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1 **Weeds: against the rules?**

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16 dynamics

17

18 **Abstract**

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

29

30 **Novelty as a challenge**

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

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

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

63 **Ecological outliers: why and how can weeds challenge functional ecology**

64 Functional ecology has long been searching for repeated patterns in the phenotypic diversity
65 of life [11–14]. These patterns reflect the existence of common physiological and biophysical
66 constraints that structure the ‘phenotypic space’ of organisms and govern their ability to adapt

67 to novel environments [13,15]. They are at the basis of major theories in functional ecology
68 and macroecology [12,16,17]. For instance, in plants, the leaf economics spectrum describes
69 leaf covariation of physiological and morphological traits that emerge from evolutionary
70 trade-offs between resource acquisition and resource conservation strategies [18]. Most plant
71 species seem to fall along this physiological trade-off [17]. However, these phenotypic
72 patterns mostly rely on correlative approaches and, as such, a comprehensive falsification
73 framework is lacking for most of them [19]. Testing the robustness of these laws would allow
74 the validation, or not, of the existence of universal ecological, evolutionary, physiological and
75 biophysical constraints for all taxa on Earth [20,21].

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

88 The possibility of original trait combinations in weeds reflects the unique environmental
89 conditions that characterize the cultivated fields. For instance, enclosed fields and the use of
90 pesticides remove top-down regulation of plant communities by invertebrate and vertebrate
91 herbivores in cropped fields. The removal of natural herbivory in cropped fields can therefore

92 change the underlying constraints that determine the leaf economics spectrum (resource
93 acquisition vs. conservation;[18]). Moreover, the original combination of disturbance and
94 resource levels in agricultural fields (Box 2) might have selected for weed ecological
95 strategies that differ from the ones observed in natural ecosystems. According to the C-S-R
96 model, the combination of disturbance and resource gradients shape three primary plant
97 ecological strategies that explain the diversity of the whole flora [31]. A high level of resource
98 availability and a low level of disturbance select for species that display a combination of
99 traits that make them good competitors ('Competitor species', C). 'Stress-tolerant' (S) species
100 occur where both resource availability and disturbance levels are low while 'Ruderal' (R)
101 species are adapted to habitats where both resource availability and the levels of disturbance
102 are high. Finally, no trait combination allows species to persist in environments where
103 disturbance level is high and resources availability is low [31]. Intriguingly, the CSR scheme
104 has been built on habitat characteristics where species are found, not on the levels of
105 resources and disturbance actually perceived by the organisms. This approach may be limited
106 in seeking to understand the functional ecology of agricultural weeds that occur in habitats
107 characterized by high levels of resources and disturbance but also experience severe resource
108 depletion, notably in light, the latter being largely preempted by the crop species that is
109 artificially dominant (Box 2). Agricultural weeds thus face repetitive disturbances in the
110 context of strongly imbalanced resource ratios [32]. This extreme situation is not considered
111 in the traditional CSR model where the ability of species to capture above and below ground
112 resources is assumed to co-vary along a stress tolerant – competitive gradient (Fig. 2B). The
113 exceptional combination of disturbances and the imbalance above and belowground resources
114 available for weeds in agricultural fields thus questions the CSR model developed from
115 observations in natural ecosystems. A greater consideration of the effect of imbalance

116 resource availability on the evolution of plant ecological strategies is required to better
117 understand the success of weeds in cultivated habitats.

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

129 **2. Challenging community assembly rules**

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

140 Whether the assembly of ecological communities follow general rules is a fundamental but
141 still unresolved question in community ecology [42]. One of the most challenging issues is to
142 understand and model the combined influences of stochastic, neutral (i.e. independent from
143 biological differences) and niche-based (i.e. biotic interactions and environmental filtering)
144 processes on community assembly [43–45]. According to the stress gradient hypothesis,
145 competition should govern community assembly in productive habitats while harsh
146 environmental conditions should filter stress-tolerant species [45]. By contrast, community
147 assembly can be neutral where both competition and environmental stress are weak, for
148 example after a disturbance that strengthens the influence of stochastic species recruitment
149 [45]. However, weed communities occupy habitats where competition, environmental
150 filtering and stochastic dynamics are all extremely strong (Box 2). Intense competition arises
151 from a pre-emption of space and light by the crop, which strongly reduces weed biomass
152 [46,47]. Abiotic constraints are caused by agricultural practices such as chemical weeding and
153 soil disturbances (i.e. tillage and mechanical weeding), which filter out species according to
154 their sensitivity to herbicides and to their phenology, respectively [48,49]. These recurring
155 disturbances further maintain the farmed ecosystem in early stages of secondary succession
156 (i.e. dominance of annuals; [50]), where stochastic colonization-extinction dynamics also play
157 an important role ([40,41,51,52]). These dynamics might however shift in no-till systems
158 where the abandonment of ploughing favour more perennial weed species [7,53]. Weed
159 communities thus represent a combination of transient species that rely on repeated
160 colonisation from field edges and resident species that are adapted to the habitat filters in the
161 field [52]. Because of the unique combination of niche-based and neutral processes in
162 cultivated fields , weed communities are particularly valuable for investigating how complex
163 assembly dynamics govern species persistence and coexistence across spatial scales.

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

189 surrounding habitats, involving stochastic processes and landscape composition [63,64].
190 Weeds thus represent an exemplary case to elaborate a “non-equilibrium” community
191 assembly theory, a theory that is urgently needed to better understand and anticipate plant
192 community responses to the ongoing global changes [65].

