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Weeds: against the rules?

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Abstract

Establishing laws of plant and ecosystems functioning has been an overarching objective of functional and evolutionary ecology. However, most theories neglect the role of human activities in creating novel ecosystems characterized by species assemblages and environmental factors not observed in natural systems. We argue that agricultural weeds, as an emblematic case of such an 'ecological novelty', constitute an original and underutilised model for challenging current concepts in ecology and evolution. We highlight key aspects of weed ecology and evolutionary biology that can help to test and recast ecological and evolutionary laws in a changing world. We invite ecologists to seize weeds as a model system to improve our understanding of short-term and long-term dynamics of ecological systems in the Anthropocene.

Novelty as a challenge

Ecologists and evolutionary biologists have always sought repeated patterns that reveal universal laws of biological function and diversification. Several general theories have been proposed to define ecological and evolutionary processes explaining diversity within and across levels of organization, and across temporal and spatial scales. However, these theories are mostly inspired from natural or semi-natural ecosystems, and theoretical models are developed under idealized conditions such as population equilibrium or non-limiting resource conditions for plant growth. These theories largely neglect the role of human activities in creating novel ecosystems with original species assemblages and environmental factors. Such 'ecological novelties' represent new frontiers of knowledge and create opportunities to challenge widely accepted theories [1], which, in line with Popper's view of science, is a key aspect of the development of theory.

The emergence of agriculture during the Neolithic period is perhaps the most widespread example of a driver of novel ecosystems. It has created new habitats for numerous plant species [2] (so-called agricultural weeds) which now cover more than 40% of the terrestrial surface [3]. At the scale of the cropped field, weed communities represent melting pots of plant species with various biogeographic and ecological backgrounds and whose local assembly results as much from the movement of crops and civilisations as ecological rules (Box 1). In addition, agricultural practices result in environmental conditions that are unique from conditions in non-cultivated habitats, notably in term of disturbances and resource gradients (Box 2). Mechanical and chemical weeding also represent highly specific and strong selection pressures on weed communities [4]. New species combinations and environmental factors in cultivated fields can, therefore, lead to new forms of ecological and evolutionary dynamics that are difficult to capture using well-established theories.

In this review, we argue that weeds in cropped fields provide a valuable but under-utilised model for challenging conceptual foundation stones in both ecology and evolution in the context of the current era that is characterised by rapid, human mediated change [5]. We discuss how our understanding of short-term and long-term diversification and dynamics of ecological systems should benefit from the study of weeds. In turn, better knowledge of weed ecology and evolutionary biology should help explain and predict their dynamics in cultivated fields, which will be necessary to develop innovative weed management schemes that consider both services (e.g. pollination; [6]; [7]) and disservices (e.g. yield loss; [8] [9]) provided by weeds [10].

Ecological outliers: why and how can weeds challenge functional ecology

Functional ecology has long been searching for repeated patterns in the phenotypic diversity of life [11–14]. These patterns reflect the existence of common physiological and biophysical constraints that structure the ‘phenotypic space’ of organisms and govern their ability to adapt to novel environments [13,15]. They are at the basis of major theories in functional ecology and macroecology [12,16,17]. For instance, in plants, the leaf economics spectrum describes leaf covariation of physiological and morphological traits that emerge from evolutionary trade-offs between resource acquisition and resource conservation strategies [18]. Most plant species seem to fall along this physiological trade-off [17]. However, these phenotypic patterns mostly rely on correlative approaches and, as such, a comprehensive falsification framework is lacking for most of them [19]. Testing the robustness of these laws would allow the validation, or not, of the existence of universal ecological, evolutionary, physiological and biophysical constraints for all taxa on Earth [20,21].

Agricultural weeds appear as good candidates to test whether organisms can overcome the constraints and tradeoffs that determine these patterns, and consequently whether (natural or artificial) selection can act against them [15,22]. Recent comparative analyses using taxa spanning continental and global scales show that weeds are located at the margins of the functional space defined by national and global floras [23,24]. Such a position makes them potential ‘functional outliers’, i.e. species functionally distinct from the rest of the global pool of species [25]. In addition, weed species are expected to have greater phenotypic plasticity than non-weeds [26,27], particularly for traits related to reproduction - allowing life cycle completion in variable conditions [28–30]. Being at the margins of the plant functional space and having high level of phenotypic plasticity are two key ingredients for weeds to eventually overcome eco-physiological and biophysical constraints that are assumed to limit the diversification of life (Fig. 1A).

