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Article type : Special Issue

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

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

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Abstract

Herbicides act as human-mediated novel selective agents and community disruptors, yet their full effects on eco-evolutionary dynamics in natural communities has only begun to be appreciated. Here we synthesize how herbicide exposures can result in dramatic phenotypic and compositional shifts within communities at the agro-ecological interface and how these 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. We advocate a holistic approach to understanding these dynamics that includes plastic changes and plant community transformations and also extends beyond this single trophic level targeted by herbicides to the effects on non-target plant-associated organisms and their potential to evolve, thereby embracing the complexity of these real-world systems. We make explicit recommendations for future research to achieve this goal and specifically address impacts of ecology on evolution, evolution on ecology, and their feedbacks so that we can gain a more predictive view of the fates of herbicide-impacted communities.

Key words

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

Introduction

Humans are modifying the environment in myriad ways and at unprecedented rates, and their activities are now recognized as leading to some of the strongest selection wild populations have ever been exposed (Alberti 2015; Pelletier & Coltman 2018; Palkovacs et al. 2012, Turcotte et al. 2017), as well as having dramatic effects on species interactions, community assembly, and ecosystem services (Johnson & Munshi-South 2017; Kiers et al 2010; Valiente-Banuet et al. 2015). As a consequence, human-mediated disturbances can represent a turning point for these natural systems. Of particular concern are human-introduced chemicals-- i.e., new herbicides, insecticides, fungicides (in chemistry, application method or scale of use), that can represent novel selective agents and community disruptors especially when coupled with exponential 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

When ecological dynamics (e.g. population growth or community assembly) and evolution occur on the same timescales there is the opportunity for new dynamics to emerge (Palkovacs et al. 2012; Pimentel 1963). Eco-evolutionary forces wherein biotic and abiotic processes lead to rapid evolution in species (Fig 1, top arrow) that then alter the ecological dynamics of the interacting species (Fig 1, bottom arrow) are now recognized to create not only 'real-time' evolution but also lead to dramatic, and potentially unpredictable, changes in ecological dynamics (Turcotte et al. 2019). While evolution in a community context is gaining empirical support (terHorst, et al. 2010; terHorst et al. 2018), we still lack a full understanding of how this evolution alters ecological dynamics, and whether this results in a feedback that affects future evolution (De Meester et al. 2019; Hendry 2018; Turcotte et al. 2019). Of particular interest are scenarios where the rapid evolution of traits alters ecological variables that then in turn affect the evolution of those same traits, creating eco-evolutionary feedbacks (Fig. 1 dotted arrows). Likewise, the recognition that evolution depends not only on direct but also on indirect evolutionary effects has prompted the inclusion of a wider community context to evolutionary studies (terHorst et al. 2018), and the study of 'diffuse coevolution' (DeMeester et al. 2019). Here, traits evolve in response to multiple interacting members of a community, and in turn evolution indirectly affects the magnitude or direction of the interactions among species (Arceo-Gómez & Ashman 2014; Janzen 1980; terHorst et al. 2018; terHorst et al 2010). The result is a 'broad sense' view of eco-evolutionary feedbacks that includes all reciprocal interactions between ecology and evolution (De Meester et al. 2019).

Herbicide-impacted communities are one of the few natural systems that have emerged as uniquely suited to demonstrate direct links between evolving traits and ecological impacts and vice versa (Baucom 2019; Bell 2017; Neve et al 2013; Prosser et al 2016). As yet, however, there has been no robust discussion of the eco-evolutionary feedbacks (e.g., Palkovacs & Hendry 2018; Turcotte et al. 2019) possible within systems experiencing herbicide application. Moreover, because an eco-evolutionary focus beyond the single trophic level that is targeted by herbicides (plants) is rare, the complexity of these real-world systems has been mostly overlooked (Figure 2). Thus, our understanding of multi-tropic interactions in these impacted systems is incomplete, and our ability to predict the outcomes of herbicide disruption limited.

We explicitly consider how herbicide exposures affect eco-evolutionary dynamics in the broad sense. In Figure 2 and the paragraphs that follow, we illustrate the ways that herbicide exposure affects the ecology and evolution of plants (the target organisms), as well as the non-target organisms plants associate with. First, we establish the known ways herbicides lead to 1) phenotypic transformation of individual plant species via plasticity or evolution, and 2) alteration of plant communities via species extinctions and invasions. Second, we consider the evidence for herbicide effects on non-target organisms that interact with plants (either above- or below- ground) and how this can affect community structure of these trophic levels, as well as evolution of the organisms within these trophic groups. Third, we explicitly describe the ways these ecological and evolutionary processes could come together to create **eco-evo** and **evo-eco** dynamics catalyzed by herbicide exposure. And finally, we conclude by recommending approaches that will reveal these processes and rapidly propel our understanding of these eco-evo dynamics forward.

