittleness at the lower nodes or of the rhizomes or rootstocks, so that it is not easily dug out of the ground.
13. If a perennial, shows an ability to regenerate from severed portions of the root-stock.
14. Has ability to compete by special means: rosette formation, choking growth, production of toxic substances (allelopathy), etc.

One of Baker's main conclusions was that there is no single path to weediness: some species succeed through a wide array of traits, others through just one or a few. He likewise developed the concept of the "general-purpose genotype," which he defined as "the kind of genotype which provides the plant bearing it with a wide environmental tolerance, and gives it the ability to grow in a multitude of climates and edaphic situations" (1965). Both concepts—"ideal weed" traits and the general-purpose genotype (GPG)—inspired decades of subsequent research on traits associated with weedy plants in global and regional flora, as well as studies of plasticity and plant adaptation to new environments (reviewed in Richards *et al.*, 2006; Pyšek & Richardson, 2007; Lau & Funk, 2023).

Notably, while Baker discussed differences between native and introduced weeds narratively (1974), he did not treat introduction status as a variable for comparisons the way later trait-based studies would; Stebbins, writing in the same 1965 volume, focused specifically on traits of weeds within the native California flora. Since that time, trait-based and GPG-inspired research has concentrated heavily on introduced, invasive species, leaving comparisons of native weeds and native non-weeds comparatively rare. Exceptions include Sutherland (2004), who compared life-history traits among native and exotic weeds and non-weeds in the US flora, and Kuester *et al.* (2014) and (Van Etten *et al.*, 2017), who extended Baker-inspired comparisons to include native weeds versus native non-weeds directly, along with the more conventional introduced-species contrasts.

/end Box 1

Are weeds human commensals?

As defined by Fawthrop *et al.* (2025), a human-commensal species exhibits both population-level dependence on anthropogenic resources and genetic differentiation from a non-commensal ancestral population (Fig. 2). This definition builds on the classic view of commensalism as a pairwise interaction in which one partner benefits while the other experiences no net benefit or harm (Maréchal & McKinney, 2020; Mathis & Bronstein, 2020). Human commensalism specifies that relationship further: the non-human partner benefits from exploiting human-modified environments, while the human experiences neither meaningful benefit nor cost—or if there is a cost, it is much smaller than the benefit to the non-human partner. Costs and benefits are assessed on fitness, not economic harm, so a plant that reduces crop yield can still be a commensal, whereas a species that harms human health (for example, through allergenic pollen or toxins) would not be. Human commensalism is different from related terms, such as synanthropic, anthrophilic, synurbic, or urban exploiter that instead describe different components of human interaction intensity (Fig. 2; Fawthrop *et al.*, 2025). Critically, the human commensalism framework requires that humans are actively living in or modifying the environment in question, not just affecting it. Most species are influenced in some way by humans *via* habitat fragmentation, global climate change, and other pressures; being affected by humans is not the same as relying on them. Both criteria of the definition of human commensalisms are testable: a dependent population declines or fails to persist when the human-provided resource is removed, and differentiation can be assessed by comparing populations from human-modified environments with non-commensal ancestral or reference populations.

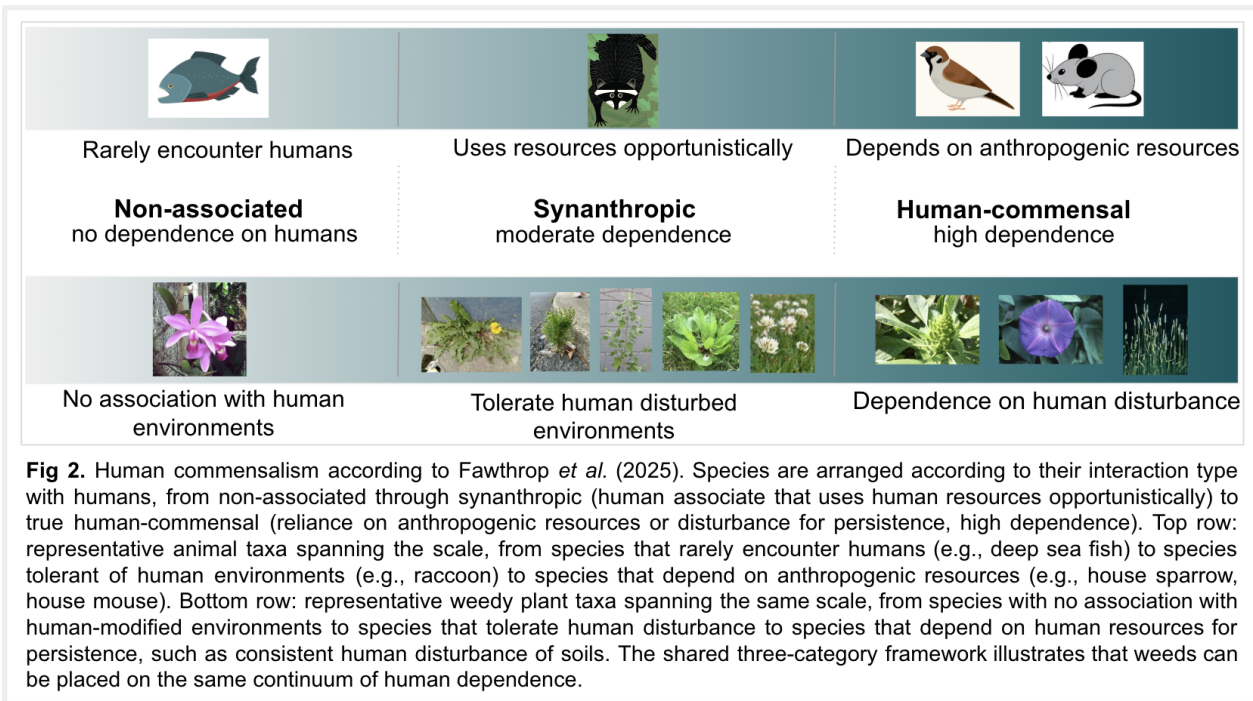
Weedy plants are strong candidates for human commensals. Many crop weeds (also known as
agrestals), such as various *Ipomoea* (morning glory) species, *Chenopodium album*
(lambsquarters), and *Setaria faberi* (giant foxtail) (Fig. 2), depend on the open, disturbed soil
created by tillage for germination (Dekker & Hargrove, 2002; Baucom *et al.*, 2011; Eslami &
Ward, 2021). If these species are commensals, their populations should decline when the
disturbance is removed (Fawthrop *et al.*, 2025). Although not yet studied explicitly within the
commensalism framework, ‘weed shifts’, in which weed communities reorganize after a change
in agricultural practice, offer a scenario ripe for testing. A management regime, such as
sustained use of a particular herbicide or tillage system (Buhler, 1995; Owen, 2008),
suppresses some species and so opens ecological space for others better able to tolerate it.
When the regime changes, species that benefited from the old conditions decline and others
expand (Storkey *et al.*, 2012). Release from competition is not among the resources Fawthrop
et al., (2025) list, so we treat it here as an extension of the framework. Weed shifts identify
species associated with a regime; determining which are commensals would be informed by
tracking populations after the regime is removed altogether, or by testing whether competitor
suppression underlies their advantage.

