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2   DR. TIA-LYNN ASHMAN (Orcid ID : 0000-0002-9884-5954)

3   DR. REGINA S BAUCOM (Orcid ID : 0000-0001-7960-498X)

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9   Herbicides as anthropogenic drivers of eco-evo feedbacks in plant communities at
10   the agro-ecological interface

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12   *Running title*: **herbicides as catalysts of eco-evo dynamics**

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14   Veronica Iriart[1], Regina S. Baucom[2] and Tia-Lynn Ashman[1*]

15   [1]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260

16   [2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI
17   48109

18

19   *Author for correspondence (and page proofs): tia1@pitt.edu

20   Abstract

21   Herbicides act as human-mediated novel selective agents and community disruptors, yet
22   their full effects on eco-evolutionary dynamics in natural communities has only begun to
23   be appreciated. Here we synthesize how herbicide exposures can result in dramatic
24   phenotypic and compositional shifts within communities at the agro-ecological interface

25 and how these in turn affect species interactions and drive plant (and plant-associates')

26 evolution in ways that can feedback to continue to affect the ecology and ecosystem

27 functions of these assemblages. We advocate a holistic approach to understanding

28 these dynamics that includes plastic changes and plant community transformations and

29 also extends beyond this single trophic level targeted by herbicides to the effects on

30 non-target plant-associated organisms and their potential to evolve, thereby embracing

31 the complexity of these real-world systems. We make explicit recommendations for

32 future research to achieve this goal and specifically address impacts of ecology on

33 evolution, evolution on ecology, and their feedbacks so that we can gain a more

34 predictive view of the fates of herbicide-impacted communities.

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36 **Key words**

37 Herbicide resistance, rapid evolution, phenotypic plasticity, eco-evo dynamics, plant-

38 animal interactions

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43 **Introduction**

44 Humans are modifying the environment in myriad ways and at unprecedented rates, and

45 their activities are now recognized as leading to some of the strongest selection wild

46 populations have ever been exposed (Alberti 2015; Pelletier & Coltman 2018; Palkovacs

47 et al. 2012, Turcotte et al. 2017), as well as having dramatic effects on species

48 interactions, community assembly, and ecosystem services (Johnson & Munshi-South

49 2017; Kiers et al 2010; Valiente-Banuet et al. 2015). As a consequence, human-

50 mediated disturbances can represent a turning point for these natural systems. Of

51 particular concern are human-introduced chemicals-- i.e., new herbicides, insecticides,

52 fungicides (in chemistry, application method or scale of use), that can represent novel

53 selective agents and community disruptors especially when coupled with exponential

54 adoption trajectories and/or broad geographic scale (Baucom & Mauricio 2004; Kniss

2017). Here, we focus on herbicides because the immediate toxicological effects of these chemicals on natural systems and human health is often the focus, but how their use may alter reciprocal interactions between ecological and evolutionary processes on contemporary timescales (eco-evolutionary dynamics) has yet to be considered. This is a striking omission, since understanding eco-evo dynamics in the broad sense, and especially in response to anthropogenic stressors, represents a grand challenge of the current decade (Alberti 2015; Bell 2017; Palkovacs et al. 2012).

In this mini-review, we synthesize the avenues by which herbicides—chemicals designed specifically to reduce weedy plant populations in agricultural systems--can lead to dramatic phenotypic and compositional shifts within crop-associated communities that in turn affect species interactions and drive plant (and plant-associates') evolution in ways that can feedback to continue to affect the ecology and ecosystem functions of these assemblages. Plant communities at the agro-ecological interface are likely to be subject to powerful herbicide-catalyzed eco-evolutionary dynamics because they 1) exist at the boundary of the rapidly expanding agricultural matrix and remnant unmanaged communities, 2) often contain crop-associated species (identified as weeds) found within agricultural fields as well as other diverse native plant taxa (Bernardo et al. 2018; Prosser et al. 2016), and 3) support mutualistic and antagonistic plant-associates, e.g., pollinators, soil microbes, herbivores, and parasitoids (Ouvrard et al. 2018; Prosser et al. 2016). Thus, these communities are recognized as both being important reservoirs of biodiversity and critical sources of nutrition and habitat for the pollinators, predators, and parasitoids that are both beneficial and detrimental to crop health (Bretagnolle & Gaba 2015; Ouvrard et al. 2018; Rollin et al. 2016). Plant communities at the agro-eco interface experience herbicides both from direct exposure at field application rates (100% FAR) as well as at sublethal levels via particle or vapor drift and run-off (e.g., 0.1-1% FAR) (Egan et al 2014; Prosser et al. 2016). Animal and microbial associates of plants are also likely to experience eco-evolutionary change in response to such novel chemicals because they not only rely on plant communities that are responding to the herbicide but also because herbicides can have direct effects on them as well (Prosser et al. 2016, also see below). The combination of direct and indirect effects could lead to synergistic outcomes on these associates as well as feedback to the plants.

Eco-evo framework for herbicide impacted systems

87   When ecological dynamics (e.g. population growth or community assembly) and

88   evolution occur on the same timescales there is the opportunity for new dynamics to

89   emerge (Palkovacs et al. 2012; Pimentel 1963). Eco-evolutionary forces wherein biotic

90   and abiotic processes lead to rapid evolution in species (Fig 1, top arrow) that then alter

91   the ecological dynamics of the interacting species (Fig 1, bottom arrow) are now

92   recognized to create not only 'real-time' evolution but also lead to dramatic, and

93   potentially unpredictable, changes in ecological dynamics (Turcotte et al. 2019). While

94   evolution in a community context is gaining empirical support (terHorst, et al. 2010;

95   terHorst et al. 2018), we still lack a full understanding of how this evolution alters

96   ecological dynamics, and whether this results in a feedback that affects future evolution

97   (De Meester et al. 2019; Hendry 2018; Turcotte et al. 2019). Of particular interest are

98   scenarios where the rapid evolution of traits alters ecological variables that then in turn

99   affect the evolution of those same traits, creating eco-evolutionary feedbacks (Fig. 1

100 dotted arrows). Likewise, the recognition that evolution depends not only on direct but

101 also on indirect evolutionary effects has prompted the inclusion of a wider community

102 context to evolutionary studies (terHorst et al. 2018), and the study of 'diffuse

103 coevolution' (DeMeester et al. 2019). Here, traits evolve in response to multiple

104 interacting members of a community, and in turn evolution indirectly affects the

105 magnitude or direction of the interactions among species (Arceo-Gómez & Ashman

106 2014; Janzen 1980; terHorst et al. 2018; terHorst et al 2010). The result is a 'broad

107 sense' view of eco-evolutionary feedbacks that includes all reciprocal interactions

108 between ecology and evolution (De Meester et al. 2019).

109 Herbicide-impacted communities are one of the few natural systems that have emerged

110 as uniquely suited to demonstrate direct links between evolving traits and ecological

111 impacts and vice versa (Baucom 2019; Bell 2017; Neve et al 2013; Prosser et al 2016).

112 As yet, however, there has been no robust discussion of the eco-evolutionary feedbacks

113 (e.g., Palkovacs & Hendry 2018; Turcotte et al. 2019) possible within systems

114 experiencing herbicide application. Moreover, because an eco-evolutionary focus

115 beyond the single trophic level that is targeted by herbicides (plants) is rare, the

116 complexity of these real-world systems has been mostly overlooked (Figure 2). Thus,

117 our understanding of multi-tropic interactions in these impacted systems is incomplete,

118 and our ability to predict the outcomes of herbicide disruption limited.