Target organisms - Plant phenotypic changes in response to herbicide

Herbicides can affect the plant phenotype via plastic or genetic changes (Table 1). If plants do not die outright following herbicide exposure, they will exhibit wide-ranging plastic phenotypic alterations such as stunted growth and delayed flowering, among other changes. Additionally, given strong, herbicide-mediated selection, the plant phenotype can evolve along with herbicide resistance either through genetic linkage or pleiotropy. These changes to the plant phenotype are expected to be equally as important as herbicide-induced species compositional effects (see below) because generally within-species phenotypic effects on ecological parameters are as strong as replacing one species with another (Des Roches et al. 2018). While either plastic or genetic changes of the phenotype could mediate ecological interactions, the genesis of plant phenotypic change has different consequences for eco-evolutionary dynamics (Hendry 2016; Levis & Pfenning 2016).

Plastic changes –While evolutionary responses take a generation or more, plastic phenotypic responses to herbicide exposure can be immediate. Plastic changes in response to non-lethal herbicide exposure is seen in many traits (Table 1) and may precede, accompany, or give rise to genetic changes. Specifically, vegetative ‘damage’ responses (e.g., stem wilting, leaf cupping or growth stunting) are common plastic phenotypic changes that occur within hours or a few days of exposure to non-lethal herbicide exposure but can vary among plant species (Figure 3, Table S1) and genotypes within species (Gassmann & Futyuma 2005). Plant growth responses to drift-level exposure vary from severely negative to nonsignificant and even to positive irrespective of the class of herbicide (Fig. 3, Table S1). These and other physiological changes in plants (e.g., leaf nitrogen, Bohnenblust et al. 2013) and longer-term stunting of above ground biomass can have consequences for plant fitness (e.g. seed production or siring success) (Table 1), which may be mediated by interactions with other organisms via traits such as floral attraction, reward production, nodule traits, or leaf palatability. Plastic changes in reproductive traits, such as flowering time, inflorescence height, flower size and pollen production have been observed (Baucom et al. 2008; Bohnenblust et al. 2013; Bohnenblust et al. 2016; Charles 2017; Kovács-Hostyánszki et al. 2017; Iriart & Ashman unpublished). For instance, drift-level exposure (1% FAR) of dicamba delayed the day of first flower by nearly two weeks in a greenhouse community of four species (*Abutilon theophrasti*, *Ipomoea lacunosa*, *Mollugo verticillata*, and *Solanum ptycanthum* (Fig. 4, Table S3). Shifts in timing and floral resources can affect not only plant interactions with pollinators and plant-plant interactions mediated by pollinators (Arceo-Gomez et al. 2019) but can also influence mating system. Changes in mating patterns alter genetic variance and thus can subsequently influence the direction and rate of evolutionary change in response to herbicide exposure (Kuester et al. 2017). While less studied, plastic changes in root morphology occur and can impact relationships with mutualistic rhizobia (Iriart & Ashman, unpublished) or other root symbionts, potentially affecting their abundance and diversity.

Genetic changes— Herbicides impose incredibly strong selection on target plants as they are designed to reduce population sizes by >90% (Jasieniuk et al. 1996). Thus, even the first generation of exposure can dramatically transform plant population-level genetic diversity.

Due to this strong selection and the presence of genetic variation for resistance within crop-associated plant populations (Jasieniuk et al. 1996), resistance often evolves within 2-10 years of the widespread, commercial use of any given herbicide, regardless of herbicide chemistry (Gould et al. 2018, Heap & Duke 2018). Over 400 weed species have evolved herbicide resistance, 40 to glyphosate alone (Gould et al. 2018). Some populations are seen to have high initial frequency of resistant individuals contributing to rapid development of herbicide resistance once they are used (Preston and Powles 2002). In addition to resistance traits (e.g., enzymes that degrade the herbicide, or reduce target protein susceptibility; Gould et al. 2018) correlated evolution of life history traits has also been seen in response to herbicide exposure (Table 1). For instance, later (or earlier) germination time (Owen et al. 2011), earlier flowering time (Wang et al 2010), increased vegetative growth (Comont et al. 2019), and higher selfing rates (Kuester et al. 2017) are associated with increased genetic resistance. While life history traits are often the focus, there is a wealth of plant traits that may change in response to herbicides that mediate interactions with non-target species (see below) and thus are also highly relevant to eco-evo dynamics. Any of these correlated phenotypes may arise as a result of pleiotropic effects of (or physical linkage to) resistance alleles or through selection for the combination of specific resistance and trait combinations (e.g., correlational selection; Baucom 2019; Kuester et al. 2017; Saltz et al. 2017).