A second tenet of the human commensalism framework is that commensals exhibit genetic
differentiation from non-commensal or ancestral lineages. Weedy radish (*Raphanus*
raphanistrum) offers a clear agricultural example: populations sampled from crop fields flower
significantly more rapidly than any other *Raphanus* population or cultivar, consistent with
genetic differentiation due to adaptation to the frequent, severe disturbance characteristic of
agricultural fields (Charbonneau *et al.*, 2018). Crop-mimic weeds provide further examples,
having diverged from non-mimetic relatives in response to selection imposed by weeding. A
weedy strain of *Camelina sativa* (false flax) evolved a suite of adaptations to mirror flax, such as
similar height, synchronous reproduction, and flax-like seed morphology, which help it escape
removal from flax fields (Harper *et al.*, 1970; Barrett, 1983; Brock *et al.*, 2018). Similarly,
Echinochloa crus-galli (barnyard grass), has evolved rice-like tiller angle and phenology to
escape detection in rice paddies (Barrett, 1983; McElroy, 2014; Ye *et al.*, 2019).

A parallel pattern has been documented in urban weeds, which show genomic (*Lepidium*
virginicum) and/or phenotypic (*L. virginicum* and *Ambrosia artemisiifolia*) divergence along
urban-rural gradients (*L. virginicum*: Yakub & Tiffin, 2017; *A. artemisiifolia*: Gorton *et al.*, 2018).
Such differentiation in response to human-modified environments may be repeatable across

agricultural and urban contexts, although it can be inconsistent across cities (Kostanecki *et al.*, 2021; Santangelo *et al.*, 2022a). These patterns provide evidence for the differentiation component of commensalism, but differentiation alone does not distinguish dependence from tolerance, so dependence must be shown separately. Detecting differentiation is also a high bar, because it requires paired ancestral and derived populations, and the rural end of a gradient is not necessarily ancestral. Historical sampling could also provide evidence of genetic differentiation during adaptation to human-modified environments (Kuester *et al.*, 2016; Kreiner *et al.*, 2022). Further, weeds may also succeed in human-modified environments without additional genetic changes, persisting instead through phenotypic plasticity, and populations may differ in plasticity itself. Here we suggest that adaptation and plasticity are complementary routes to persistence in human-modified environments, and that plasticity deserves investigation as a pathway toward commensalism.

Weeds differ in how strongly they depend on human-modified environments, and not all require human-modifications. Some persist through tolerance or dispersal adaptations that make them better characterized as 'synanthropic' (Fig. 2) or opportunistic species (Hulme-Beaman *et al.*, 2016). These species exploit novel spaces humans create, such as sidewalk and asphalt cracks, or persist in abandoned lots and lawns (e.g., *Convolvulus arvensis*; Del Tredici, 2010). Synanthropic or opportunistic species can likewise be found in agricultural areas, taking advantage of that space without relying on it. Some species may depend on one component of human modification (i.e., disturbance) while remaining opportunistic with regard to other resources—for example, *Ipomoea* vines that climb maize plants for access to light, or nitrophilous weeds such as common lambsquarters (*Chenopodium album*) that exploit fertilizer inputs (Blackshaw *et al.*, 2003) without depending on them for persistence (Simard & Ziadi, 2024).



Since dependence on humans is not necessarily a fixed property of a species but a variable relationship that must be measured, our suggested entry criterion for weediness does not itself require it. Following Baker (1965) and, to some extent, Harlan and deWet (1965), a plant qualifies as a weed if it is found, uncultivated and reproducing, in a human-modified environment. We depart from Baker by centering the human-modified environment rather than disturbance, and by treating dependence on human resources, a hallmark of human commensalism (Fawthrop *et al.*, 2025), as something to measure. This change does not make cross-environment questions newly possible, but it should encourage them.

We next characterize how human-modified environments differ and overlap in the type, frequency, and predictability of their stressors and resources, and what this suggests about the selective pressures weedy plants contend with in each.

Human-modified environments as selective landscapes for weedy plants

Human modifications in urban, suburban, and agricultural landscapes challenge plants and the potential effects of these modifications have been heavily reviewed (Cousens & Mortimer, 1995; Murphy & Lemerle, 2006; Grimm *et al.*, 2008; Radosevich *et al.*, 2008; Johnson & Munshi-South, 2017; Rivkin *et al.*, 2019; Alberti *et al.*, 2020). Some of these challenges are shared

across environments. For example, these landscapes all experience high levels of chemical stress. In response to heavy use of chemical herbicides, plants have repeatedly evolved herbicide resistance, creating agricultural challenges (Délye *et al.*, 2013; Baucom, 2019). Suburban species may also face strong herbicide pressure and urban species face additional toxic chemicals due to soil pollution (Vanni *et al.*, 2015). In addition, both urban and agricultural environments can experience increased levels of drought than natural areas (Lambrecht *et al.*, 2016), although this pattern is reversed in cities in arid climates (Hope *et al.*, 2003) and in irrigated fields. These shared environmental pressures could select for similar responses: for example, urban plants often flower earlier than plants from rural populations in situ (Li *et al.*, 2019) and in common garden (Yakub & Tiffin, 2017; Gorton *et al.*, 2018; Stanley & Ashman, 2025; Chan *et al.*, 2026; *but see* Lambrecht *et al.*, 2016; Taichi *et al.*, 2025). Early flowering is also a hallmark of adaptation in agricultural weeds (Le Corre *et al.*, 2020; Li *et al.*, 2023; Garrison *et al.*, 2024) and early flowering can contribute to herbicide resistance (Raingeval *et al.*, 2024).

However, not all environmental stresses are shared across human-modified environments. Urban environments are characterized by higher temperatures than surrounding rural areas, suggesting that urban environments may select for resilience to high temperatures in ways that rural environments will not (Taichi *et al.*, 2025). In addition, (sub)urban and agricultural habitats likely differ in nutrient levels. Agricultural weeds have evolved to exploit higher levels of nutrients from fertilizer (Bravo *et al.*, 2018) while in urban yards, fertilization reduces the presence of weeds relative to cultivated species (Cavender-Bares *et al.*, 2020). Interestingly, the crop mimicry example described earlier points to a further difference between urban and agricultural environments: there is no straightforward analog to this kind of adaptive scenario in urban settings. There may, however, be a parallel process at work: urban weeds that grow low to the ground may be favored for escaping mowing (Baucom & Holt, 2010), and since homeowner preferences shape species diversity in urban yards (Cavender-Bares *et al.*, 2020), aesthetically appealing weeds may carry a fitness advantage in these environments as well.