119   We explicitly consider how herbicide exposures affect eco-evolutionary dynamics in the

120   broad sense. In Figure 2 and the paragraphs that follow, we illustrate the ways that

121   herbicide exposure affects the ecology and evolution of plants (the target organisms), as

122   well as the non-target organisms plants associate with. First, we establish the known

123   ways herbicides lead to 1) phenotypic transformation of individual plant species via

124   plasticity or evolution, and 2) alteration of plant communities via species extinctions and

125   invasions. Second, we consider the evidence for herbicide effects on non-target

126   organisms that interact with plants (either above- or below- ground) and how this can

127   affect community structure of these trophic levels, as well as evolution of the organisms

128   within these trophic groups. Third, we explicitly describe the ways these ecological and

129   evolutionary processes could come together to create **eco-evo** and **evo-eco** dynamics

130   catalyzed by herbicide exposure. And finally, we conclude by recommending

131   approaches that will reveal these processes and rapidly propel our understanding of

132   these eco-evo dynamics forward.

133   **Target organisms - Plant phenotypic changes in response to herbicide**

134   Herbicides can affect the plant phenotype via plastic or genetic changes (Table 1). If

135   plants do not die outright following herbicide exposure, they will exhibit wide-ranging

136   plastic phenotypic alterations such as stunted growth and delayed flowering, among

137   other changes. Additionally, given strong, herbicide-mediated selection, the plant

138   phenotype can evolve along with herbicide resistance either through genetic linkage or

139   pleiotropy. These changes to the plant phenotype are expected to be equally as

140   important as herbicide-induced species compositional effects (see below) because

141   generally within-species phenotypic effects on ecological parameters are as strong as

142   replacing one species with another (Des Roches et al. 2018). While either plastic or

143   genetic changes of the phenotype could mediate ecological interactions, the genesis of

144   plant phenotypic change has different consequences for eco-evolutionary dynamics

145   (Hendry 2016; Levis & Pfenning 2016).

146   **Plastic changes –**While evolutionary responses take a generation or more, plastic

147   phenotypic responses to herbicide exposure can be immediate. Plastic changes in

148   response to non-lethal herbicide exposure is seen in many traits (Table 1) and may

149   precede, accompany, or give rise to genetic changes. Specifically, vegetative 'damage'

150   responses (e.g., stem wilting, leaf cupping or growth stunting) are common plastic

151   phenotypic changes that occur within hours or a few days of exposure to non-lethal

152 herbicide exposure but can vary among plant species (Figure 3, Table S1) and

153 genotypes within species (Gassmann & Futyuma 2005). Plant growth responses to drift-

154 level exposure vary from severely negative to nonsignificant and even to positive

155 irrespective of the class of herbicide (Fig. 3, Table S1). These and other physiological

156 changes in plants (e.g., leaf nitrogen, Bohnenblust et al. 2013) and longer-term stunting

157 of above ground biomass can have consequences for plant fitness (e.g. seed production

158 or siring success) (Table 1), which may be mediated by interactions with other

159 organisms via traits such as floral attraction, reward production, nodule traits, or leaf

160 palatability. Plastic changes in reproductive traits, such as flowering time, inflorescence

161 height, flower size and pollen production have been observed (Baucom et al. 2008;

162 Bohnenblust et al. 2013; Bohnenblust et al. 2016; Charles 2017; Kovács-Hostyánszki et

163 al. 2017; Iriart & Ashman unpublished). For instance, drift-level exposure (1% FAR) of

164 dicamba delayed the day of first flower by nearly two weeks in a greenhouse community

165 of four species (*Abutilon theophrasti*, *Ipomoea lacunosa*, *Mollugo verticillata*, and

166 *Solanum ptycanthum* (Fig. 4, Table S3). Shifts in timing and floral resources can affect

167 not only plant interactions with pollinators and plant-plant interactions mediated by

168 pollinators (Arceo-Gomez et al. 2019) but can also influence mating system. Changes in

169 mating patterns alter genetic variance and thus can subsequently influence the direction

170 and rate of evolutionary change in response to herbicide exposure (Kuester et al. 2017).

171 While less studied, plastic changes in root morphology occur and can impact

172 relationships with mutualistic rhizobia (Iriart & Ashman, unpublished) or other root

173 symbionts, potentially affecting their abundance and diversity.

174 **Genetic changes—** Herbicides impose incredibly strong selection on target plants as

175 they are designed to reduce population sizes by >90% (Jasieniuk et al. 1996). Thus,

176 even the first generation of exposure can dramatically transform plant population-level

177 genetic diversity.

178 Due to this strong selection and the presence of genetic variation for resistance within

179 crop-associated plant populations (Jasieniuk et al. 1996), resistance often evolves within

180 2-10 years of the widespread, commercial use of any given herbicide, regardless of

181 herbicide chemistry (Gould et al. 2018, Heap & Duke 2018). Over 400 weed species

182 have evolved herbicide resistance, 40 to glyphosate alone (Gould et al. 2018). Some

183 populations are seen to have high initial frequency of resistant individuals contributing to

184 rapid development of herbicide resistance once they are used (Preston and Powles

185   2002). In addition to resistance traits (e.g., enzymes that degrade the herbicide, or

186   reduce target protein susceptibility; Gould et al. 2018) correlated evolution of life history

187   traits has also been seen in response to herbicide exposure (Table 1). For instance, later

188   (or earlier) germination time (Owen et al. 2011), earlier flowering time (Wang et al 2010),

189   increased vegetative growth (Comont et al. 2019), and higher selfing rates (Kuester et

190   al. 2017) are associated with increased genetic resistance. While life history traits are

191   often the focus, there is a wealth of plant traits that may change in response to

192   herbicides that mediate interactions with non-target species (see below) and thus are

193   also highly relevant to eco-evo dynamics. Any of these correlated phenotypes may arise

194   as a result of pleiotropic effects of (or physical linkage to) resistance alleles or through

195   selection for the combination of specific resistance and trait combinations (e.g.,

196   correlational selection; Baucom 2019; Kuester et al. 2017; Saltz et al. 2017).

197   Resistance may evolve one of two ways, target-site resistance (resistance caused by

198   mutations that arise in the targeted region) or nontarget-site resistance (alteration of one

199   or more physiological processes that prevent the herbicide to reach its target site). And

200   the type or extent of resistance, and of changes in correlated traits, may depend on the

201   strength of herbicide selection (i.e., depending on the intensity and application rate and

202   frequency; Gould et al. 2018, Neve et al. 2014, Baucom 2019). It has been predicted

203   that high 'field application strength' doses lead to strong selection for resistance genes of

204   major effect (target-site resistance) whereas low 'drift-level' dose (or low frequency)

205   applications lead to selection for quantitative resistance based on numerous genes of

206   small effect (nontarget-site resistance, Neve et al. 2014). Thus, if 'gene-level' pleiotropy

207   and pleiotropic effects of multiple individual genetic variants result in different

208   evolutionary fates for the trait correlations they produce (Saltz et al. 2017), then the type

209   of correlated outcomes will differ under low and high dose selective pressure, and this

210   could have consequences for eco-evolutionary feedbacks. Likewise, cross-environment

211   (i.e., presence and absence of herbicide) genetic correlations can affect the response to