Resistance may evolve one of two ways, target-site resistance (resistance caused by mutations that arise in the targeted region) or nontarget-site resistance (alteration of one or more physiological processes that prevent the herbicide to reach its target site). And the type or extent of resistance, and of changes in correlated traits, may depend on the strength of herbicide selection (i.e., depending on the intensity and application rate and frequency; Gould et al. 2018, Neve et al. 2014, Baucom 2019). It has been predicted that high 'field application strength' doses lead to strong selection for resistance genes of major effect (target-site resistance) whereas low 'drift-level' dose (or low frequency) applications lead to selection for quantitative resistance based on numerous genes of small effect (nontarget-site resistance, Neve et al. 2014). Thus, if 'gene-level' pleiotropy and pleiotropic effects of multiple individual genetic variants result in different evolutionary fates for the trait correlations they produce (Saltz et al. 2017), then the type of correlated outcomes will differ under low and high dose selective pressure, and this could have consequences for eco-evolutionary feedbacks. Likewise, cross-environment (i.e., presence and absence of herbicide) genetic correlations can affect the response to selection in variable environments (e.g. Czesak et al 2006),

Target organisms - Plant community shifts in response to herbicide

As the primary producers and targeted taxonomic group of herbicides, plant communities can quickly reconfigure in response to herbicide exposure. Specifically, highly susceptible plant species may go locally extinct while resistant or preadapted species may expand or invade, filling vacated niches (Bohnenblust et al. 2013). While low-level variation in resistance within some plant species is thought to underlie compositional changes in crop-associated plant communities when new herbicide classes are introduced (Bohnenblust et al. 2013), different plant taxonomic groups may vary in susceptibility for other reasons such as phenological avoidance (e.g., opportunistic germination time [Grundy et al. 2011; Owen & Zelya 2005] or circadian rhythms [Belbin 2019]), physiological sensitivity (grasses are resistant to 2-4-D; Mayerova et al. 2018), or because they rely on mutualistic microorganisms that themselves are susceptible to herbicide (e.g., rhizobia or mycorrhizae, see below). For instance, abundance of forbs is reduced by dicot-specific herbicide use (e.g., dicamba, Egan et al 2014), whereas grasses are suppressed by monocot-specific herbicides, and both types of plants by broad-spectrum herbicides (Marshall et al. 2003). While highly sensitive plant species may not be eradicated outright from these communities, those that remain may incur a significant ‘extinct debt’ (Cronk 2016; Kuussaari et al 2009) worsened by isolation, decline in genetic variation (see below), or loss of biotic interactions (Valiente-Banuet et al., 2015).

Shifts in species composition and reduced diversity in weed communities have been observed in response to several herbicides when applied at field concentrations and repeatedly over years (Hald 1999; Mayerova et al. 2018). These may be perpetuated beyond the time of application by changes in seedbanks in some soils (Barberi et al. 1997). Even low-dose herbicide exposures can have substantial effects on plant communities. For instance, Egan et al. (2014) saw declines in forb cover, but not species richness, in response to drift-level dicamba exposure, thereby shifting dominance (i.e., evenness) of plant functional classes (e.g. nitrogen-fixing forbs vs. grasses) within the community.

Non-target organisms - Performance and community changes

While most herbicides have been designed to take advantage of biochemical pathways that are unique to plants (Capinera 2019; Motta et al 2018), it is not uncommon that organisms that are not the intended target to also be affected by herbicide exposure. As a result, there is the potential for performance effects and community shifts in these trophic levels (Figure 2) as well as for diffuse co-evolution between them and plants in the affected communities. Yet attempts to investigate this constellation of ecologically relevant linkages is generally lacking (Prosser et al. 2016). Below we highlight some findings concerning herbicide impacts on plant-associates both above and below ground to illustrate the wide range of species interactions affected by herbicides, and the reader is referred to recent compilations for more extensive reviews (e.g., Capinera 2019; Stanley & Preetha 2016).

Above-ground plant associates -- Most herbicides have not been shown to have direct effects on arthropods or birds (Capinera 2019), so projected effects on pollinators are through herbicide-mediated plant community shifts that monotonize pollinator diets or reduce the abundance or availability of resources (see plastic effects on flowers above, Egan et al. 2014, Stanley & Preetha 2016) and thereby threaten pollinator health and resistance to disease (Goulson et al. 2015). Nevertheless, there is evidence that under some conditions herbicides can affect pollinators directly by affecting their physiology, survivorship, and/or foraging effectiveness. For instance, honeybees were killed when directly sprayed, or when they came into contact with plants that have been freshly sprayed, with glyphosate-based herbicides at higher than recommended doses (Abraham et al. 2018). Furthermore, flight trajectories and the spatial learning processes of honeybees are impaired, and beneficial gut microbiota are impacted by ingestion of glyphosate (Balbuena et al. 2015; Motta et al. 2018), and these in turn affect honeybee health and effectiveness as pollinators. Exposure at other life stages not as commonly studied is possible, for instance at larval stages in ground nesting bees (e.g. Kopit & Pitts-Singer 2018). Several studies have focused on the effect of herbicides (e.g. glyphosate) on butterflies and moths yielding mixed results, possibly owing to varied application rates or complexity of multiple life stages (reviewed in Prosser et al. 2016). As one example, dicamba had no direct effect on butterflies but indirectly influenced the performance of their caterpillars, possibly via altering plant nutritional content of their hosts (Bohneblust et al. 2013). The potential effects of herbicides (or any pesticide) on the vast majority of other pollinating taxa beyond those described above (e.g., solitary bees, flies, beetles) in agro-ecological communities is unknown (Franklin & Raine 2019). Studies of effects of herbicide on pollinator community composition are also lacking (but see Egan et al. 2014).