One benefit of comprehensively studying weeds across (sub)urban and rural contexts will be uncovering the common features of these human-modified landscapes that benefit weeds. For example, human-modified landscapes often have reduced herbivore diversity (Maunder *et al.*, 2025) that could select to lower levels of chemical defenses in weeds (Santangelo *et al.*, 2022a) although patterns of herbivory across urban and natural landscapes are heterogeneous

(Santangelo *et al.*, 2022b). Similarly, the stresses of (sub)urban and rural environments could reduce competition from other species, benefiting weeds that can tolerate harsher conditions (DiTommaso, 2004; Bae *et al.*, 2016). This effect may be stronger for urban weeds than agricultural weeds, at least as seen in studies that find that, compared to rural populations, urban weeds are less resilient to competition (Fukano *et al.*, 2020) and herbivory (Pisman *et al.*, 2020).

While we have discussed specific examples, making broad conclusions about the shared nature of stresses and adaptive strategies across human-modified environments is difficult because agricultural stresses are mostly studied by weed scientists while urban stresses are studied by evolutionary ecologists (Rivkin *et al.*, 2019) although some studies of urban weed adaptation use agricultural populations as a non-urban control (Fukano *et al.*, 2020). A broader definition of a plant as a weed allows for comprehensive studies of that species across environments, which can ultimately test the question that will seemingly never go away— “what makes a weed a weed?”

Casting a wide net will allow us to ask novel questions about the factors that underlie weediness

As noted above, weeds studied in agricultural spaces are typically examined in isolation from their presence in (sub)urban spaces, and *vice versa*. Because these contexts have largely been studied separately, no framework has emerged for uniting the study of weeds across human-modified environments. Such a framework would make it possible to ask questions that are difficult to ask with context-specific data, such as the ubiquity question raised previously (Fig. 1): is a plant’s presence across multiple human-modified environments due to a long-term association with humans, high stress tolerance, a dispersal mechanism that enables presence regardless of context, or some combination of these? The commensalism framework adds questions about dependence: how strongly does a given species depend on human-modified environments, what trait or set of traits confers high persistence, and does dependence on humans imply that some trade-off exists in adapting to human environments? Further, how does a plant’s introduction history influence the likelihood that a species will be considered weedy or problematic in multiple human-modified environments?

Answering questions like these requires data that do not yet exist in a unified, comparable

form—presence, abundance, and dependence are rarely recorded across agricultural, urban, and suburban contexts for the same species. We therefore advocate for a broad database of human-associated plant species, built around two core principles: an inclusive entry point (i.e., Is this plant found, uncultivated and reproducing, in a human-modified environment?), and measured variables that allow for developing structured hypotheses about such plant species. Table 2 lists variables that we envision as the basis for re-framing our understanding of weedy plants (presence, abundance, human-modified environment or land type), as well as the variable that would allow us to assess a weed’s degree of dependence on human-modified environments—namely, whether it is disturbance-requiring or dependent on some other human-provided resource. Beyond this, incorporating introduction history will further disentangle introduced non-weeds from introduced weeds, also known as invasive species—a strategy taken in (Kuester *et al.*, 2014) that identified distinctions between introduced plants that are considered ‘problematic’ versus introduced plants that have yet to merit concern. Further, including a noxiousness variable can allow for a separate axis of consideration: noxious is a legal and regulatory designation, assigned differently across federal, state, and international entities (Skinner *et al.*, 2000; Quinn *et al.*, 2013; Beaury *et al.*, 2021). Exactly how best to incorporate this variable—whether as a binary federal designation, a count of state-level listings, a categorization by harm domain (e.g., agricultural, ecological, human health), or some combination of these—remains an open and important question for consideration. We emphasize that what we propose here is a framework and starting set of variables (Table 2) and not a completed design—rather, a conceptual foundation for future adaptation. Box 2 outlines several of the novel hypotheses and research directions this restructured definition and database can open up.

Variable	What it captures	Why it matters
Presence (y/n)	Whether an uncultivated plant occurs in a human-modified environment.	Operationalizes the ubiquity/specificity axis (found in all environments vs. one).
Reproduction (y/n)	Whether the plant reproduces in the environment versus transient due to immigration.	Separates persistent populations from transient ones.
Abundance	Population size/density where present.	Distinguishes ubiquitous-but-rare from ubiquitous-and-dominant, a distinction presence/absence alone does not capture.
Context or land type	The specific human-modified environment the species occupies. Can be captured in a variety of ways.	Allows for a test of whether presence across environments reflects a shared underlying stressor or independent, environment-specific pressures.
Disturbance type and frequency	The kind of disturbance (e.g., mowing, tilling, herbicide, etc) and frequency of such disturbance.	Makes disturbance a measured variable, allowing tests of whether ubiquity is tied to particular regimes.
Dependence on human resource	Whether persistence depends on human inputs, such as consistent disturbance. Other relevant human-based resources could be included.	Closest measured proxy for dependence; a species can fail this test and remain in the dataset rather than being excluded <i>a priori</i> .
Introduction history (y/n)	Introduced vs native status.	Allows for contrasts of native vs introduced species, may help to disentangle the concepts of weediness and invasiveness.
Noxiousness metric	Degree of harm/economic damage/undesirability.	Fashioned as a measured outcome rather than the criteria for entrance in the database.

Table 2. Variables to record when developing a structured database of weedy plants found in human-modified environments. These variables enable hypothesis-driven comparisons of presence and abundance across contexts and allow additional information—such as plant traits (Box 1)—to be layered on to assess what underlies prevalence and persistence.

Box 2

Testable hypotheses enabled by this framework

Overarching question: *Why are some weedy species found across every human-modified environment they encounter, while others are restricted to one?*

One could take a multi-tiered approach to testing hypotheses about general adaptation to multiple human-modified environments. First, systematic floristic surveys across agricultural, suburban, and urban environments would establish presence and abundance (categorized, e.g., absent to dominant) for each species, identifying core weeds found across all environments versus those restricted to one. This presence/abundance matrix would then support phylogenetic and trait-based analysis: testing whether ubiquity and abundance show phylogenetic clustering—indicating a shared, conserved basis for ubiquity—or phylogenetic overdispersion, indicating convergent, independent origins; identifying which traits associate with high ubiquity versus specificity, and whether trait associations differ by environment type. Further, incorporating introduction status (introduced vs. native) would allow one to examine potential differences between native and introduced weeds (invasives). Finally, a sub-sample of core weeds identified through this process would move into experimental eco-evolutionary work: common garden studies to test whether trait differences persist under shared conditions (e.g., smaller size in urban-origin lineages?), and reciprocal transplants to test for local adaptation via home-site performance advantages.