212   selection in variable environments (e.g. Czesak et al 2006),

213   **Target organisms - Plant community shifts in response to herbicide**

214   As the primary producers and targeted taxonomic group of herbicides, plant

215   communities can quickly reconfigure in response to herbicide exposure. Specifically,

216   highly susceptible plant species may go locally extinct while resistant or preadapted

217   species may expand or invade, filling vacated niches (Bohnenblust et al. 2013). While

218 low-level variation in resistance within some plant species is thought to underlie

219 compositional changes in crop-associated plant communities when new herbicide

220 classes are introduced (Bohnenblust et al. 2013), different plant taxonomic groups may

221 vary in susceptibility for other reasons such as phenological avoidance (e.g.,

222 opportunistic germination time [Grundy et al. 2011; Owen & Zelya 2005] or circadian

223 rhythms [Belbin 2019]), physiological sensitivity (grasses are resistant to 2-4-D;

224 Mayerova et al. 2018), or because they rely on mutualistic microorganisms that

225 themselves are susceptible to herbicide (e.g., rhizobia or mycorrhizae, see below). For

226 instance, abundance of forbs is reduced by dicot-specific herbicide use (e.g., dicamba,

227 Egan et al 2014), whereas grasses are suppressed by monocot-specific herbicides, and

228 both types of plants by broad-spectrum herbicides (Marshall et al. 2003). While highly

229 sensitive plant species may not be eradicated outright from these communities, those

230 that remain may incur a significant 'extinct debt' (Cronk 2016; Kuussaari et al 2009)

231 worsened by isolation, decline in genetic variation (see below), or loss of biotic

232 interactions (Valiente-Banuet et al., 2015).

233 Shifts in species composition and reduced diversity in weed communities have been

234 observed in response to several herbicides when applied at field concentrations and

235 repeatedly over years (Hald 1999; Mayerova et al. 2018). These may be perpetuated

236 beyond the time of application by changes in seedbanks in some soils (Barberi et al.

237 1997). Even low-dose herbicide exposures can have substantial effects on plant

238 communities. For instance, Egan et al. (2014) saw declines in forb cover, but not species

239 richness, in response to drift-level dicamba exposure, thereby shifting dominance (i.e.,

240 evenness) of plant functional classes (e.g. nitrogen-fixing forbs vs. grasses) within the

241 community.

242 **Non-target organisms - Performance and community changes**

243 While most herbicides have been designed to take advantage of biochemical pathways

244 that are unique to plants (Capinera 2019; Motta et al 2018), it is not uncommon that

245 organisms that are not the intended target to also be affected by herbicide exposure. As

246 a result, there is the potential for performance effects and community shifts in these

247 trophic levels (Figure 2) as well as for diffuse co-evolution between them and plants in

248 the affected communities. Yet attempts to investigate this constellation of ecologically

249 relevant linkages is generally lacking (Prosser et al. 2016). Below we highlight some

250 findings concerning herbicide impacts on plant-associates both above and below ground

251   to illustrate the wide range of species interactions affected by herbicides, and the reader

252   is referred to recent compilations for more extensive reviews (e.g., Capinera 2019;

253   Stanley & Preetha 2016).

254   **Above-ground plant associates --** Most herbicides have not been shown to have direct

255   effects on arthropods or birds (Capinera 2019), so projected effects on pollinators are

256   through herbicide-mediated plant community shifts that monotonize pollinator diets or

257   reduce the abundance or availability of resources (see plastic effects on flowers above,

258   Egan et al. 2014, Stanley & Preetha 2016) and thereby threaten pollinator health and

259   resistance to disease (Goulson et al. 2015). Nevertheless, there is evidence that under

260   some conditions herbicides can affect pollinators directly by affecting their physiology,

261   survivorship, and/or foraging effectiveness. For instance, honeybees were killed when

262   directly sprayed, or when they came into contact with plants that have been freshly

263   sprayed, with glyphosate-based herbicides at higher than recommended doses

264   (Abraham et al. 2018). Furthermore, flight trajectories and the spatial learning processes

265   of honeybees are impaired, and beneficial gut microbiota are impacted by ingestion of

266   glyphosate (Balbuena et al. 2015; Motta et al. 2018), and these in turn affect honeybee

267   health and effectiveness as pollinators. Exposure at other life stages not as commonly

268   studied is possible, for instance at larval stages in ground nesting bees (e.g. Kopit &

269   Pitts-Singer 2018). Several studies have focused on the effect of herbicides (e.g.

270   glyphosate) on butterflies and moths yielding mixed results, possibly owing to varied

271   application rates or complexity of multiple life stages (reviewed in Prosser et al. 2016).

272   As one example, dicamba had no direct effect on butterflies but indirectly influenced the

273   performance of their caterpillars, possibly via altering plant nutritional content of their

274   hosts (Bohneblust et al. 2013). The potential effects of herbicides (or any pesticide) on

275   the vast majority of other pollinating taxa beyond those described above (e.g., solitary

276   bees, flies, beetles) in agro-ecological communities is unknown (Franklin & Raine 2019).

277   Studies of effects of herbicide on pollinator community composition are also lacking (but

278   see Egan et al. 2014).

279   Herbicides have been shown to stimulate or benefit some arthropods (Capinera 2019).

280   This is because some herbicides function as plant growth regulators (e.g., auxenic

281   herbicides: 2-4-D, dicamba), and thus, by increasing plant growth (Figure 3, Table S1),

282   can reduce plant defenses (Hout et al. 2014), potentially affecting plant susceptibility to

283   herbivores (Egan et al 2014) and herbivore performance. For example, Wu et al. (2001)

284 found that 4 of 11 herbicides increased the growth rate and reproduction of the brown

285 planthopper. Similarly, aphids performed better on herbicide-exposed plants (Oka &

286 Pimental 1976). The abundance of whitefly larvae was higher on plants that have been

287 exposed to drift levels of dicamba in velvet leaf (*A. theophrasti*; Johnson & Baucom

288 unpublished). However, on a *Carduus* thistle, native butterfly caterpillars and pupae

289 were smaller on dicamba-damaged plants than controls (Bohneblust et al. 2013).

290 Herbicides can also indirectly impact microbial and fungal pathogens (Duke 2018). For

291 instance, glyphosate-based herbicides (that act by inhibiting a key enzyme in plants,

292 fungi, and bacteria) can suppress rust fungal activity (Feng et al. 2005). Nevertheless,

293 herbicides can also affect plant susceptibility to plant pathogens by either inducing or

294 inhibiting disease resistance mechanisms (Duke 2018), and thus indirectly affect

295 pathogen populations and disease spread. Taken together, there are many possible

296 indirect effects of herbicides on plant-antagonist interactions, and an understanding of

297 the broad effects of herbicides on plant antagonists will require knowledge of these.

298

299 **Below-ground plant associates --**Herbicides are often intentionally applied directly to

300 the soil (pre-treatments) or enter soil indirectly by off target spray or drift, and thus can

301 affect soil-dwelling microbes, arthropods and nematodes.

302 Herbicides have been seen to reduce diversity, and shift the composition and functional

303 aspects of soil microbe communities (Helander et al. 2018; Jacobsen and Hjelmsøl

304 2014). While some microbes can actively degrade herbicides (Głodowska & Wozniak

305 2019), toxicity on microbial activities especially of enzyme activities is well documented

306 (Stanley & Preetha 2016). Herbicide residues can persist in soil for several months or

307 even years leading to persistent changes in microbial community composition and

308 function (Helander et al. 2018; Jacobsen and Hjelmsøl 2014). Best studied is

309 glyphosate's effect on microbial communities in the soil, but these appear to be complex,

310 depending on dosage, timing and functional and taxonomic community membership

311 (reviewed in Dennis et al 2018; Tyler & Locke 2018). Some taxa benefit from glyphosate.