The possibility of original trait combinations in weeds reflects the unique environmental conditions that characterize the cultivated fields. For instance, enclosed fields and the use of pesticides remove top-down regulation of plant communities by invertebrate and vertebrate herbivores in cropped fields. The removal of natural herbivory in cropped fields can therefore change the underlying constraints that determine the leaf economics spectrum (resource acquisition vs. conservation;[18]). Moreover, the original combination of disturbance and resource levels in agricultural fields (Box 2) might have selected for weed ecological strategies that differ from the ones observed in natural ecosystems. According to the C-S-R model, the combination of disturbance and resource gradients shape three primary plant ecological strategies that explain the diversity of the whole flora [31]. A high level of resource availability and a low level of disturbance select for species that display a combination of traits that make them good competitors (‘Competitor species’, C). ‘Stress-tolerant’ (S) species occur where both resource availability and disturbance levels are low while ‘Ruderal’ (R) species are adapted to habitats where both resource availability and the levels of disturbance are high. Finally, no trait combination allows species to persist in environments where disturbance level is high and resources availability is low [31]. Intriguingly, the CSR scheme has been built on habitat characteristics where species are found, not on the levels of resources and disturbance actually perceived by the organisms. This approach may be limited in seeking to understand the functional ecology of agricultural weeds that occur in habitats characterized by high levels of resources and disturbance but also experience severe resource depletion, notably in light, the latter being largely preempted by the crop species that is artificially dominant (Box 2). Agricultural weeds thus face repetitive disturbances in the context of strongly imbalanced resource ratios [32]. This extreme situation is not considered in the traditional CSR model where the ability of species to capture above and below ground resources is assumed to co-vary along a stress tolerant – competitive gradient (Fig. 2B). The exceptional combination of disturbances and the imbalance above and belowground resources available for weeds in agricultural fields thus questions the CSR model developed from observations in natural ecosystems. A greater consideration of the effect of imbalance resource availability on the evolution of plant ecological strategies is required to better understand the success of weeds in cultivated habitats.

Functional ecology approaches to studying weeds are at their infancy. While the ruderal strategy has traditionally been related to weeds, empirical evidence shows that a wider range of ecological strategies also exist in weeds [24]. Particularly, weeds species differ between those that compete with the crop and those that avoid it as well as between species that resist or avoid disturbances [33,34]. These results suggest that the same environmental constraints may select for a variety of ecological strategies that can co-exist in the same field. Improving the characterization of the whole weed biota through the lens of functional traits will allow the species able to establish and persist in arable habitats to be identified (so-called 'regional pool' in community ecology). This will inform the profiling of future weed communities and the assessment of the physiological and biophysical constraints that regulate weed success and their potential to adapt.

2. Challenging community assembly rules

Weed science has largely focused on understanding the biology and control of individual weeds infesting cropland. However, plant species do not act independently but are imbedded in complex interaction networks, both within and between local communities. This evidence has motivated the seminal article of Booth & Swanton [35] that calls for a shift from species to community level studies in weed science. Yet, despite an increasingly number of studies addressing weed community assembly, the rules that govern weed community dynamics remain far from clear, making predictions of the impact of any change in farming practices difficult (e.g., refs. [36–41]). Here, we argue that this may result from the fact that weed communities display particular dynamics that cannot be fully capture by classical ecological theories.