Herbicides have been shown to stimulate or benefit some arthropods (Capinera 2019). This is because some herbicides function as plant growth regulators (e.g., auxenic herbicides: 2-4-D, dicamba), and thus, by increasing plant growth (Figure 3, Table S1), can reduce plant defenses (Hout et al. 2014), potentially affecting plant susceptibility to herbivores (Egan et al 2014) and herbivore performance. For example, Wu et al. (2001) found that 4 of 11 herbicides increased the growth rate and reproduction of the brown planthopper. Similarly, aphids performed better on herbicide-exposed plants (Oka & Pimental 1976). The abundance of whitefly larvae was higher on plants that have been exposed to drift levels of dicamba in velvet leaf (*A. theophrasti*; Johnson & Baucom unpublished). However, on a *Carduus* thistle, native butterfly caterpillars and pupae were smaller on dicamba-damaged plants than controls (Bohneblust et al. 2013). Herbicides can also indirectly impact microbial and fungal pathogens (Duke 2018). For instance, glyphosate-based herbicides (that act by inhibiting a key enzyme in plants, fungi, and bacteria) can suppress rust fungal activity (Feng et al. 2005). Nevertheless, herbicides can also affect plant susceptibility to plant pathogens by either inducing or inhibiting disease resistance mechanisms (Duke 2018), and thus indirectly affect pathogen populations and disease spread. Taken together, there are many possible indirect effects of herbicides on plant-antagonist interactions, and an understanding of the broad effects of herbicides on plant antagonists will require knowledge of these.

Below-ground plant associates --Herbicides are often intentionally applied directly to the soil (pre-treatments) or enter soil indirectly by off target spray or drift, and thus can affect soil-dwelling microbes, arthropods and nematodes.

Herbicides have been seen to reduce diversity, and shift the composition and functional aspects of soil microbe communities (Helander et al. 2018; Jacobsen and Hjelmsøl 2014). While some microbes can actively degrade herbicides (Głodowska & Wozniak 2019), toxicity on microbial activities especially of enzyme activities is well documented (Stanley & Preetha 2016). Herbicide residues can persist in soil for several months or even years leading to persistent changes in microbial community composition and function (Helander et al. 2018; Jacobsen and Hjelmsøl 2014). Best studied is glyphosate's effect on microbial communities in the soil, but these appear to be complex, depending on dosage, timing and functional and taxonomic community membership (reviewed in Dennis et al 2018; Tyler & Locke 2018). Some taxa benefit from glyphosate. For example, the plant growth promoting rhizobacterium *Enterobacter cloacae* degrades glyphosate and can use it as a phosphorus source (Duke 2018). Bacterial resistance to active agents of herbicides is common (e.g., Mohr & Tebbe 2006), owing to large populations, standing resistance, and horizonal gene exchange (Brockhurst et al. 2019). Genetic variation in tolerance to several herbicides was observed in 76 strains of rhizobia (Zabaloy & Gomez 2005), however whether resistance to herbicide comes at a cost to other functions, like growth in soil (e.g., Porter & Rice 2012) or effectiveness as a mutualist is unknown but such effects would also impact wild plant hosts (e.g. Burghardt 2019).

There is evidence of immediate negative effects of herbicides on colonization of plants by mycorrhizal fungi. For instance, Zaller et al (2014) found that glyphosate significantly decreased colonization by mycorrhizae, vesicles and soil spore biomass. In some cases, these effects appear to resolve in a few weeks, suggesting that plants can compensate for the loss, though this varies with herbicide and plant host (Abd-Alla et al. 2000). While the composition of fungal communities is not well understood, a recent metanalysis of the effects of herbicides on soil nematodes showed herbicides reduced total nematode abundances, but did so differentially among trophic groups—while fungivores and predators decreased, bacterivores, plant parasites and omnivores increased (Zhao et al. 2013). Because nematodes contribute to many soil ecosystem processes (e.g., soil decomposition and N mineralization) shifts in functional community structure could affect plants indirectly as well as directly (e.g., via an increase in plant parasites).