312 For example, the plant growth promoting rhizobacterium *Enterobacter cloacae* degrades

313 glyphosate and can use it as a phosphorus source (Duke 2018). Bacterial resistance to

314 active agents of herbicides is common (e.g., Mohr & Tebbe 2006), owing to large

315 populations, standing resistance, and horizonal gene exchange (Brockhurst et al. 2019).

316 Genetic variation in tolerance to several herbicides was observed in 76 strains of

317 rhizobia (Zabaloy & Gomez 2005), however whether resistance to herbicide comes at a

318 cost to other functions, like growth in soil (e.g., Porter & Rice 2012) or effectiveness as a

319 mutualist is unknown but such effects would also impact wild plant hosts (e.g. Burghardt

320 2019).

321 There is evidence of immediate negative effects of herbicides on colonization of plants

322 by mycorrhizal fungi. For instance, Zaller et al (2014) found that glyphosate significantly

323 decreased colonization by mycorrhizae, vesicles and soil spore biomass. In some cases,

324 these effects appear to resolve in a few weeks, suggesting that plants can compensate

325 for the loss, though this varies with herbicide and plant host (Abd-Alla et al. 2000). While

326 the composition of fungal communities is not well understood, a recent metanalysis of

327 the effects of herbicides on soil nematodes showed herbicides reduced total nematode

328 abundances, but did so differentially among trophic groups—while fungivores and

329 predators decreased, bacterivores, plant parasites and omnivores increased (Zhao et al.

330 2013). Because nematodes contribute to many soil ecosystem processes (e.g., soil

331 decomposition and N mineralization) shifts in functional community structure could affect

332 plants indirectly as well as directly (e.g., via an increase in plant parasites).

333 **Putting them together - Ecological-evolutionary feedbacks**

334 While it has been acknowledged that herbicide use can be viewed as an eco-

335 evolutionary problem (Baucom 2019; Neve et al 2014), the focus has largely been on

336 rapid evolution of herbicide-resistant weeds and on the ecological costs of this

337 resistance in the absence of herbicide (Baucom 2019; **Evo-Eco**). Yet, it is now clear that

338 herbicide use can induce plastic trait changes and transform entire ecological

339 communities, thus multiple unpredictable eco-evo trajectories can result. Moreover,

340 because these communities are complex and herbicides affect more than the intended

341 primary producers there is need for a broader view of this evolution in a community

342 context. We believe there is a need to explicitly consider herbicide impact via 1)

343 cascading effects of evolution to the ecological interactions **(Evo-Eco-Evo)**, 2) plastic

344 trait changes on ecology and evolution **(Eco-Evo-Eco)**, 3) shifts in community structure

345 (**Eco & Evo**) that affect species interactions and evolution **(Eco/Evo-Eco-Evo)** and

346 finally, 4) the interplay of these modified communities back to the evolution of the other

347 interacting species (**Eco/Evo-Eco/Evo)**. By specifically considering all of the pathways

348 within eco-evo dynamics (Figure 1), we can hope to formulate a more predictive view of

349 the fates of herbicide-impacted communities.

350 **Evolution changes Ecology: Cascading effects of resistance on species**

351 **interactions--**The evolution of herbicide resistance can have second-order effects on

352 ecological interactions (Table 2; Fig 2) because expression of resistance genes directly

353 affects these interactions or because resistance leads to trade-offs with other traits as a

354 result of competing resource demands (e.g., Uesugi et al. 2017). For instance, relative

355 to herbicide susceptible plants, resistant ones have metabolic changes (Vila-Aiub et al.,

356 2019) that can affect their quality as hosts or partners in interspecific interactions.

357 Indeed, resistant plants have been seen to have weaker competitive ability (Comont et

358 al. 2019), increased susceptibility to herbivorous insects (Gassmann 2005), greater

359 mortality when exposed to rust infection (Salzmann et al. 2008), and reduced floral

360 biomass in the presence of herbivores (Gassmann & Futuyma 2005). Thus, in the

361 context of complex communities, evolution of herbicide resistance could affect ecological

362 interactions, such as competitive hierarchies and the outcome of other plant-antagonist

363 interactions, in a multitude of ways that can feedback on trait evolution and reshape

364 genetic architecture, as has been seen in other settings (Uesugi et al. 2017). Likewise,

365 the correlated changes in traits of herbicide resistant plants can affect their interactions

366 with mutualists. For instance, Atrazine resistant *Brassica rapa* produced significantly less

367 pollen per flower and flowered later than atrazine susceptible plants (Bingham et al.

368 2017), which could potentially affect their interactions with pollinators. Likewise, shifts in

369 flowering time (Wang et al 2010; Fig 4, Table S3) or traits associated with selfing

370 (Kuester et al. 2017) can reduce availability of resources to pollinator communities

371 leading to shifts in their visitation rates or diversity in ways that feedback on evolution of

372 these floral traits. Indeed, changes in pollinator quantity and quality *via* loss of effective

373 pollinators or phenological mismatches between plants and pollinators are main drivers

374 of floral evolution and could occur rapidly in the highly disrupted pollinator communities

375 of the agro-ecological interface (Knight et al. 2018).

376

377 **Plasticity changes Ecology and facilitates Evolution--** Plastic responses to

378 herbicides have been documented for several functional traits that mediate ecological

379 interactions (Tables 1,2). While plasticity can be maladaptive (Hendry 2016), when the

380 plasticity in a trait is in the direction favored by selection, it may facilitate adaptation to

381 novel environments ('plasticity first' reviewed in Levis & Pfenning 2016). This is because

382 plasticity in response to a novel stressor (e.g., herbicide) may uncover cryptic genetic

383 variation and expose it to selection (Gilbert et al 2015; Levis & Pfenning 2016) or, align

with additive genetic variation and thus enhance the efficacy of selection (Nobel et al. 2019). As selection acts on this variation, the trait undergoes genetic accommodation leading to the evolution of a novel phenotype (Levis & Pfenning 2016). Environments where natural populations experience rapid environmental change have been identified as the most likely places that 'plasticity first' will contribute to evolution (Levis & Pfenning 2016). Indeed, the wide range of functional traits that are phenotypically plastic in response to herbicide exposure (Table 1) and affect ecological interactions (Table 2) could lead to a wealth of opportunities for evolution through genetic accommodation in response to herbicides.

For instance, non-lethal herbicide exposure can delay flowering (Table 1, Fig 4, Table S3) and there is extensive genetic variation in flowering time plasticity (Blackman 2017). So, if individual plant genotypes vary in their plastic response to herbicides with respect to flowering time, and this leads to variable degrees of ecological mismatch (i.e., between plants and their pollinators), then this could increase fitness variation (i.e., opportunity for selection) and the potential for flowering time to evolve to reduce the mismatch. Likewise, floral form and mating system could evolve under herbicide exposure, because plastic reductions in flower size, stigma-anther distance, or pollen production in response to herbicide exposure can affect selfing rate (Table 1,2), and these traits can be adaptive when pollinators are limited (e.g., in response to loss of pollinators, Roels & Kelly 2011). These scenarios make clear that if there is genetic variation in trait plasticity in response to non-lethal herbicide exposure then there is the potential for trait plasticity to facilitate evolution, especially via modified ecological interactions.