Overarching question: *Do various human-modified environments have similar impacts on dispersal and gene flow?*

Human modifications are likely to affect not just the stresses that plants experience, but also broader patterns of movement across the landscape. These changes have led to specific hypotheses for how human modifications could affect gene flow, leading to selection for specific dispersal traits. First, there is an expectation that human-modified environments will be more fragmented than natural environments (Haddad *et al.*, 2015; Miles *et al.*, 2019). Fragmentation can shape the evolution of mating systems, floral traits, and life history traits (Jacquemyn *et al.*, 2012). In line with this, (Cheptou *et al.*, 2008) found that the fragmented nature of urban environments selects for reduced dispersal.

Second, human actions could themselves modify dispersal patterns, if humans or their vehicles are likely to move seeds (Baduel *et al.*, 2018), if human modifications provide barriers to movement, or if human-modifications affect communities of dispersors (Stanley & Arceo-Gómez, 2020). However, while urban areas tend to contain species with different dispersal traits than rural areas (Knapp *et al.*, 2012), there is not clear evidence of urbanization affecting gene flow patterns within species (Miles *et al.*, 2019; Chan *et al.*, 2026; Hoffman *et al.*, 2026). Meanwhile, agricultural weeds often show evidence of low differentiation among populations, potentially due to human-mediated dispersal (Alvarado-Serrano *et al.*, 2019; Ravet *et al.*, 2021).

As more researchers connect genomic datasets for human commensal species, it will be possible to assess patterns of gene flow across environments and develop a unified framework for how human modifications affect gene flow and how plant dispersal evolves in response to these modifications.

Overarching question: *How does plasticity contribute to success in human-modified environments?*

Plasticity is often hypothesized to be important for persistence through environmental stress and establishment in new environments (Chevin & Hoffmann, 2017), making it a key potential contributor to weed success across urban and agricultural habitats (Baker, 1974; Rivkin *et al.*, 2019). Studies in agricultural weeds have suggested that plasticity likely contributes to adaptation to human-modified environments (Josephs *et al.*, 2021; Garrison *et al.*, 2024). While there have been fewer studies of urban weeds, many of the weed trait differences observed along urbanization gradients are plastic (Sotillo *et al.*, 2024; Taichi & Ushimaru, 2024). Combined, these results suggest that plasticity could in general allow plants to thrive in human-modified environments, but we lack comprehensive evidence of this pattern across environments.

Addressing the role of plasticity in adaptation to human commensality will first require common garden experiments and, especially, reciprocal transplant experiments, that can clearly demonstrate links between plasticity and fitness. While these studies are limited in urban environments, the ones conducted so far do not find strong evidence for a role for plasticity. In a reciprocal transplant experiment, (Gorton *et al.*, 2018) found both rural and urban plants were equally plastic to rural vs urban environments, suggesting that changes in plasticity did not contribute to any potential adaptation to human commensalism. Similarly, (Géron *et al.*, 2022) did not find differences in plasticity between urban and rural populations. Meanwhile, in agricultural weeds, common garden experiments have shown that plasticity could contribute to persistence but that agricultural populations have evolved a mixture of increased and decreased plasticity across traits (Hermanutz & Weaver, 1996; Garrison *et al.*, 2024).

/end Box 2

Synthesis and forward look: Benefits of studying weeds in proposed framework

There are numerous benefits in being inclusive about what makes a plant a weed from the outset and in taking a structured, empirical approach to studying weedy plants. Primarily, the inclusive entry criterion and the framework we have detailed replace an *a priori* assumption about a plant species with data-driven characterization. For example, prior work has leaned on lists of plants classified as a ‘weed’ by knowledgeable entities—each with their own way of deciding which plants should be included (WSSA, 2026; Daehler, 1998; Holm & Holm, 2014)—and then identified traits or characters associated with weeds compared to non-weeds (Williamson, 1993; Sutherland, 2004; Kuester *et al.*, 2014). The approach we advocate makes no prior designation a bar for inclusion; instead, a plant found, uncultivated and reproducing, in a human-modified environment is itself the entry point, with abundance and other measurable properties then recorded and compared across contexts. Variation among species then emerges from the data (e.g., Is the species dependent on human resources? How abundant is

it? Is it found in each of the human-modified environments under study? What is its introduction history?) and is not assumed from the outset. The framework is thus generative rather than classificatory and aimed at broadening the scope of study of weedy plant ecology and evolution.

Further, we treat commensal status as an outcome of data collection, rather than criteria for inclusion. We likewise re-center the definition of a weed on plants occurring in human-modified environments, rather than on disturbance; within these environments, the type of human-based disturbance becomes a recorded variable. Doing so allows one to examine the ubiquity and specificity of a weed across different human-modified contexts, exposed to different frequencies and intensities of disturbance. Additionally, under this framework, the concept of noxiousness as established by federal or state entities could be included as a measured variable in the dataset, allowing new testable questions (e.g., Are noxious species disproportionately ubiquitous across human-modified environments?).

To be sure, broadening the definition of a weed to be more inclusive will invariably expand the list of qualifying species well beyond those on official inventories like the WSSA list, which currently contains ~3.8k species (WSSA, 2026). This could be viewed as practically counterproductive: land managers and regulatory bodies often need to prioritize eradication efforts on species of the highest economic or ecological concern, not on every plant capable of persisting in a human-modified space (Skinner *et al.*, 2000). Additionally, and as we have pointed out before, there are numerous definitions of the term ‘weed’—do we really need a restructuring or reframing? Further, where do plants that can invade natural areas, and are sometimes labeled as ‘weeds’ fit within this framework? There are likewise large-scale efforts already characterizing plants at a global level—GloNAF (Global Naturalized Alien Flora), for instance, compiles distribution data for naturalized alien plant species worldwide (van Kleunen *et al.*, 2019), and there would certainly be species overlap between initiatives. Finally, reframing weeds as plants that can persist in human-modified spaces necessitates action—careful taxonomic inventories of plants in agricultural and (sub)urban spaces will need to be made (e.g., presence and abundance data), and, to describe and differentiate types of weeds from one another, additional categories of data will need to be recorded (Table 2). Who is to generate these data, individual researchers, coordinated groups of researchers, etc?

Others have identified pieces of this problem. Radosевич *et al.*, (2008) argued for a neutral, non-value-laden definition of a weed, and noted that evaluations of a successful species should

consider the number of individuals, the range of habitats occupied, and the ability to continue the species through time. Morin *et al.*, (2013) made the same core observation that we do here: the classification of a plant as a weed rests largely on human perception of being ‘troublesome’ rather than on objective criteria. Past efforts have pointed to the same problem, but none provided a structure that describes a testable path forward. Meanwhile, the same weed species, weedy traits, and evolutionary processes are frequently studied in agricultural and (sub)urban settings in isolation from one another, with little overlap between urban ecology and evolution and agricultural weed science. Applying one inclusion rule across all human-modified environments, and treating both disturbance (type, frequency) and dependence as measurable quantities makes it easier to ask questions about a species’ presence, persistence, and adaptation across the full range of contexts it occupies, rather than having separate subdisciplinary studies on the same species, as is current practice.