Putting them together - Ecological-evolutionary feedbacks

While it has been acknowledged that herbicide use can be viewed as an eco-evolutionary problem (Baucom 2019; Neve et al 2014), the focus has largely been on rapid evolution of herbicide-resistant weeds and on the ecological costs of this resistance in the absence of herbicide (Baucom 2019; **Evo-Eco**). Yet, it is now clear that herbicide use can induce plastic trait changes and transform entire ecological communities, thus multiple unpredictable eco-evo trajectories can result. Moreover, because these communities are complex and herbicides affect more than the intended primary producers there is need for a broader view of this evolution in a community context. We believe there is a need to explicitly consider herbicide impact via 1) cascading effects of evolution to the ecological interactions **(Evo-Eco-Evo)**, 2) plastic trait changes on ecology and evolution **(Eco-Evo-Eco)**, 3) shifts in community structure (**Eco & Evo**) that affect species interactions and evolution **(Eco/Evo-Eco-Evo)** and finally, 4) the interplay of these modified communities back to the evolution of the other interacting species (**Eco/Evo-Eco/Evo)**. By specifically considering all of the pathways within eco-evo dynamics (Figure 1), we can hope to formulate a more predictive view of the fates of herbicide-impacted communities.

Evolution changes Ecology: Cascading effects of resistance on species interactions--The evolution of herbicide resistance can have second-order effects on ecological interactions (Table 2; Fig 2) because expression of resistance genes directly affects these interactions or because resistance leads to trade-offs with other traits as a result of competing resource demands (e.g., Uesugi et al. 2017). For instance, relative to herbicide susceptible plants, resistant ones have metabolic changes (Vila-Aiub et al., 2019) that can affect their quality as hosts or partners in interspecific interactions. Indeed, resistant plants have been seen to have weaker competitive ability (Comont et al. 2019), increased susceptibility to herbivorous insects (Gassmann 2005), greater mortality when exposed to rust infection (Salzmann et al. 2008), and reduced floral biomass in the presence of herbivores (Gassmann & Futuyma 2005). Thus, in the context of complex communities, evolution of herbicide resistance could affect ecological interactions, such as competitive hierarchies and the outcome of other plant-antagonist interactions, in a multitude of ways that can feedback on trait evolution and reshape genetic architecture, as has been seen in other settings (Uesugi et al. 2017). Likewise, the correlated changes in traits of herbicide resistant plants can affect their interactions with mutualists. For instance, Atrazine resistant *Brassica rapa* produced significantly less pollen per flower and flowered later than atrazine susceptible plants (Bingham et al. 2017), which could potentially affect their interactions with pollinators. Likewise, shifts in flowering time (Wang et al 2010; Fig 4, Table S3) or traits associated with selfing (Kuester et al. 2017) can reduce availability of resources to pollinator communities leading to shifts in their visitation rates or diversity in ways that feedback on evolution of these floral traits. Indeed, changes in pollinator quantity and quality *via* loss of effective pollinators or phenological mismatches between plants and pollinators are main drivers of floral evolution and could occur rapidly in the highly disrupted pollinator communities of the agro-ecological interface (Knight et al. 2018).

Plasticity changes Ecology and facilitates Evolution-- Plastic responses to herbicides have been documented for several functional traits that mediate ecological interactions (Tables 1,2). While plasticity can be maladaptive (Hendry 2016), when the plasticity in a trait is in the direction favored by selection, it may facilitate adaptation to novel environments ('plasticity first' reviewed in Levis & Pfenning 2016). This is because plasticity in response to a novel stressor (e.g., herbicide) may uncover cryptic genetic 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 also affect the abundances or diversity of higher trophic levels and thus selection on traits associated with those interactions, such as herbivore defense or pollinator attraction.

Herbicide-mediated loss or gain of plant species can result in major changes in the plant community membership and thus add an evolutionary-driven (extinction and invasion) species composition-dependent dimension to the dynamics within these communities (i.e., terHorst et al. 2018, van Moorsel et al. 2019). Ecological interactions depend on the members of the community, and loss of those with niche constructing, non-redundant functions or specialized traits that make them keystone species (e.g., N fixing mutualisms, unique floral morphologies or rewards), will affect local interaction types, intensity and resulting selection (e.g., Biella et al. 2019; Gomez et al. 2009; Lankau & Strauss 2007). For instance, flower traits mediated the impact of species loss in co-flowering communities, because pollinator foraging decisions (and potentially selection) changed after removal of specific morphospecies (Biella et al. 2019). Likewise, invasion by *Medicago polymorpha* altered the strength and direction of selection on antiherbivore defenses, but not competitive ability, of a native *Lotus* (Lau 2008). Interestingly, the strength of effects also depended on the presence of herbivores (Lau 2008), reinforcing the importance of a holistic approach to eco-evo feedbacks. Thus, extinctions/invasions that result from repeated herbicide exposure can fundamentally feedback on the ecology and trait evolution of the interacting species. In some circumstances, evolution may even compensate for extreme species loss. For instance, van Moorsel et al. (2019) found that prolonged growth in monoculture led to an increase in within-species trait variation suggesting widening of intraspecific niche via character displacement.