Ecology feeds back and changes Evolution, and vice versa --Changes in plant species relative abundances (or percent cover) have been observed in response to herbicide exposure (see above) and these are expected to occur well before plant extinction. Changes in functional or taxonomic evenness of the plant community can affect plant-plant interactions as well as interactions with other trophic levels (Symstad et al 2000). For instance, when an herbicide differentially impacts functional groups of plants (e.g., Figure 3, Table S1, dicots) it can simplify functional aspects of the community, reducing the opportunity for complementarity in resource use and thus shifting selection to functional traits related to resource acquisition (e.g., van Moorsel et al. 2019). Moreover, when an herbicide affects the dominance of plant species, it could

417   also affect the abundances or diversity of higher trophic levels and thus selection on

418   traits associated with those interactions, such as herbivore defense or pollinator

419   attraction.

420   Herbicide-mediated loss or gain of plant species can result in major changes in the plant

421   community membership and thus add an evolutionary-driven (extinction and invasion)

422   species composition-dependent dimension to the dynamics within these communities

423   (i.e., terHorst et al. 2018, van Moorsel et al. 2019). Ecological interactions depend on the

424   members of the community, and loss of those with niche constructing, non-redundant

425   functions or specialized traits that make them keystone species (e.g., N fixing

426   mutualisms, unique floral morphologies or rewards), will affect local interaction types,

427   intensity and resulting selection (e.g., Biella et al. 2019; Gomez et al. 2009; Lankau &

428   Strauss 2007). For instance, flower traits mediated the impact of species loss in co-

429   flowering communities, because pollinator foraging decisions (and potentially selection)

430   changed after removal of specific morphospecies (Biella et al. 2019). Likewise, invasion

431   by *Medicago polymorpha* altered the strength and direction of selection on antiherbivore

432   defenses, but not competitive ability, of a native *Lotus* (Lau 2008). Interestingly, the

433   strength of effects also depended on the presence of herbivores (Lau 2008), reinforcing

434   the importance of a holistic approach to eco-evo feedbacks. Thus, extinctions/invasions

435   that result from repeated herbicide exposure can fundamentally feedback on the ecology

436   and trait evolution of the interacting species. In some circumstances, evolution may even

437   compensate for extreme species loss. For instance, van Moorsel et al. (2019) found that

438   prolonged growth in monoculture led to an increase in within-species trait variation

439   suggesting widening of intraspecific niche via character displacement.

440   **Evolution feeds back and changes Evolution: Coevolution of two trophic levels-**

441   Anthropogenic impacts modify communities and can alter the quality of species

442   interactions, leading to evolution and coevolution of the interactors within these

443   communities. Coevolution of host-pathogen interactions may be modified by herbicide

444   exposure because herbicide can affect levels of polymorphism in resistance and

445   infectivity (Duke 2018; Feng et al. 2005), and thus affect trajectories of pathogen-plant

446   arms races. Likewise, evolution may work to maintain, or restore disrupted mutualistic

447   interactions (Gundel et al. 2012, Kiers 2010). For instance, herbicides could shift the

448   quality of mutualistic interactions toward antagonism (changing the cost/benefit

449   relationships of the partners), or threaten coextinction by dramatically reducing the

450 population size of one partner. These changes could precipitate evolutionary shifts to

451 reduce reliance on the declining partner or shifts in partner quality (Kiers et al. 2010;

452 Veron et al. 2018). Herbicide dose has been seen to interact with plant genetic

453 background to influence the expression of mutualism between endophytes and grass

454 species, where the mutualism improved seedling survival at low but not high doses

455 (Gundel 2012). Nevertheless, rhizobia or fungal endophytes may adapt rapidly and in

456 novel ways to herbicide-altered plant phenotypes because their fitness depends on that

457 of the holobont (Gundel 2012; Kiers et al. 2010). Likewise, in pollination mutualisms,

458 plants may evolve towards use of abiotic pollen vectors (e.g., wind) or exclusive self-

459 pollination when faced with poor biotic pollination service (Kaiser-Bunbury et al. 2010,

460 Roels & Kelly 2009). Thus, herbicide-impacted communities may be subject to

461 coevolutionary 'rescue' wherein coevolution between community members mitigates the

462 impacts of ongoing anthropogenic disturbance by rewiring the network structure of the

463 community in a way that compensates for the extinction of individual species and their

464 interactions (Nusimer et al. 2019).

465 **Conclusions, future goals and approaches**

466 Herbicide use leads to some of the most well documented cases of rapid evolution

467 (Palkovacs et al. 2012), but the cascading effects for ecological systems, especially in

468 terms of community composition and quantity and quality of species interactions remain

469 to be explored. Through this mini-synthesis we have shown that herbicides have the

470 potential to transform communities and create eco-evo trajectories for multiple

471 interacting trophic groups, but also that the multiple avenues for interaction in naturally

472 complex communities make it difficult to predict net ecological effects of plant evolution

473 and *vice versa*. As a way forward to assess the potential for eco-evo dynamics, we

474 suggest that we need to start by characterizing several basic axes of variation in

475 impacted natural communities, as well as to begin to conduct the types of manipulative

476 experiments that specifically reveal impacts of ecology on evolution, evolution on

477 ecology, and their feedbacks.

478 With respect to plants as the focal taxonomic level, there are multiple axes of variation

479 that should be quantified in observational studies. First, the extent of within-population

480 genetic variation in response to herbicides across coexisting plant species, and the

481 extent of within-population genetic variation in plastic responses to non-lethal herbicide

482 exposure. In both cases, the response should be measured in terms of a wide range of

483 functional traits, especially those that may be genetically correlated with resistance, as
484 well as those that mediate different types of ecological interactions (i.e., floral attraction,
485 reward production, nodule traits, or leaf palatability or nutritional quality). Assessing
486 resistance in natural settings will be key as resistance is not likely to be consistent
487 across abiotic or biotic environments (e.g., Comont et al. 2019; Du et al. 2018). Levels of
488 herbicide exposure should include sublethal doses, not just field application rates,
489 because sublethal doses impose different strengths of selection which is experienced by
490 the broad range of organisms at the agro-eco interface. In addition to functional traits,
491 studies should explore the effect of herbicide exposure on variance in relative fitness
492 (measured as seed production and seed siring success), because if herbicide exposure
493 increases fitness variation, then it increases the opportunity for selection. For instance,
494 fitness variance (the 'opportunity for selection') increases when populations are in
495 decline (Reiss 2013). Likewise, studies should determine whether plastic responses to
496 herbicides align with additive genetic variation and covariation for those phenotypes as
497 this can increase the efficacy of selection (Nobel et al. 2019). Studies should
498 characterize the ecologically-relevant linkages between direct effects of herbicides on
499 plants, associated indirect effects on plant-dependent communities (i.e., pollinators,
500 rhizobia, herbivores) and the potential direct effect on these communities, as well as
501 determine whether herbicide exposure changes the net strength of existing ecological
502 interactions. In all cases, an effort should be made to incorporate the totality of
503 interactions which will inform on the potential for diffuse coevolution (De Meester 2019).
504 Finally, studies should document plant community shifts in terms of species membership
505 and evenness not only throughout the growing season as phenological shifts are
506 common responses to herbicide, but also across years (Table 2, Figure 3, Table S1).