This approach can also help to disaggregate weediness from the sometimes inconsistently defined ‘noxious’ label, which tends to rely on regulatory judgments or economic filters. It is distinct from GloNAF (van Kleunen *et al.*, 2019), which documents where naturalized alien plants occur worldwide but not the land-use contexts they occupy, their dependence on human-modified environments, or native weeds; GloNAF is therefore a natural source of data for the database and not a competing effort. We view the remaining concerns raised above, the number of species and who will generate the data, as ones that any large conceptual advance would need to examine in practice.

Finally, another benefit of this reframing is that it helps distinguish plants that are invasive from plants that are weeds. A species is considered invasive if it is non-native, has been introduced either intentionally or unintentionally, and is likely to cause economic harm (Iannone *et al.*, 2020). Invasive plants are labeled invasive weeds by the WSSA (WSSA, 2016), yet this terminology is discouraged by others since not all weeds are invasive (Iannone *et al.*, 2020). Invasive plants can invade natural areas (e.g., cheatgrass) and maintain their population sizes without further disruption or input from humans, so by the definition and framework presented here we would not consider natural-area invaders to be weeds. The two categories can overlap: an introduced plant that also occurs and reproduces in human-modified environments would qualify as a weed there. Introduction history and noxiousness are therefore incorporated (Table 2) so that invasive status can be examined across contexts.

Summary

Prior definitions of the term weed relied on human opinion, ecological characteristics, or economic harm, typically in isolation from one another. While each perspective can be useful, relying on them in isolation constrains our understanding of weediness. In contrast, viewing weedy plant ecology and evolution through the lens of human association allows for a broader, more neutral definition—and, with it, an operationalized way forward. For example, definitions that focus on abundance in a particular context—*i.e.*, an ecological lens—or that imply some threshold of economic harm would fail to generate hypotheses about the characteristics and processes underlying ubiquitous but low-abundance species. A further tangible outcome of this framework is that it gives weed scientists and urban evolutionary ecologists a shared vocabulary and data structure to ask the same questions of the same species. By defining weeds as plants found in human-modified environments, and by proposing an inclusive entry point to a structured, testable dataset, we aim to offer a more rigorous way to ask why some species succeed virtually everywhere humans are.

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References

- 647 Alberti, M., Palkovacs, E. P., Des Roches, S., De Meester, L., Brans, K. I., Govaert, L., et al.
648 (2020). The complexity of urban eco-evolutionary dynamics. *BioScience*, 70, 772–793.
- 649 Alvarado-Serrano, D. F., Van Etten, M. L., Chang, S.-M., & Baucom, R. S. (2019). The relative
650 contribution of natural landscapes and human-mediated factors on the connectivity of a noxious
651 invasive weed. *Heredity*, 122, 29–40.
- 652 Anderson, E. (1952). *Plants, man and life*. Little, Brown.
- 653 Baduel, P., Hunter, B., Yeola, S., & Bomblies, K. (2018). Genetic basis and evolution of rapid
654 cycling in railway populations of tetraploid *Arabidopsis arenosa*. *PLOS Genetics*, 14, e1007510.
- 655 Bae, J., Benoit, D. L., & Watson, A. K. (2016). Effect of heavy metals on seed germination and
656 seedling growth of common ragweed and roadside ground cover legumes. *Environmental*
657 *Pollution*, 213, 112–118.
- 658 Baker, H. G. (1965). Characteristics and modes of origin of weeds. In H. G. Baker & G. L.
659 Stebbins (Eds.), *The genetics of colonizing species* (pp. 147–168). Academic Press.
- 660 Baker, H. G. (1974). The evolution of weeds. *Annual Review of Ecology and Systematics*, 5, 1–
661 24.
- 662 Barrett, S. C. H. (1983). Crop mimicry in weeds. *Economic Botany*, 37, 255–282.
- 663 Baucom, R. S. (2019). Evolutionary and ecological insights from herbicide-resistant weeds:
664 What have we learned about plant adaptation, and what is left to uncover? *New Phytologist*,
665 223, 68–82.
- 666 Baucom, R. S., Chang, S.-M., Kniskern, J. M., Rausher, M. D., & Stinchcombe, J. R. (2011).
667 Morning glory as a powerful model in ecological genomics: Tracing adaptation through both
668 natural and artificial selection. *Heredity*, 107, 377–385.
- 669 Baucom, R. S., & Holt, J. S. (2010). Weeds of agricultural importance: Bridging the gap between
670 evolutionary ecology and crop and weed science. *New Phytologist*, 184, 741–743.
- 671 Beaury, E. M., Fusco, E. J., Allen, J. M., & Bradley, B. A. (2021). Plant regulatory lists in the
672 United States are reactive and inconsistent. *Journal of Applied Ecology*, 58, 1957–1966.
- 673 Blackshaw, R. E., Brandt, R. N., Janzen, H. H., Entz, T., Grant, C. A., & Derksen, D. A. (2003).
674 Differential response of weed species to added nitrogen. *Weed Science*, 51, 532–539.
- 675 Blatchley, W. S. (1912). *The Indiana weed book*. The Nature Publishing Company.
- 676 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., & Wood, C. W. (2018). Evolutionary
677 adaptations of Palmer amaranth (*Amaranthus palmeri*) to nitrogen fertilization and crop rotation
678 history affect morphology and nutrient-use efficiency. *Weed Science*, 66, 180–189.
- 679 Brenchley, W. E. (1920). *Weeds of farm land*. Longmans, Green.

680 Brock, J. R., Dönmez, A. A., Beilstein, M. A., & Olsen, K. M. (2018). Phylogenetics of *Camelina*
681 Crantz. (Brassicaceae) and insights on the origin of gold-of-pleasure (*Camelina sativa*).
682 *Molecular Phylogenetics and Evolution*, 127, 834–842.

683 Buhler, D. D. (1995). Influence of tillage systems on weed population dynamics and
684 management in corn and soybean in the central USA. *Crop Science*, 35, 1247–1258.

685 Bunting, A. H. (1960). Some reflections on the ecology of weeds. In J. L. Harper (Ed.), *The*
686 *biology of weeds*. Blackwell Scientific Publications.

687 Cavender-Bares, J., Padullés Cubino, J., Pearse, W. D., Hobbie, S. E., Lange, A. J., Knapp, S.,
688 et al. (2020). Horticultural availability and homeowner preferences drive plant diversity and
689 composition in urban yards. *Ecological Applications*, 30, e02082.

690 Chan, Y. F., Scopece, G., Guzzetti, L., Pellegrini, L., Cafasso, D., Labra, M., et al. (2026).
691 Phenotypic and genomic signatures of adaptation in urban populations of the wild radish
692 *Raphanus raphanistrum*. *Evolutionary Applications*, 19, e70212.

693 Charbonneau, A., Tack, D., Lale, A., Goldston, J., Caple, M., Conner, E., et al. (2018). Weed
694 evolution: Genetic differentiation among wild, weedy, and crop radish. *Evolutionary Applications*,
695 11, 1964–1974.