Whether the assembly of ecological communities follow general rules is a fundamental but still unresolved question in community ecology [42]. One of the most challenging issues is to understand and model the combined influences of stochastic, neutral (i.e. independent from biological differences) and niche-based (i.e. biotic interactions and environmental filtering) processes on community assembly [43–45]. According to the stress gradient hypothesis, competition should govern community assembly in productive habitats while harsh environmental conditions should filter stress-tolerant species [45]. By contrast, community assembly can be neutral where both competition and environmental stress are weak, for example after a disturbance that strengthens the influence of stochastic species recruitment [45]. However, weed communities occupy habitats where competition, environmental filtering and stochastic dynamics are all extremely strong (Box 2). Intense competition arises from a pre-emption of space and light by the crop, which strongly reduces weed biomass [46,47]. Abiotic constraints are caused by agricultural practices such as chemical weeding and soil disturbances (i.e. tillage and mechanical weeding), which filter out species according to their sensitivity to herbicides and to their phenology, respectively [48,49]. These recurring disturbances further maintain the farmed ecosystem in early stages of secondary succession (i.e. dominance of annuals; [50]), where stochastic colonization-extinction dynamics also play an important role ([40,41,51,52]). These dynamics might however shift in no-till systems where the abandonment of ploughing favour more perennial weed species [7,53]. Weed communities thus represent a combination of transient species that rely on repeated colonisation from field edges and resident species that are adapted to the habitat filters in the field [52]. Because of the unique combination of niche-based and neutral processes in cultivated fields , weed communities are particularly valuable for investigating how complex assembly dynamics govern species persistence and coexistence across spatial scales.

Another critical issue in the Anthropocene is to predict the responses of communities to anthropogenic environmental changes [54,55]. Spatial variation contributes to species coexistence via the spatial storage effect [56] that allows less competitive species to migrate and persist in communities (source-sink dynamics, [57]). By contrast, temporal variation can modify the competitive hierarchy between species, allowing species to coexist over the long-term (i.e. temporal storage effect, [56]). However, ecological theories implicitly assume stationary regimes of environmental variation so that some coexistence equilibrium is reached at a given time (reviewed in [55]). In the case of agricultural weeds, this fundamental assumption is violated by abrupt changes imposed by changing human activities, which prevents the system reaching any long-term stability. Over decadal time scales, the development of new agricultural practices and the abandonment of ancient ones has strongly affected the dynamics of weed populations, as some formerly rare weeds become more successful and *vice et versa* [49,58]. Similarly, the introduction of new cultivated species within a region (*e.g.* rapeseed, sugar beet, sunflower in France) creates unprecedented environmental conditions that can radically change the composition of weed communities in just a few years [59]. From year to year, the sequential cultivation of different crop species within a field also causes large fluctuations of disturbance regimes and competitive interactions [60]. Such non-stationary environmental constraints should theoretically drive deviations from community equilibrium within an environment at a given time by favouring transient and delayed species responses (*lag response hypothesis*;[55,61]). This has been verified empirically with agricultural weeds where temporal dispersal from the dormant seedbank allows the presence of weed species that reproduced successfully under previous, more suitable conditions (i.e. temporal source-sink dynamics, [38,41,62]). The ability of weeds to colonise novel cropping environments over short time scales will also be related to spatial dynamics of introductions of seed in crops and on machinery or dispersal from surrounding habitats, involving stochastic processes and landscape composition [63,64]. Weeds thus represent an exemplary case to elaborate a “non-equilibrium” community assembly theory, a theory that is urgently needed to better understand and anticipate plant community responses to the ongoing global changes [65].

3-Weeds: evolutionary roadrunners?

Although scientists long assumed that evolution proceeds slowly, an increasing number of examples of rapid evolution have been documented in wild plant species (e.g. [66,67]). Evidence of rapid phenotypic and molecular evolution challenge the classical view of the standard model of population genetics [68]. Furthermore, because ecological and evolutionary time scales overlap, ecological and evolutionary process are now known to interact and we need to understand how evolutionary process can affect population growth rates and ecological dynamics [69]. A better understanding of rapid evolution and eco-evolutionary dynamics is particularly crucial given that these phenomena may become increasingly frequent in the Anthropocene [70] due to the dramatic acceleration of human driven ecological changes ("the Great Acceleration," [5]).