507 Future work should leverage experimental manipulations to explicitly assess the impacts
508 of ecology on evolution and vice versa, and their feedback. First, classic selection
509 experiments can be used to assess the impacts of ecology on evolution. For instance,
510 the canonical experiment involves exposing plant populations to different levels of
511 herbicide application (including relevant controls), sowing the seeds for the next
512 generation in proportion to fitness in the prior, conducting this over several generations
513 and finally scoring herbicide resistance and other functional traits. But if this experiment
514 is conducted with and without the potential for biotic interactions (e.g., mutualistic
515 partners) then one can compare the sum of direct and indirect ecological effects of
516 herbicide evolution to the direct effects of herbicide alone.

517   If selection experiments are conducted with numerous community members, then one

518   can conduct a second type of experiment where the standing genetic variation in

519   resistance is manipulated to explicitly assess the impacts of evolution on ecology. For

520   instance, ecological interactions can be characterized for populations (or communities)

521   inhabited with varying compositions of resistant or susceptible genotypes (i.e., products

522   of previous selection experiments). Manipulating community composition in a crossed

523   design with within-species resistance variation would allow one to assess the synergistic

524   effect of species extinctions (or migrations) and resistance evolution on ecology of a

525   focal species. Finally, resistant or susceptible plants could be compared when inhabiting

526   artificial communities assembled to reflect foundational compositions or to reflect

527   herbicide-shifted compositions. This would allow one to disentangle the direct effects of

528   herbicide resistance from the community-contextual changes in species interactions.

529   It will also be important to determine if the mutualist partners evolve in response to

530   herbicides directly or via plant evolution. It is possible that partners with fast generations

531   times and large population sizes, like microbes, will evolve faster than plants in response

532   to herbicides and could facilitate evolutionary rescue of the plant species (Bell 2017).

533   Such experiments could involve artificial selection on microbes and assessment of plant

534   fitness when in the presence of evolved or original microbial associates.

535   Finally, experiments that put a 'break' on evolution are recommended to assess

536   feedback of evolution on ecology (Turcotte et al. 2013). Here, alongside a selection

537   experiment (as above) where each generation is started with the most fit individuals from

538   a prior generation, control populations are created wherein each generation the initial

539   genotypes are used to repopulate the community, rather than those that have evolved in

540   the previous generation. The effects of evolved populations on species interactions are

541   then compared to those with initial populations. It is worth mentioning that all of these

542   experiments should be conducted in accordance with state and local pesticide

543   regulations, and with the utmost care to avoid escape of evolved organisms.

544   In conclusion, an eco-evo perspective provides a framework for understanding the

545   impact of herbicides on evolution and ecology and their interaction on the same time

546   scale. Thus, it will provide a better understanding of how these human-mediated

547   disturbances are transforming species and community functions in real time.

548

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553

554 **References**

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933 **Author contributions**

934 All authors contributed to design and concept development. TLA wrote first draft of the
935 paper which VI and RSB edited. VI collected data and created figures and tables.

936 **Tables and Figures**

937 Table 1. Plant functional trait changes in response to herbicide exposure. Plastic
938 category represents trait response to immediate ecological effect of herbicide exposure
939 while genetic reflects those that were the result evolved response to herbicide exposure.
940 Herbicide dose is categorized as "drift" (0.01-1% of the field application rate), "field rates"
941 (100%), and "sublethal" (between drift and field rates).

942 Table 2. Ecological interactions affected by herbicide exposure. Categorized by
943 interaction partner-- the organism type interacting with herbicide-exposed plants. Effects
944 are divided into immediate ecological (plastic) effects and evolved effects of herbicide
945 exposure. Mechanism and effect give specific and general information about the
946 responses recorded. Herbicide dose is categorized by "drift" (0.01-1% of the field
947 application rate), "field rates" (100%), and "sublethal" (between drift and field rates).
948 Dashes indicate information is lacking.

949 **Figure 1.** Schematic representation of eco-evolutionary dynamics. Ecological changes
950 drive evolutionary response (top bold arrow), evolutionary change drives ecological
951 dynamics (bottom bold arrow), feedbacks after rapid evolution (inner dotted arrow) and
952 feedbacks in ecological change (outer dotted arrow).

953 **Figure 2.** Schematic representation of eco-evolutionary dynamics in herbicide (red
954 chemical icon) affected communities. The middle green trophic level contains the target
955 organisms (plants), while the top multicolored trophic level and the bottom brown trophic
956 level contain the non-target organisms that associate with plants above- and below-

957 ground, respectively. Middle right arrows indicate progression through time showing

958 shifts in community compositions and resistance evolution (red symbols) in members of

959 different trophic levels. Arrows from the chemical icon on the left represent direct effects,

960 while curved arrows on the right and double-headed arrows illustrate ecological

961 feedbacks within and between trophic levels, respectively.

962 **Figure 3.** Examples of species variation in growth-related responses to sublethal

963 exposure for three common herbicides, chlorsulfuron (circle, Fletcher et al. 1996),

964 dicamba (blue triangle, Table S3; red triangle, Olszyk et al. 2015), and glyphosate

965 (square, Olszyk et al. 2015) (see Table S1 and S2 for details). Filled symbols represent

966 significant effects of herbicide noted in original study. Growth is represented as

967 percentage of control.

968 **Figure 4.** Dicamba drift (1% FAR) delays the day of first flower, represented in days

969 since planting, in a greenhouse community of four wildflower species (Table S3). Density

970 represents the smooth kernel density estimate of day of first flower, which estimates the

971 probability of a value falling in a given interval of a continuous variable based on the

972 distribution of the data, and the overall density plot is similar in concept to a histogram

973 (Trosset 2011). This density plot was constructed with R (R Core Team 2019) using the

974 *geom_density* function in the package *ggplot2* (Wickham 2016). Dotted lines indicate

975 treatment means.

976

977

978 **Data accessibility**

979 The data that support the findings of this study are available in the Supplemental

980 Information in the online version of this article.

Table 1. Plant functional trait changes in response to herbicide exposure. Plastic category represents trait response to immediate ecological effect of herbicide exposure while genetic reflects those that were the result evolved response to herbicide exposure. Herbicide dose is categorized as "drift" (0.01-1% of the field application rate), "field rates" (100%), and "sublethal" (between drift and field rates).

Trait	Plastic/Genetic	Direction	Herbicide	Dose	Plant Species	Source
Biomass	genetic	decreased	sulfonylurea	field rates	*Lactuca serriola*	Alcocer-Ruthling et al. 1992
					Bupleurum rotundifolium, Scandix pecten-veneris subsp. pectenveneris, Neslia paniculata subsp. Thracica,	
	plastic	decreased	2,4-D	sublethal	*Rapistrum rugosu, Papaver argemone*	Rotchés-Ribalta et al 2015
	plastic	reduced	glyphosate	drift	*Geranium robertianum, P. vulgaris*	Gove et al. 2007
Defense against disease	genetic	decreased	triazine	field rates	*Senecio vulgaris*	Salzmann et al 2008
Nitrogen composition of leaves	plastic	decreased	dicamba	drift	*Carduus thistle*	Bohnenblust et al 2013
Root architecture	plastic	altered	dicamba	drift	*Medicago sativa*	Iriart and Ashman unpublished
Flower production	plastic	reduced	dicamba	drift	*Medicago sativa, Eupatorium perfoliatum L.*	Bohnenblust et al 2016
	plastic	reduced	glyphosate	drift	*Geranium robertianum, P. vulgaris*	Gove et al. 2007
Flowering time	plastic	delayed	dicamba	drift	*Medicago sativa, Eupatorium perfoliatum L*	Bohnenblust et al 2016
	plastic	delayed	glyphosate	drift	*Tanacetum vulgare*	Dupont et al 2018
	plastic	delayed	dicamba	drift	*Ipomoea lacunosa, Solanum ptycanthum, Abutilon theophrasti*	Iriart & Ashman unpublished
	genetic	accelerated	glyphosate	field rates	*Setaria viridis (L.) Beauv, Setaira italica (L.) Beauv*	Wang et al 2010