696 Cheptou, P.-O., Carrue, O., Rouifed, S., & Cantarel, A. (2008). Rapid evolution of seed
697 dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National*
698 *Academy of Sciences of the United States of America*, 105, 3796–3799.

699 Chevin, L.-M., & Hoffmann, A. A. (2017). Evolution of phenotypic plasticity in extreme
700 environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372.

701 Cousens, R., & Mortimer, A. M. (1995). *Dynamics of weed populations*. Cambridge University
702 Press.

703 Daehler, C. C. (1998). The taxonomic distribution of invasive angiosperm plants: Ecological
704 insights and comparison to agricultural weeds. *Biological Conservation*, 84, 167–180.

705 Dekker, J., & Hargrove, M. (2002). Weedy adaptation in *Setaria* spp. V. Effects of gaseous
706 environment on giant foxtail (*Setaria faberii*) (Poaceae) seed germination. *American Journal of*
707 *Botany*, 89, 410–416.

708 Del Tredici, P. (2010). Excerpts from *Wild urban plants of the Northeast: A field guide*. *Arnoldia*,
709 68, 13–25.

710 Délye, C., Jasieniuk, M., & Le Corre, V. (2013). Deciphering the evolution of herbicide
711 resistance in weeds. *Trends in Genetics*, 29, 649–658.

712 DiTommaso, A. (2004). Germination behavior of common ragweed (*Ambrosia artemisiifolia*)
713 populations across a range of salinities. *Weed Science*, 52, 1002–1009.

- 714 Doubleday, Z. A., & Connell, S. D. (2018). Weedy futures: Can we benefit from the species that
715 thrive in the marine Anthropocene? *Frontiers in Ecology and the Environment*, 16, 599–604.
- 716 Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: Anthropogenic biomes of the
717 world. *Frontiers in Ecology and the Environment*, 6, 439–447.
- 718 Eslami, S. V., & Ward, S. (2021). *Chenopodium album* and *Chenopodium murale*. In B. S.
719 Chauhan (Ed.), *Biology and management of problematic crop weed species* (pp. 89–112).
720 Academic Press.
- 721 Fawthrop, R., Cerca, J., Pacheco, G., Sætre, G.-P., Scordato, E. S. C., Ravinet, M., et al.
722 (2025). Understanding human-commensalism through an ecological and evolutionary
723 framework. *Trends in Ecology & Evolution*, 40, 159–169.
- 724 Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., et al. (2005).
725 Global consequences of land use. *Science*, 309, 570–574.
- 726 Fukano, Y., Guo, W., Uchida, K., & Tachiki, Y. (2020). Contemporary adaptive divergence of
727 plant competitive traits in urban and rural populations and its implication for weed management.
728 *Journal of Ecology*, 108, 2521–2530.
- 729 Garrison, A. J., Norwood, L. A., & Conner, J. K. (2024). Plasticity-mediated persistence and
730 subsequent local adaptation in a global agricultural weed. *Evolution*, 78, 1804–1817.
- 731 Georgia, A. E. (1916). *A manual of weeds*. Macmillan.
- 732 Geron, C., Lembrechts, J. J., Hamdi, R., Berckmans, J., Nijs, I., & Monty, A. (2022). Phenotypic
733 variation along urban-to-rural gradients: An attempt to disentangle the mechanisms at play
734 using the alien species *Matricaria discoidea* (Asteraceae). *Plant Ecology*, 223, 1219–1231.
- 735 Gorton, A. J., Moeller, D. A., & Tiffin, P. (2018). Little plant, big city: A test of adaptation to urban
736 environments in common ragweed (*Ambrosia artemisiifolia*). *Proceedings of the Royal Society
737 B: Biological Sciences*, 285.
- 738 Gray, A. (1879). The pertinacity and predominance of weeds. *American Journal of Science*, s3-
739 18, 161–167.
- 740 Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008).
741 Global change and the ecology of cities. *Science*, 319, 756–760.
- 742 Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., et al. (2015).
743 Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1,
744 e1500052.
- 745 Harlan, J. R., & deWet, J. M. J. (1965). Some thoughts about weeds. *Economic Botany*, 19, 16–
746 24.
- 747 Harper, J. L. (Ed.). (1960). *The biology of weeds: A symposium of the British Ecological Society*.
748 Blackwell Scientific Publications.

749 Harper, J. L., Lovell, P. H., & Moore, K. G. (1970). The shapes and sizes of seeds. *Annual*
750 *Review of Ecology and Systematics*, 1, 327–356.

751 Hermanutz, L. A., & Weaver, S. E. (1996). Agroecotypes or phenotypic plasticity? Comparison
752 of agrestal and ruderal populations of the weed *Solanum ptycanthum*. *Oecologia*, 105, 271–280.

753 Hoffman, A. M., Cocciardi, J. M., Manna, P., Alvarado-Serrano, D. F., Cavender-Bares, J.,
754 Groffman, P. M., et al. (2026). Genetic diversity and population structure in cities is not
755 consistent among cosmopolitan plant species. *Molecular Ecology*, 35, e70261.

756 Holm, L., & Holm, L. G. (2014). *A geographical atlas of world weeds*. Krieger Publishing
757 Company.

758 Hope, D., Gries, C., Zhu, W., Fagan, W. F., Redman, C. L., Grimm, N. B., et al. (2003).
759 Socioeconomics drive urban plant diversity. *Proceedings of the National Academy of Sciences*
760 *of the United States of America*, 100, 8788–8792.

761 Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and
762 evolutionary framework for commensalism in anthropogenic environments. *Trends in Ecology &*
763 *Evolution*, 31, 633–645.

764 Iannone, B., Carnevale, S., Main, M., Hill, J., McConnell, J., Johnson, S., et al. (2020). Invasive
765 species terminology: Standardizing for stakeholder education. *Journal of Extension*, 58.

766 Isely, D. (1960). *Weed identification and control*. Iowa State University Press.

767 Jacquemyn, H., De Meester, L., Jongejans, E., & Honnay, O. (2012). Evolutionary changes in
768 plant reproductive traits following habitat fragmentation and their consequences for population
769 fitness. *Journal of Ecology*, 100, 76–87.

770 Johnson, M. T. J., & Munshi-South, J. (2017). Evolution of life in urban environments. *Science*,
771 358.

772 Josephs, E. B., Van Etten, M. L., Harkess, A., Platts, A., & Baucom, R. S. (2021). Adaptive and
773 maladaptive expression plasticity underlying herbicide resistance in an agricultural weed.
774 *Evolution Letters*, 5, 432–440.

775 Klingman, G. C. (1961). *Weed control as a science*. John Wiley & Sons.

776 Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S. E., Jakobsdottir, I., Kattge, J., et al. (2012).
777 Phylogenetic and functional characteristics of household yard floras and their changes along an
778 urbanization gradient. *Ecology*, 93, S83–S98.