Rapid evolution is particularly frequent in agricultural fields where farming practices have caused intense but unintended selective pressures on weeds since the Neolithic. The contribution of the genetic attributes of weeds and their evolutionary dynamics (in term of mating systems, phenotypic plasticity, and many other adaptive traits) to their capacity for rapid evolution in a new human-made environment have been repeatedly pointed out [2,4,29,71–73]. The evolution of herbicide resistance is probably the most emblematic and well-documented case of rapid evolution in plants (reviewed in [74]). Beyond herbicide resistance, rapid evolution can also affect weed demography by controlling weed-crop or and weed-pathogens interactions. For example, Guo et al. [75] demonstrated the rapid evolution of allelopathy and pathogen resistance in the barnyard grass (*Echinochloa crus-galli*) in response to co-cultivation with rice and to infection by pathogenic *Pyricularia oryzae*, respectively. In addition, many weed species rapidly evolve traits that mimic the crops to survive the selective constraints historically imposed by the farmers (Vavilovian mimicry, [76,77]). For instance, there is evidence that populations of *Agrostemma githago* have adapted to mimic the size and shape of crop seed to avoid being removed during seed cleaning ([78]). This species is also virtually indistinguishable from wheat during the vegetative stage (Figure 2), which also probably allows it to escape from manual weeding in traditional farming systems. Another example is the evolution of the crop mimicry syndrome in *Camelina alyssum (Mill.) Thell.* that has led to the weed reducing its phenotypic plasticity ([28]). If the evolution of vegetative or seed traits has been driven by crop mimicry, by contrast floral traits may have differentiated from crops due to divergent selection. For example, *Agrostema githago* produces flowers that are clearly visible among wheat plants; presumably, to attract pollinators and ensure reproduction at low plant densities in self-pollinating crop stands (Figure 2). Thomann et al. [79] also reported the evolution of increased capitula size in the cornflower (*Cyanus segetum*), in parallel with pollinator decline in 1990's agrosystems in northern Europe. However, the generalization of contrasted selection pressures on vegetative and floral traits in weeds, as well as the mechanisms of convergent and divergent evolution, remain an open question.

The realization that evolution can occur on short time suggests the existence of reciprocal interactions between ecological and evolutionary dynamics [69]. Although a growing number of studies show that rapid trait evolution can drive ecological dynamics on contemporary time scales, there are few empirical evidence of feedbacks from these altered ecological interactions on the evolutionary responses of plant communities [80]. Recently, Baucom [74] argue that weed communities exposed to herbicides provide an attractive system to study such eco-evolutionary feedbacks. Indeed, the emergence of resistance boosts the demography of resistant populations in agrosystems that can in turn affect pollinator communities and disease prevalence. The resulting changes in biotic interactions between weeds and other trophic levels can in turn promote the evolution of new weed species traits (see Fig. 1 in [74]). Here, an important and still unresolved question is to identify functional traits that can drive rapid evolution and eco-evolutionary dynamics. Plant genome size (GS) might be such a trait as it simultaneously controls evolutionary rates and several important plant functional traits such as plant relative growth rate and generation time [81,82]. Intriguingly, Bennett [77] reported that GS was smaller in weeds than in non-weeds although polyploidy was more common in weeds. This is surprising given that plant GS positively correlates with the amount of repetitive DNA that result from hybridization and/or polyploidy (at least soon after such polyploidization events occur; [78]). Antagonistic forces may therefore drive plant GS size and ploidy level in agricultural weeds.

Finally, archeological findings provide both a chronology of agricultural innovations and a parallel record of associated weed floras from archaeological remains (e.g. [85,86]), making agricultural weeds remarkable models to understand the genetic basis of rapid evolution as well as the evolutionary trajectories of complex traits in natural populations. The progress in ancient DNA sequencing techniques makes it possible to scan whole genomes of weed historical samples to detect candidate genes under selection. On a shorter time scale, resurrection ecology [87] and museum specimen analysis [88] can also be a relevant methodologies to investigate weed trait evolution and its genetic and epigenetic underpinning over hundreds to a few dozens of generations. Weeds are particularly useful for this approach since most of these species are annuals producing numerous seeds that persist in soil seedbank for decades [89]. Recent resurrection experiments on weed species have for example revealed rapid evolution on herbicide and drought resistance, pathogen susceptibility, phenology, floral traits and pollination biology and adaptive plasticity [79,87,90]. Coupling resurrection ecology with genome wide association mapping will be a key approach to understand the genetic basis of rapid evolution of multiple and complex traits in response to documented selective pressures (e.g. [91]).