						Baucom, Mauricio, & Chang
Anther length	plastic	reduced	glyphosate	drift	*Brassica rapa*	2008; Londo et al. 2014
Pollen production	plastic	reduced	atrazine	field rates	*Brassica rapa*	Bingham et al. 2017
Pistil function	plastic	reduced	glyphosate	drift	*Brassica rapa*	Londo et al. 2014
Selfing rate	genetic	increased	glyphosate	field rates	*Ipomoea purpurea*	Kuester et al 2017
Tiller length	genetic	increased	mesosulfuron and iodosulfuron	field rates	*Alopecurus myosuroides*	Comont et al. 2019
Immature seed weight	plastic	increased	dicamba and glyphosate mix	drift	*Eriophyllum lanatum*	Olszyk et al. 2017
Seed dormancy requirement	plastic	decreased	glyphosate	drift	*Avena fatua L.*	Shuma et al. 1995
Seed production	plastic	reduced	sulfometuron	drift	*Pisium sativum L.*	Olszyk et al. 2009
Seed weight	plastic	reduced	dicamba and glyphosate mix	drift	*Camassia leichtlinii, Elymus glaucus, Eriophyllum lanatum, Festuca idahoensis, Iris tenax, Prunella vulgaris, Eriophyllum lanatum*	Olszyk et al. 2017
Germination	plastic	reduced	glyphosate	drift	*Avena fatua L.*	Shuma et al. 1995

Table 2. Ecological interactions affected by herbicide exposure. Categorized by interaction partner-- the organism type interacting with herbicide-exposed plants. Effects are divided into immediate ecological (plastic) effects and evolved effects of herbicide exposure. Mechanism and effect give specific and general information about the responses recorded. Herbicide dose is categorized by "drift" (0.01-1% of the field application rate), "field rates" (100%), and "sublethal" (between drift and field rates). Dashes indicate information is lacking.

	Interaction Partner	Effects	Mechanism	Herbicide	Dose	Source
Immediate Ecological Effects						
Above ground	herbivore	increased aphid herbivory on *Abutilon theophrasti*	vegetative damage	dicamba	drift	Johnson & Baucom unpublished
		reduced *Vanessa cardui* larval and pupal mass and thistle biomass in presence of *V. cardui* larvae	plant nitrogen content	dicamba	drift	Bohnenblust et al. 2013
	pollinator	reduced abundance of Heteroptera and Coleoptera species in plots of mixed herbaceous species	floral resources	combination of autumn herbicides	field rates	Moreby & Southway 1999
		reduced visitation rate of honey bees to *Medicago sativa L.* and *Eupatorium perfoliatum L*	floral resources	dicamba	drift	Bohnenblust et al. 2016
	fungal pathogen	increased susceptibility of soybean to fungal pathogen *P. sojae*	defense against disease	glyphosate	sublethal	Keen et al. 1982
Below ground	arbuscular mycorrhizal fungi (AMF)	shifted plant community dominance from spotted knapweed (good AMF host) to bulbous bluegrass (poor host)	species-specific fitness	picloram	field rates	Lekberg et al. 2017
	earthworm	decreased earthworm reproduction and surface burrowing activity	soil chemistry	glyphosate	sublethal	Zaller et al. 2015

|	root nematode	increased total abundance of omnivorous nematodes	soil food web	atrazine	field rates	Zhao et al. 2012
	rhizobia	decreased nodulation and nodule dry weight of rhizobia on cowpea	rhizobial growth	2,4-D, round-up, atrazine	field rates	Shankar et al. 2012; Ahemad 2012
		Depleted number of actively Nitrogen-fixing nodules in *Medicago sativa* and *Trifolium pratense*	root architecture	dicamba	drift	Iriart & Ashman unpublished

Evolved Effects

Above ground	fungal pathogen	increased defenses against leaf and stripe rusts in wheat cultivar	fungal pathogen growth	glyphosate	field rate	Feng et al. 2005
		decreased resistance in *Senecio vulgaris* against fungal pathogen *Puccinia lagenophorae*	photosynthetic capacity	triazine	field rates	Salzmann et al 2008
	plant	reduced intraspecific competitive ability in *Kochia scoparia*	time to development and fecundity	glyphosate	field rates	Comont et al. 2019; Martin et al. 2017
	endophytic fungi	Decreased efficiency in the mutalism between grass species *Lolium multiflorum* and endophytic fungi	symbiont compatibility	dichlofop-methyl	sublethal	Gundel et al. 2012
	herbivore	increased susceptibility of *Amaranthus hybridus* to specialist herbivore *Disonycha glabrata* and generalist *Trichoplusia ni*	herbivore preference	triazine	field rates	Gassmann 2005
	herbivore	reduced reproductive biomass of *A. hybridus* in presence of foliverous beetle *Disonycha glabrata*	susceptibility to herbivory	triazine	field rates	Gassmann & Futuyma 2005