Evolution feeds back and changes Evolution: Coevolution of two trophic levels-Anthropogenic impacts modify communities and can alter the quality of species interactions, leading to evolution and coevolution of the interactors within these communities. Coevolution of host-pathogen interactions may be modified by herbicide exposure because herbicide can affect levels of polymorphism in resistance and infectivity (Duke 2018; Feng et al. 2005), and thus affect trajectories of pathogen-plant arms races. Likewise, evolution may work to maintain, or restore disrupted mutualistic interactions (Gundel et al. 2012, Kiers 2010). For instance, herbicides could shift the quality of mutualistic interactions toward antagonism (changing the cost/benefit relationships of the partners), or threaten coextinction by dramatically reducing the population size of one partner. These changes could precipitate evolutionary shifts to reduce reliance on the declining partner or shifts in partner quality (Kiers et al. 2010; Veron et al. 2018). Herbicide dose has been seen to interact with plant genetic background to influence the expression of mutualism between endophytes and grass species, where the mutualism improved seedling survival at low but not high doses (Gundel 2012). Nevertheless, rhizobia or fungal endophytes may adapt rapidly and in novel ways to herbicide-altered plant phenotypes because their fitness depends on that of the holobont (Gundel 2012; Kiers et al. 2010). Likewise, in pollination mutualisms, plants may evolve towards use of abiotic pollen vectors (e.g., wind) or exclusive self-pollination when faced with poor biotic pollination service (Kaiser-Bunbury et al. 2010, Roels & Kelly 2009). Thus, herbicide-impacted communities may be subject to coevolutionary ‘rescue’ wherein coevolution between community members mitigates the impacts of ongoing anthropogenic disturbance by rewiring the network structure of the community in a way that compensates for the extinction of individual species and their interactions (Nusimer et al. 2019).

Conclusions, future goals and approaches

Herbicide use leads to some of the most well documented cases of rapid evolution (Palkovacs et al. 2012), but the cascading effects for ecological systems, especially in terms of community composition and quantity and quality of species interactions remain to be explored. Through this mini-synthesis we have shown that herbicides have the potential to transform communities and create eco-evo trajectories for multiple interacting trophic groups, but also that the multiple avenues for interaction in naturally complex communities make it difficult to predict net ecological effects of plant evolution and *vice versa*. As a way forward to assess the potential for eco-evo dynamics, we suggest that we need to start by characterizing several basic axes of variation in impacted natural communities, as well as to begin to conduct the types of manipulative experiments that specifically reveal impacts of ecology on evolution, evolution on ecology, and their feedbacks.

With respect to plants as the focal taxonomic level, there are multiple axes of variation that should be quantified in observational studies. First, the extent of within-population genetic variation in response to herbicides across coexisting plant species, and the extent of within-population genetic variation in plastic responses to non-lethal herbicide exposure. In both cases, the response should be measured in terms of a wide range of functional traits, especially those that may be genetically correlated with resistance, as well as those that mediate different types of ecological interactions (i.e., floral attraction, reward production, nodule traits, or leaf palatability or nutritional quality). Assessing resistance in natural settings will be key as resistance is not likely to be consistent across abiotic or biotic environments (e.g., Comont et al. 2019; Du et al. 2018). Levels of herbicide exposure should include sublethal doses, not just field application rates, because sublethal doses impose different strengths of selection which is experienced by the broad range of organisms at the agro-eco interface. In addition to functional traits, studies should explore the effect of herbicide exposure on variance in relative fitness (measured as seed production and seed siring success), because if herbicide exposure increases fitness variation, then it increases the opportunity for selection. For instance, fitness variance (the ‘opportunity for selection’) increases when populations are in decline (Reiss 2013). Likewise, studies should determine whether plastic responses to herbicides align with additive genetic variation and covariation for those phenotypes as this can increase the efficacy of selection (Nobel et al. 2019). Studies should characterize the ecologically-relevant linkages between direct effects of herbicides on plants, associated indirect effects on plant-dependent communities (i.e., pollinators, rhizobia, herbivores) and the potential direct effect on these communities, as well as determine whether herbicide exposure changes the net strength of existing ecological interactions. In all cases, an effort should be made to incorporate the totality of interactions which will inform on the potential for diffuse coevolution (De Meester 2019). Finally, studies should document plant community shifts in terms of species membership and evenness not only throughout the growing season as phenological shifts are common responses to herbicide, but also across years (Table 2, Figure 3, Table S1).

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

If selection experiments are conducted with numerous community members, then one can conduct a second type of experiment where the standing genetic variation in resistance is manipulated to explicitly assess the impacts of evolution on ecology. For instance, ecological interactions can be characterized for populations (or communities) inhabited with varying compositions of resistant or susceptible genotypes (i.e., products of previous selection experiments). Manipulating community composition in a crossed design with within-species resistance variation would allow one to assess the synergistic effect of species extinctions (or migrations) and resistance evolution on ecology of a focal species. Finally, resistant or susceptible plants could be compared when inhabiting artificial communities assembled to reflect foundational compositions or to reflect herbicide-shifted compositions. This would allow one to disentangle the direct effects of herbicide resistance from the community-contextual changes in species interactions.