Concluding remarks

Understanding the impacts of human activities on ecological and evolutionary dynamics will require revisiting ecological theories initially developed for natural ecosystems (see also oustanding questions). Pivotal to this is the integration of reciprocal interactions between human activities and ecological and evolutionary processes. Because weed evolutionary history and ecological dynamics are linked intrinsically to human activities, these species have great potential to become a valuable model in ecology and evolution. Yet, weeds are absent from most ongoing efforts of global biodiversity and trait databases, or at least their peculiarities are not recognized (due to e.g., lack of vegetation plot data in cropping systems, lack of data on intraspecific trait variation). We urge (numerical) ecologists not to discard the amazing source of information coming from weed species and their associated habitats. Field ecologists might have also overlooked widespread cultivated habitats compared to rare and emblematic ones. However, studying plant community assembly using weed communities is an attractive prospect given that assembly processes can be more easily identified, deciphered and quantified. Finally, weeds, by their short life cycle and relatively simple genome, appear as preferential experimental models for ecology and evolution. Let ecologists and evolutionists seize the weeds!

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Box 1. How to become an agricultural weed?

Three roads can lead a plant species to become a weed: wild species invading fields, crop-wild hybridization and crop de-domestication [72,92].

First, crop domestication during the Neolithic has resulted in the construction of a new human-made ecological niche, the agricultural fields in different part of the world [93]. At this moment, and in each center of plant domestication, numerous local pre-adapted plants were able to colonize cultivated fields [94]. These proto-weeds probably locally evolved according to the man-made selective pressures (the first agricultural practices) during millennia, as plant cultivation started long before crop domestication, at least in the Levant [95]. Some of these species still exist in both cultivated and non-cultivated habitat (*i.e.* apophytes), while others such as *Lolium temulentum, Bromus secalinus, Agrostemma githago* or *Vaccaria hispanica*, are only known in agricultural habitats (*i.e.* anecophytes).

Second, the expansion phase of agriculture has then carried out secondary contact among previously isolated populations or species, both domesticated and wild, generating admixture or hybridization [96,97]. Hybridization has triggered the emergence and diversification of many emblematic weed species such as *Capsella bursa-pastoris* [98], *Veronica persica* [99], or *Chenopodium album* [100]. Moreover, during the expansion phase, pre-adapted plant species from the newly cultivated areas could enter in the field adding new species [2].

Finally, some contemporary weed species are the result of de-domestication from cultivated ancestors (e.g. weedy rice, *Oryza sp.* [101]; weedy radish, *Raphanus sp*. [102]). By definition, these feral species are highly adapted to their early agricultural practices. This can explain why these weed species are notoriously ones of the most problematic weeds in contemporary farming [102].

These various processes make modern weed communities a unique assemblage of species with various biogeographic origins and evolutionary histories.

Box 2. Environmental gradients in cultivated fields.