Below ground

Figure 1. Schematic representation of eco-evolutionary dynamics. Ecological changes drive evolutionary response (top bold arrow), evolutionary change drives ecological dynamics (bottom bold arrow), feedbacks after rapid evolution (inner dotted arrow) and feed backs in ecological change (outer dotted arrow).
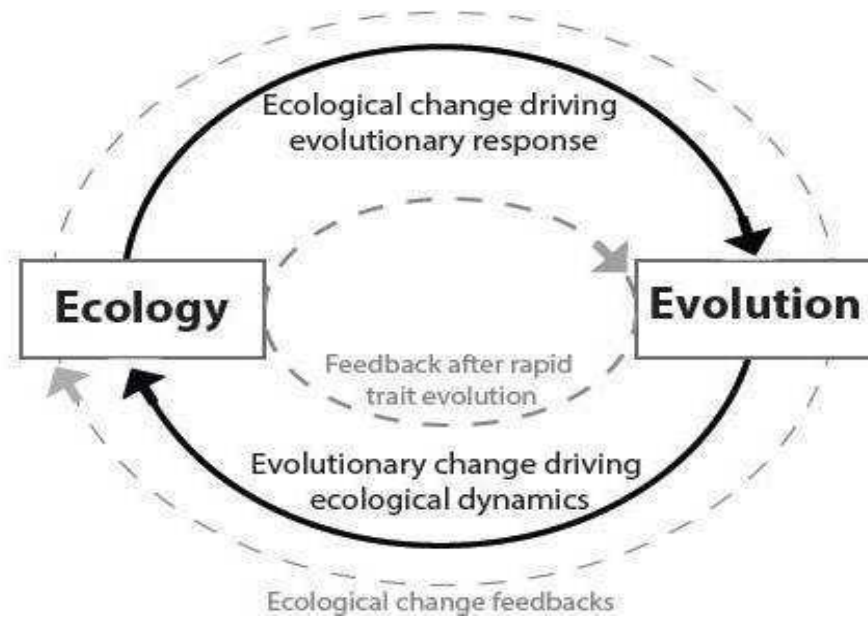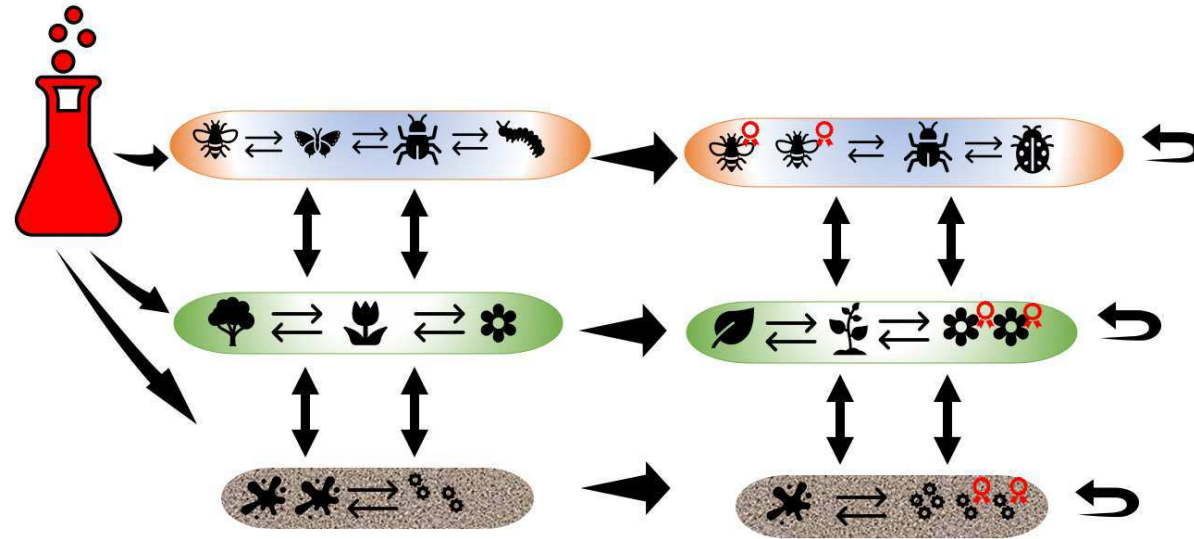
Figure 2. Schematic representation of eco-evolutionary dynamics in herbicide (red chemical icon) affected communities. The middle green trophic level contains the target organisms (plants), while the top multicolored trophic level and the bottom brown trophic level contain the non-target organisms that associate with plants above- and below-ground, respectively. Middle right arrows indicate progression through time showing shifts in community compositions and resistance evolution (red symbols) in members of different trophic levels. Arrows from the chemical icon on the left represent direct effects, while curved arrows on the right and double-headed arrows illustrate ecological feedbacks within and between trophic levels, respectively.

Figure 3. Examples of species variation in growth-related responses to sublethal exposure for three common herbicides, chlorsulfuron (circle, Fletcher et al. 1996), dicamba (blue triangle, Table S3; red triangle, Olszyk et al. 2015), and glyphosate (square, Olszyk et al. 2015) (see Table S1 and S2 for details). Filled symbols represent significant effects of herbicide noted in original study. Growth is represented as percentage of control.
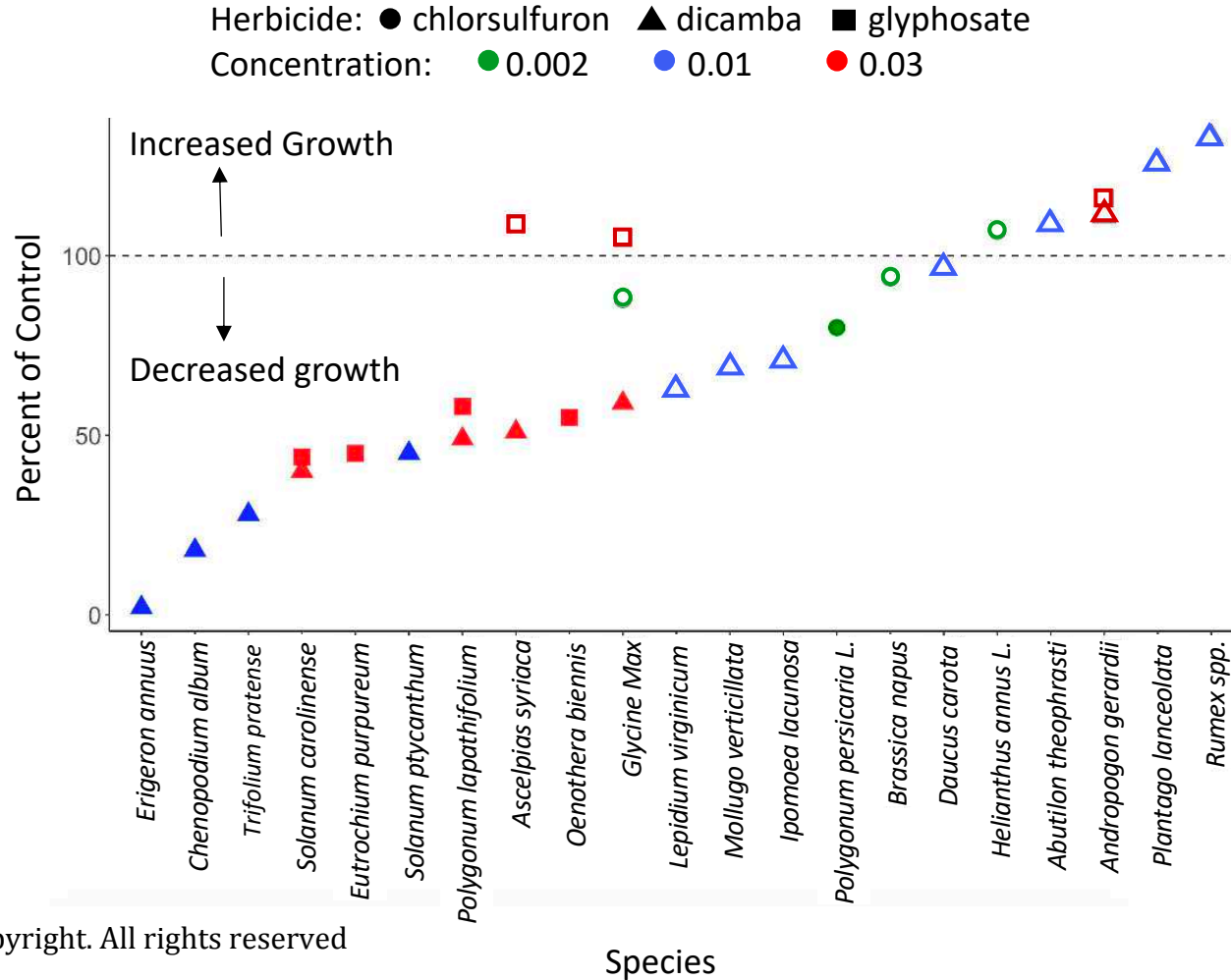
Figure 4. Dicamba drift (1% FAR) delays the day of first flower, represented in days since planting, in a greenhouse community of four wildflower species (Table S3). Density represents the smooth kernel density estimate of day of first flower, which estimates the probability of a value falling in a given interval of a continuous variable based on the distribution of the data, and the overall density plot is similar in concept to a histogram (Trosset 2011). This density plot was constructed with R (R Core Team 2019) using the *geom_density* function in the package *ggplot2* (Wickham 2016). Dotted lines indicate treatment means.