It will also be important to determine if the mutualist partners evolve in response to herbicides directly or via plant evolution. It is possible that partners with fast generations times and large population sizes, like microbes, will evolve faster than plants in response to herbicides and could facilitate evolutionary rescue of the plant species (Bell 2017). Such experiments could involve artificial selection on microbes and assessment of plant fitness when in the presence of evolved or original microbial associates.

Finally, experiments that put a ‘break’ on evolution are recommended to assess feedback of evolution on ecology (Turcotte et al. 2013). Here, alongside a selection experiment (as above) where each generation is started with the most fit individuals from a prior generation, control populations are created wherein each generation the initial genotypes are used to repopulate the community, rather than those that have evolved in the previous generation. The effects of evolved populations on species interactions are then compared to those with initial populations. It is worth mentioning that all of these experiments should be conducted in accordance with state and local pesticide regulations, and with the utmost care to avoid escape of evolved organisms.

In conclusion, an eco-evo perspective provides a framework for understanding the impact of herbicides on evolution and ecology and their interaction on the same time scale. Thus, it will provide a better understanding of how these human-mediated disturbances are transforming species and community functions in real time.

Acknowledgements

This work was supported by NSF DEB-1834496 and USDA 2017-09529/1016564 to TLA and RB. VI was additionally supported by UPitt Dietrich School of Arts and Sciences Hot Metal Bridge and first year Fellowships.

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Author contributions

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

Tables and Figures

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).

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.

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 feedbacks 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.

Data accessibility

The data that support the findings of this study are available in the Supplemental Information in the online version of this article.

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Trait	Plastic/Genetic	Direction	Herbicide	Dose	Plant Species	Source
Biomass	genetic	decreased	sulfonylurea	field rates	*Lactuca serriola*	Alcocer-Ruthling et al. 1992
	plastic	decreased	2,4-D	sublethal	*Bupleurum rotundifolium, Scandix pecten-veneris subsp. pectenveneris, Neslia paniculata subsp. Thracica, 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

Anther length	plastic	reduced	glyphosate	drift	*Brassica rapa*	Baucom, Mauricio, & Chang 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	Salzmannet 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	-	-	-	-	-	-

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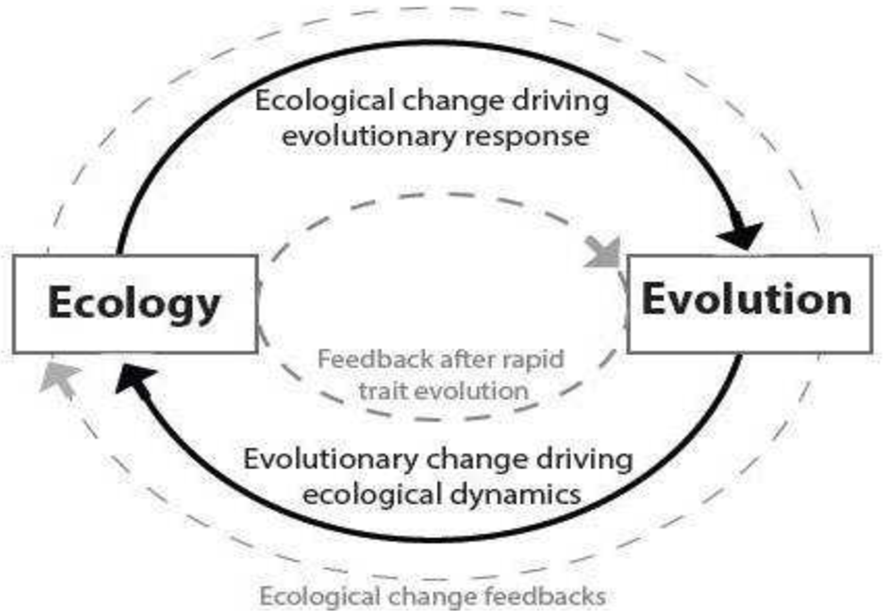