779 Kostanecki, A., Gorton, A. J., & Moeller, D. A. (2021). An urban–rural spotlight: Evolution at
780 small spatial scales among urban and rural populations of common ragweed. *Journal of Urban*
781 *Ecology*, 7.

782 Kreiner, J. M., Latorre, S. M., Burbano, H. A., Stinchcombe, J. R., Otto, S. P., Weigel, D., et al.
783 (2022). Rapid weed adaptation and range expansion in response to agriculture over the past
784 two centuries. *Science*, 378, 1079–1085.

785 Kuester, A., Conner, J. K., Culley, T., & Baucom, R. S. (2014). How weeds emerge: A
786 taxonomic and trait-based examination using United States data. *New Phytologist*, 202, 1055–
787 1068.

788 Kuester, A., Wilson, A., Chang, S.-M., & Baucom, R. S. (2016). A resurrection experiment finds
789 evidence of both reduced genetic diversity and potential adaptive evolution in the agricultural
790 weed *Ipomoea purpurea*. *Molecular Ecology*, 25, 4508–4520.

791 Lambrecht, S. C., Mahieu, S., & Cheptou, P.-O. (2016). Natural selection on plant physiological
792 traits in an urban environment. *Acta Oecologica*, 77, 67–74.

793 Lau, J. A., & Funk, J. L. (2023). How ecological and evolutionary theory expanded the “ideal
794 weed” concept. *Oecologia*, 203, 251–266.

795 Le Corre, V., Siol, M., Vigouroux, Y., Tenaillon, M. I., & Délye, C. (2020). Adaptive introgression
796 from maize has facilitated the establishment of teosinte as a noxious weed in Europe.
797 *Proceedings of the National Academy of Sciences of the United States of America*, 117, 25618–
798 25627.

799 Li, D., Stucky, B. J., Deck, J., Baiser, B., & Guralnick, R. P. (2019). The effect of urbanization on
800 plant phenology depends on regional temperature. *Nature Ecology & Evolution*, 3, 1661–1667.

801 Li, L.-Z., Xu, Z.-G., Chang, T.-G., Wang, L., Kang, H., Zhai, D., et al. (2023). Common
802 evolutionary trajectory of short life-cycle in Brassicaceae ruderal weeds. *Nature*
803 *Communications*, 14, 290.

804 Maréchal, L., & McKinney, T. (2020). The (mis)use of the term “commensalism” in primatology.
805 *International Journal of Primatology*, 41, 1–4.

806 Mathis, K. A., & Bronstein, J. L. (2020). Our current understanding of commensalism. *Annual*
807 *Review of Ecology, Evolution, and Systematics*, 51, 167–189.

808 Maunder, K. G., Dawson, K., Joslin, L., Eckert, L., Kraml, M. M., Dean-Moore, C., et al. (2025).
809 Random and non-random variation in flower color along an urban–rural gradient in the
810 introduced mustard *Hesperis matronalis*. *bioRxiv*.

811 McElroy, J. S. (2014). Vavilovian mimicry: Nikolai Vavilov and his little-known impact on weed
812 science. *Weed Science*, 62, 207–216.

813 Menalled, F., Peterson, R., Smith, R., Curran, W., Páez, D., & Maxwell, B. (2016). The eco-
814 evolutionary imperative: Revisiting weed management in the midst of an herbicide resistance
815 crisis. *Sustainability*, 8, 1297.

816 Miles, L. S., Rivkin, L. R., Johnson, M. T. J., Munshi-South, J., & Verrelli, B. C. (2019). Gene
817 flow and genetic drift in urban environments. *Molecular Ecology*, 28, 4138–4151.

- 818 Morin, L., Paini, D. R., & Randall, R. P. (2013). Can global weed assemblages be used to
819 predict future weeds? *PLOS ONE*, 8, e55547.
- 820 Muenscher, W. C. (1946). *Weeds*. Macmillan.
- 821 Murphy, C. E., & Lemerle, D. (2006). Continuous cropping systems and weed selection.
822 *Euphytica*, 148, 61–73.
- 823 Neve, P., Vila-Aiub, M., & Roux, F. (2009). Evolutionary-thinking in agricultural weed
824 management. *New Phytologist*, 184, 783–793.
- 825 Owen, M. D. K. (2008). Weed species shifts in glyphosate-resistant crops. *Pest Management*
826 *Science*, 64, 377–387.
- 827 Palumbi, S. R. (2001). Humans as the world's greatest evolutionary force. *Science*, 293, 1786–
828 1790.
- 829 Pieper, J. J. (1930). *The increasing menace of weeds: A national problem*. Illinois Farmers'
830 Institute.
- 831 Pisman, M., Bonte, D., & de la Peña, E. (2020). Urbanization alters plastic responses in the
832 common dandelion *Taraxacum officinale*. *Ecology and Evolution*, 10, 4082–4090.
- 833 Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants:
834 Where do we stand? In W. Nentwig (Ed.), *Biological invasions* (Ecological Studies, Vol. 193, pp.
835 97–125). Springer.
- 836 Quinn, L. D., Barney, J. N., McCubbins, J. S. N., & Endres, A. B. (2013). Navigating the
837 “noxious” and “invasive” regulatory landscape: Suggestions for improved regulation.
838 *BioScience*, 63, 124–131.
- 839 Radosevich, S. R., Holt, J. S., & Ghera, C. M. (2008). *Ecology of weeds and invasive plants*
840 (3rd ed.). Wiley-Blackwell.
- 841 Raingeval, M., Leduque, B., Baduel, P., Edera, A., Roux, F., Colot, V., et al. (2024).
842 Retrotransposon-driven environmental regulation of *FLC* leads to adaptive response to
843 herbicide. *Nature Plants*, 10, 1672–1681.
- 844 Ravet, K., Sparks, C. D., Dixon, A. L., Küpper, A., Westra, E. P., Pettinga, D. J., et al. (2021).
845 Genomic-based epidemiology reveals independent origins and gene flow of glyphosate
846 resistance in *Bassia scoparia* populations across North America. *Molecular Ecology*, 30, 5343–
847 5359.
- 848 Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all
849 trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*,
850 9, 981–993.

851 Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F. J., de Keyzer, C. W., Diamond, S. E.,
852 et al. (2019). A roadmap for urban evolutionary ecology. *Evolutionary Applications*, 12, 384–
853 398.

854 Robbins, W. W., Crafts, A. S., & Raynor, R. N. (1952). *Weed control*. McGraw-Hill.

855 Salisbury, E. J. (1961). *Weeds and aliens*. Collins.

856 Santangelo, J. S., Ness, R. W., Cohan, B., Fitzpatrick, C. R., Innes, S. G., Koch, S., et al.
857 (2022a). Global urban environmental change drives adaptation in white clover. *Science*, 375,
858 1275–1281.

859 Santangelo, J. S., Roux, C., & Johnson, M. T. J. (2022b). The effects of environmental
860 heterogeneity within a city on the evolution of clines. *Journal of Ecology*, 110, 2950–2959.