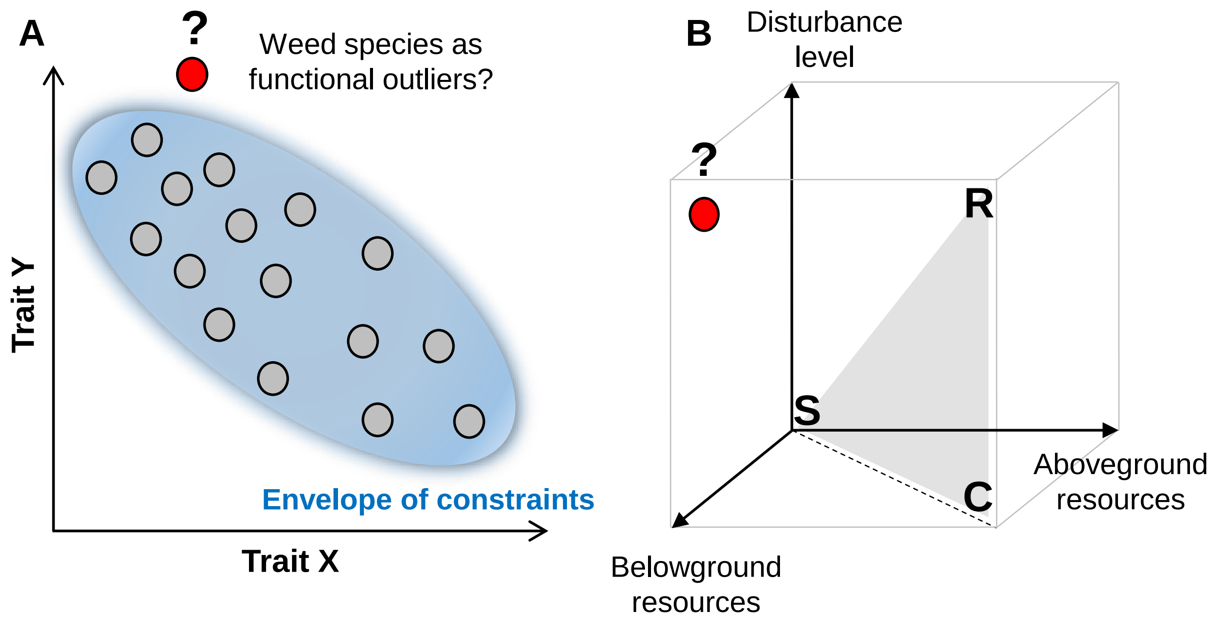
Environmental conditions in cultivated fields refer to both local pedo-climatic conditions and farming practices. Farming practices such as tillage and weeding operation correspond to major disturbance events in arable fields [60]. Crop phenology (e.g. sowing date, harvest date) notably determines the timing of disturbance during while herbicide intensity and tillage depth dictate the intensity of disturbance. In addition, the soils of cultivated habitat are extremely rich in resources as fertilization and irrigation provide large amounts of nutrient and water. Although fertilization and irrigation mostly benefit the crop species, the amount of nutrient and water supplies are such that they remain largely non-limiting for weeds [103]. By contrast, the amount of space and light that are available for weeds are strongly limited by the presence of the crop species that produce most of the standing biomass in agricultural fields. The amount of aboveground resources pre-empted by the crop varies according to crop height, lateral spread and sowing density [104].

The rapid monopolization of space and light by one species in a regularly disturbed habitat is specific to cultivated fields [4]. In non-cultivated ecosystems, disturbance releases resources by destroying biomass, so that regularly disturbed habitat generally show high level of resources availability [105]. By contrast, in cultivated fields, crop characteristics more than disturbances dictates the amount of available resources for weeds so that the positive covariance between disturbance and resource gradients do no longer exist. Finally, the succession of different crop species and associated farming practices within a field (i.e. crop sequences) causes major year-to-year changes in both disturbances and resources availability [60].

Figure 1. Whether and how weed species can break functional ecology rules: theoretical expectations. (A) Functional ecology has highlighted cross-taxa trait-trait relationships that mirror physiological and biophysiological constraints at the origin of the diversification of life. For instance, the leaf economics spectrum describes a trade-off between photosynthetic rate (trait Y) and leaf lifespan (trait X) among many plant species [16]. Each gray dot represents a given species. Weed species have been characterized as functional outliers because they were located at the margins of the multi-trait space (so-called functional space) in recent cross-taxa comparative studies. In addition, weed species are expected to display high phenotypic plasticity ability, which can help them to overcome the envelope of constraints delineated by functional ecological laws. (B) The CSR theory delineates a triangle of tenable strategies of species based on the characteristics of the habitat where they live, namely resources and disturbances. However, when decoupling resources into aboveground and belowground resources to account for the levels of resources that are available for weeds, weeds might be considered as functional outliers in this untenable triangle. Indeed, they undergo high disturbance level, high belowground resources but low aboveground resources due to high depletion of light availability by the crop species. Such imbalance between belowground and aboveground resources is not considered in the traditional CSR model.

Figure 2. Phenotypic convergence and divergence between wheat and the common corn cockle (*Agrostemma githago*). Left: At the vegetative stage, the common corn cockle is

virtually indistinguishable from wheat. Right: By contrast, floral traits strongly diverge. Photo credit: Guillaume Fried.


A
?
Weed species as functional outliers?
Trait Y
Trait X
Envelope of constraints
B
Disturbance level
?
R
S
C
Aboveground resources
Belowground resources