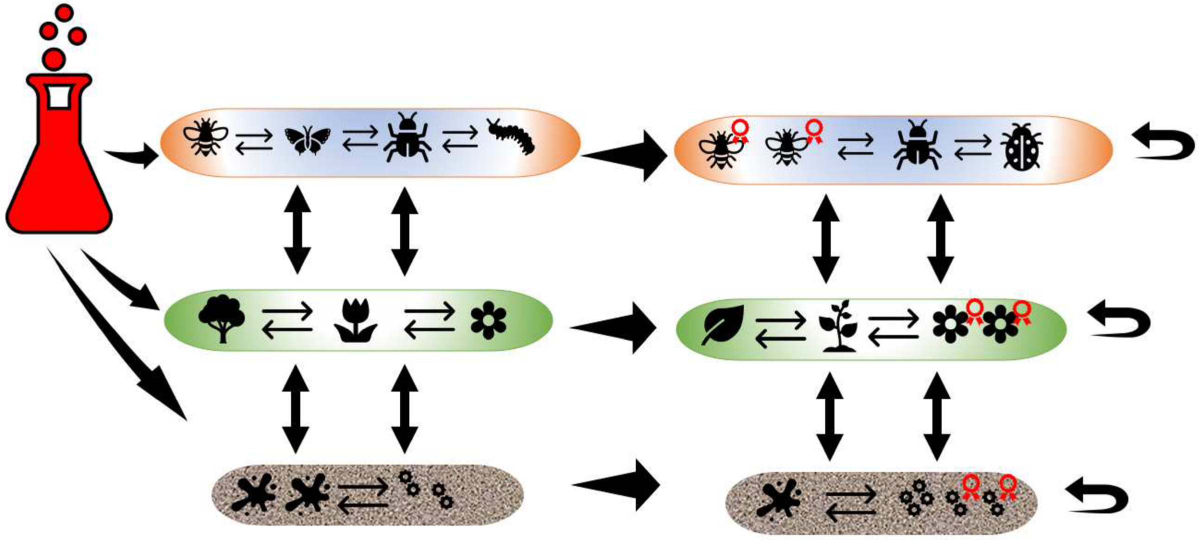

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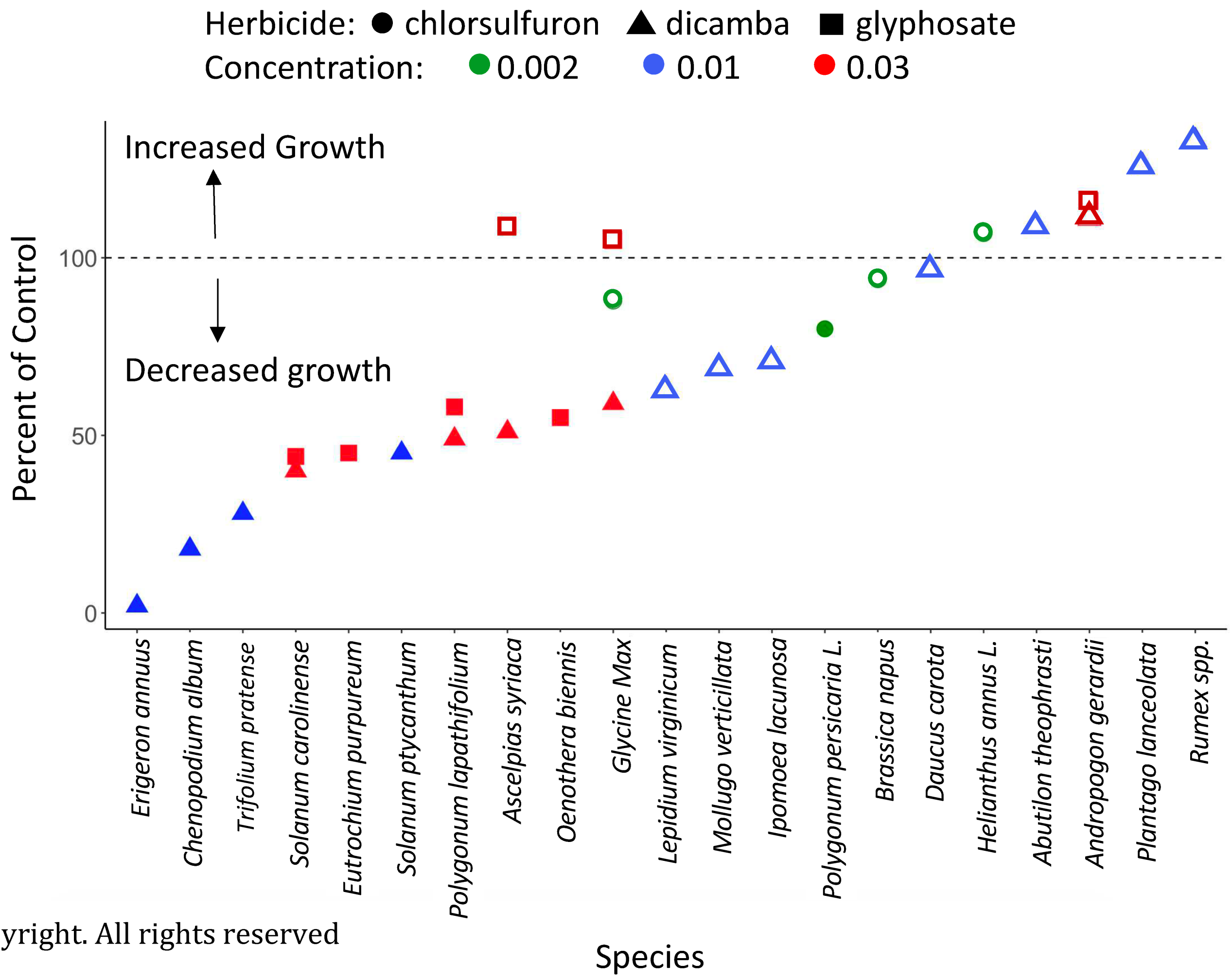

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