193 **3-Weeds: evolutionary roadrunners?**

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

204 Rapid evolution is particularly frequent in agricultural fields where farming practices have
205 caused intense but unintended selective pressures on weeds since the Neolithic. The
206 contribution of the genetic attributes of weeds and their evolutionary dynamics (in term of
207 mating systems, phenotypic plasticity, and many other adaptive traits) to their capacity for
208 rapid evolution in a new human-made environment have been repeatedly pointed out
209 [2,4,29,71–73]. The evolution of herbicide resistance is probably the most emblematic and
210 well-documented case of rapid evolution in plants (reviewed in [74]). Beyond herbicide
211 resistance, rapid evolution can also affect weed demography by controlling weed-crop or and
212 weed-pathogens interactions. For example, Guo et al. [75] demonstrated the rapid evolution of
213 allelopathy and pathogen resistance in the barnyard grass (*Echinochloa crus-galli*) in response

214 to co-cultivation with rice and to infection by pathogenic *Pyricularia oryzae*, respectively. In
215 addition, many weed species rapidly evolve traits that mimic the crops to survive the selective
216 constraints historically imposed by the farmers (Vavilovian mimicry, [76,77]). For instance,
217 there is evidence that populations of *Agrostemma githago* have adapted to mimic the size and
218 shape of crop seed to avoid being removed during seed cleaning ([78]). This species is also
219 virtually indistinguishable from wheat during the vegetative stage (Figure 2), which also
220 probably allows it to escape from manual weeding in traditional farming systems. Another
221 example is the evolution of the crop mimicry syndrome in *Camelina alyssum* (Mill.) Thell.
222 that has led to the weed reducing its phenotypic plasticity ([28]). If the evolution of vegetative
223 or seed traits has been driven by crop mimicry, by contrast floral traits may have
224 differentiated from crops due to divergent selection. For example, *Agrostema githago*
225 produces flowers that are clearly visible among wheat plants; presumably, to attract
226 pollinators and ensure reproduction at low plant densities in self-pollinating crop stands
227 (Figure 2). Thomann et al. [79] also reported the evolution of increased capitula size in the
228 cornflower (*Cyanus segetum*), in parallel with pollinator decline in 1990's agrosystems in
229 northern Europe. However, the generalization of contrasted selection pressures on vegetative
230 and floral traits in weeds, as well as the mechanisms of convergent and divergent evolution,
231 remain an open question.

232 The realization that evolution can occur on short time suggests the existence of reciprocal
233 interactions between ecological and evolutionary dynamics [69]. Although a growing number
234 of studies show that rapid trait evolution can drive ecological dynamics on contemporary time
235 scales, there are few empirical evidence of feedbacks from these altered ecological
236 interactions on the evolutionary responses of plant communities [80]. Recently, Baucom [74]
237 argue that weed communities exposed to herbicides provide an attractive system to study such
238 eco-evolutionary feedbacks. Indeed, the emergence of resistance boosts the demography of

239 resistant populations in agrosystems that can in turn affect pollinator communities and disease
240 prevalence. The resulting changes in biotic interactions between weeds and other trophic
241 levels can in turn promote the evolution of new weed species traits (see Fig. 1 in [74]). Here,
242 an important and still unresolved question is to identify functional traits that can drive rapid
243 evolution and eco-evolutionary dynamics. Plant genome size (GS) might be such a trait as it
244 simultaneously controls evolutionary rates and several important plant functional traits such
245 as plant relative growth rate and generation time [81,82]. Intriguingly, Bennett [77] reported
246 that GS was smaller in weeds than in non-weeds although polyploidy was more common in
247 weeds. This is surprising given that plant GS positively correlates with the amount of
248 repetitive DNA that result from hybridization and/or polyploidy (at least soon after such
249 polyploidization events occur; [78]). Antagonistic forces may therefore drive plant GS size
250 and ploidy level in agricultural weeds.

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

264 ecology with genome wide association mapping will be a key approach to understand the
265 genetic basis of rapid evolution of multiple and complex traits in response to documented
266 selective pressures (e.g. [91]).

267 **Concluding remarks**

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

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293

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496 **Box 1. How to become an agricultural weed?**

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

499 First, crop domestication during the Neolithic has resulted in the construction of a new
500 human-made ecological niche, the agricultural fields in different part of the world [93]. At
501 this moment, and in each center of plant domestication, numerous local pre-adapted plants
502 were able to colonize cultivated fields [94]. These proto-weeds probably locally evolved
503 according to the man-made selective pressures (the first agricultural practices) during
504 millennia, as plant cultivation started long before crop domestication, at least in the Levant
505 [95]. Some of these species still exist in both cultivated and non-cultivated habitat (*i.e.*
506 apophytes), while others such as *Lolium temulentum*, *Bromus secalinus*, *Agrostemma githago*
507 or *Vaccaria hispanica*, are only known in agricultural habitats (*i.e.* anecophytes).

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

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

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

521

522 **Box 2. Environmental gradients in cultivated fields.**

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

535 The rapid monopolization of space and light by one species in a regularly disturbed habitat is
536 specific to cultivated fields [4]. In non-cultivated ecosystems, disturbance releases resources
537 by destroying biomass, so that regularly disturbed habitat generally show high level of

538 resources availability [105]. By contrast, in cultivated fields, crop characteristics more than
539 disturbances dictates the amount of available resources for weeds so that the positive
540 covariance between disturbance and resource gradients do no longer exist. Finally, the
541 succession of different crop species and associated farming practices within a field (i.e. crop
542 sequences) causes major year-to-year changes in both disturbances and resources availability
543 [60].

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

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

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

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