861 Sharma, G., Barney, J. N., Westwood, J. H., & Haak, D. C. (2021). Into the weeds: New insights
862 in plant stress. *Trends in Plant Science*, 26, 1050–1060.

863 Simard, M.-J., & Ziadi, N. (2024). Weed communities after decades of mineral fertilization and
864 tillage treatments in a corn–soybean rotation. *Weed Technology*, 38.

865 Simberloff, D. (2022). A future planet of weeds? In D. R. Clements, M. K. Upadhyaya, S. Joshi,
866 & A. Shrestha (Eds.), *Global plant invasions* (pp. 361–373). Springer.

867 Skinner, K., Smith, L., & Rice, P. (2000). Using noxious weed lists to prioritize targets for
868 developing weed management strategies. *Weed Science*, 48, 640–644.

869 Sotillo, A., Hardion, L., Chanez, E., Fujiki, K., & Muratet, A. (2024). Plant responses to urban
870 gradients: Extinction, plasticity, adaptation. *Journal of Ecology*, 112, 2861–2875.

871 Stanley, A., & Arceo-Gómez, G. (2020). Urbanization increases seed dispersal interaction
872 diversity but decreases dispersal success in *Toxicodendron radicans*. *Global Ecology and*
873 *Conservation*, 22, e01019.

874 Stanley, A. M., & Ashman, T.-L. (2025). Urbanization alters phenology, mating system
875 allocation, and life history of *Impatiens capensis* (Balsaminaceae) via trait-specific plasticity and
876 genetic differentiation. *Ecology and Evolution*, 15, e71583.

877 Storkey, J., Meyer, S., Still, K. S., & Leuschner, C. (2012). The impact of agricultural
878 intensification and land-use change on the European arable flora. *Proceedings of the Royal*
879 *Society B: Biological Sciences*, 279, 1421–1429.

880 Sutherland, S. (2004). What makes a weed a weed: Life history traits of native and exotic plants
881 in the USA. *Oecologia*, 141, 24–39.

882 Taichi, N., Nakahama, N., Ohmido, N., & Ushimaru, A. (2025). Adaptive trait divergence of
883 annual plants in response to urban habitat diversity in a megacity. *Journal of Ecology*, 113,
884 3748–3761.

885 Taichi, N., & Ushimaru, A. (2024). Trait variation along an urban–rural gradient in Asian
886 dayflower: The contribution of phenotypic plasticity and genetic divergence. *Plant Biology*, 26,
887 74–81.

888 Thomas, W. L. (Ed.). (1959). *Man's role in changing the face of the earth*. University of Chicago
889 Press.

890 Van Etten, M. L., Conner, J. K., Chang, S.-M., & Baucom, R. S. (2017). Not all weeds are
891 created equal: A database approach uncovers differences in the sexual system of native and
892 introduced weeds. *Ecology and Evolution*, 7, 2636–2642.

893 van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., et al. (2019). The Global
894 Naturalized Alien Flora (GloNAF) database. *Ecology*, 100, e02542.

895 Vanni, G., Cardelli, R., Marchini, F., Saviozzi, A., & Guidi, L. (2015). Are the physiological and
896 biochemical characteristics in dandelion plants growing in an urban area (Pisa, Italy) indicative
897 of soil pollution? *Water, Air, and Soil Pollution*, 226, 124.

898 Williamson, M. (1993). Invaders, weeds and the risk from genetically manipulated organisms.
899 *Experientia*, 49, 219–224.

900 Wodehouse, R. P. (1963). Weed. In *Encyclopaedia Britannica*.

901 WSSA. (2026). *Composite list of weeds*. Compiled by the Standardized Plant Names
902 Subcommittee, Weed Science Society of America. wssa.net/wssa/weed/composite-list-of-weeds

903 WSSA. (2016). *Do you have a weed, noxious weed, invasive weed or “superweed”? Simple*
904 *distinctions make all the difference* [Fact sheet]. Public Awareness Committee, Weed Science
905 Society of America.

906 Yakub, M., & Tiffin, P. (2017). Living in the city: Urban environments shape the evolution of a
907 native annual plant. *Global Change Biology*, 23, 2082–2089.

908 Ye, C.-Y., Tang, W., Wu, D., Jia, L., Qiu, J., Chen, M., et al. (2019). Genomic evidence of
909 human selection on Vavilovian mimicry. *Nature Ecology & Evolution*, 3, 1474–1482.

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S1 Table. Sources and licenses for photographs in Fig 1. All photographs were cropped to fit the figure panels; no other changes were made. Locations are approximate, as reported on iNaturalist.

Panel	Species	Photographer (iNaturalist user)	Location, date observed	Source	License
Top 1	<i>Convolvulus arvensis</i>	er-birds	Long Island, NY, USA; 27 Jun 2026	https://www.inaturalist.org/photos/689619334	CC BY 4.0
Top 2	<i>Conyza canadensis</i>	Erin (mylegsareitchy)	East Gwillimbury, ON, Canada; 17 Oct 2026	https://www.inaturalist.org/observations/409593768	CC BY-NC 4.0
Top 3	<i>Amaranthus retroflexus</i>	ivansemenkov	Primorsky Krai, Russia; 17 Oct 2026	https://www.inaturalist.org/observations/408906636	CC BY 4.0
Top 4	<i>Chenopodium album</i>	Bas van Hulst-Kuiper (basvanhulst-kuiper)	Enschede, Netherlands; 5 Sep 2026	https://www.inaturalist.org/observations/405803211	CC BY-NC 4.0
Top 5	<i>Taraxacum officinale</i>	Elena Valova (elenavalova)	Pechengsky District, Murmansk Oblast, Russia; 31 May 2026	https://www.inaturalist.org/observations/410085074	CC BY-NC 4.0
Bottom 1	<i>Ipomoea hederacea</i>	mami_t_t	Tokyo, Japan; 13 Oct 2026	https://www.inaturalist.org/observations/408032284	CC BY 4.0
Bottom 2	<i>Ambrosia artemisiifolia</i>	Andrey Novgorodsky (andrey_novgorodsky)	Kharkiv, Ukraine; 13 Sep 2026	https://www.inaturalist.org/observations/408476587	CC BY-NC 4.0
Bottom 3	<i>Amaranthus tuberculatus</i>	Bob (rnheld)	Hopkins, MN, USA; 31 Aug 2025	https://www.inaturalist.org/observations/310508863	CC BY 4.0
Bottom 4	<i>Cyperus esculentus</i>	ailingstorm	Philadelphia, PA, USA; 30 Sep 2026	https://www.inaturalist.org/observations/405079821	CC BY-NC 4.0
Bottom 5	<i>Cirsium arvense</i>	Natalia Gamova (natalia_gamova)	Reutov, Moscow Oblast, Russia; 17 Oct 2026	https://www.inaturalist.org/observations/409117082	CC BY-NC 4.0