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## ARTICLE

## Agroecosystems

# Cereal rye mulch biomass and crop density affect weed suppression and community assembly in no-till planted soybean

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## Abstract

The use of multiple ecological weed management tactics may be an effective solution to weed management challenges associated with reducing tillage. An experiment was conducted to assess how soybean *Glycine max* (L.) Merr. density and cereal rye *Secale cereale* L. mulch biomass affected weed suppression and community assembly in no-till production. Soybean was planted at five rates from 0 to 74 seeds m<sup>-2</sup>, and five cereal rye mulch levels were established from 0 to 2 times the ambient cereal rye biomass within each site-year. We assessed the effects of soybean density and cereal rye mulch biomass on weed suppression, weed community composition, and the functional structure of weed life cycle, emergence timing, seed weight, height, and specific leaf area traits. Weed suppression was influenced by a synergistic interaction between soybean density and cereal rye biomass. The functional dispersion (FDis) of all weed traits, when combined, was reduced by increased soybean density and mulch biomass, suggesting that high treatment intensities induced trait convergence. However, soybean density and cereal rye biomass had differing effects on the FDis and composition of individual traits, suggesting that these management practices represent unique filters during weed community assembly. Mulch biomass had a larger effect on annual weed suppression and weed community composition than soybean density. Farmers who utilize high biomass cover crop mulch for weed management may experience shifts in weed community composition toward an increased proportion of perennials and weeds with later emergence, heavier seeds, and shorter stature. Increasing soybean density may reduce perennial weed biomass, making it a valuable complement to high cereal rye mulch biomass. As such, weed management in no-till soybean is enhanced by combining multiple practices, which can enable synergistic weed suppression and the management of diverse weed functional groups.

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**KEYWORDS**

agroecology, functional structure, *Glycine max*, multitactic weed management, *Secale cereale*, taxonomic diversity, weed traits

**INTRODUCTION**

No-till crop production requires less labor and fuel (Gozubuyuk et al., 2020; Swenson & Johnson, 1982), produces fewer greenhouse gas emissions (Mangalassery et al., 2014; Six et al., 2004), and promotes soil health (Nunes et al., 2018) relative to tillage-based crop production. However, weed management can be challenging without tillage, particularly in organic systems. In such cases, ecological weed management can facilitate successful crop production. Ecological weed management is based on an understanding of weed ecology and involves using cultural practices to modify the agroecosystem and create conditions that reduce weed abundance and weed-crop competition (Bastiaans et al., 2008). Using multiple practices that are weak in isolation but highly effective when combined is often called the “many little hammers” approach (Bastiaans et al., 2008; Liebman & Gallandt, 1997). Combining practices provides insurance if one practice fails and can result in synergistic interactions, where weed suppression is greater than expected based on suppression observed from each practice in isolation.

As with any approach to weed management, it is important to understand how cultural practices affect weed communities. Plant community diversity and structure metrics help evaluate management effects on weed communities. Taxonomic diversity metrics describe species richness and relative abundance, making them useful for quantifying changes in weed community composition and the competitive effects of weeds on crops. For example, weed communities with high species richness and evenness may be less suppressive to crop yield because they lack the dominance of highly competitive species (Adeux et al., 2019; Storkey & Neve, 2018). Functional structure metrics elaborate upon taxonomic diversity by describing changes in plant community trait attributes. A functional approach can elucidate the effects of agronomic practices on weed community composition (Booth & Swanton, 2002) and weed-crop competition (Bennett et al., 2016; Derrouch et al., 2021; Funk & Wolf, 2016; Pakeman et al., 2015). Analysis of functional metrics enables predictions of weed community responses to farm practices across diverse settings because the effect of agricultural practices on species traits is expected to be consistent across different species pools (Booth & Swanton, 2002). The

ability to predict weed community response to management practices can help farmers design systems that are less conducive to the proliferation of problematic weeds.

Community assembly theory can describe how cropping systems affect the functional structure of a weed community. Under this framework, geographic location, environmental conditions, and the internal dynamics of a system are filters that determine a plant community by allowing species with specific trait attributes to survive while filtering out those that do not meet a set of trait requirements (Booth & Swanton, 2002; Diamond, 1975; Weiher & Keddy, 1999). Agronomic practices filter weed communities because they impact the internal dynamics of a plant system, changing resource availability, biotic interactions, and habitat stability (Smith & Mortensen, 2017). Correspondingly, trait-based assessments of weed communities have found that management practices such as tillage (Derrouch et al., 2021; Smith, 2006), fertilizer application (Cordeau et al., 2021; Storkey et al., 2010), and herbicide use (Storkey et al., 2010) filter weed communities. Furthermore, past research has reported that management practices filter weed community traits with differing intensities (Légère et al., 2005; Ryan et al., 2010; Smith & Mortensen, 2017). Despite the understanding of how major management practices, such as tillage and herbicide use, affect weed community assembly, little is known about how cultural practices may function as weed community filters.

In no-till crop production, increasing crop density and the use of a high biomass cover crop mulch are two cultural weed management practices that may filter weed communities through changes in resource availability (Lowry & Smith, 2018). Dense crop stands hasten canopy closure (Schwinning & Weiner, 1998; Weiner, 1990) and reduce the amount of light available to weeds (Steckel & Sprague, 2004). Similarly, cover crop mulches suppress weeds by acting as a physical barrier (Teasdale & Mohler, 2000) and altering light (Teasdale & Mohler, 2000; Webster et al., 2016), temperature (Gauer et al., 1982; Teasdale & Mohler, 1993), water, and nutrient availability (Wells et al., 2013; Williams et al., 2018). Therefore, based on community assembly theory, we expect that changes in resource availability from increased crop density and mulch biomass should filter weeds based on traits determining light requirements, relative growth rates, and seed resources for emergence (Gaba et al., 2017). Confirmation of these

predictions would improve our ability to anticipate and direct shifts in weed communities when using increased crop density and high mulch biomass as a means of cultural weed management.

An experiment was conducted to assess the individual and interactive effects of soybean *Glycine max* (L.) Merr. density and cereal rye *Secale cereale* L. mulch biomass on weed suppression, community composition, and trait distribution in a no-till production system. In 2019, soybeans were the fourth largest crop in terms of global production area (Food and Agriculture Organization of the United Nations, 2021), and they can be grown profitably in organic no-till systems using a cereal rye mulch (Liebert & Ryan, 2017; Menalled et al., 2021). Using weed biomass data from this experiment, Ryan et al. (2011) reported a synergistic interaction between soybean seeding rate and mulch biomass on weed suppression. However, the individual and interactive effects of these two cultural practices on weed community taxonomic diversity and functional structure have not been examined. Understanding how weed communities respond taxonomically and functionally to increased soybean density and mulch biomass will encourage the adoption of organic no-till systems by enabling farmers to better anticipate shifts in weed communities arising from these practices. In this study, we assessed (1) weed suppression, community composition, taxonomic diversity, and functional structure across gradients of no-till planted soybean and cereal rye mulch, and (2) how each cultural management practice affects a set of weed traits.

## MATERIALS AND METHODS

### Study sites

The experiment was conducted across four site-years: the Beltsville Agricultural Research Center in Beltsville, MD, in 2008 and 2009 (MD 2008 and MD 2009, respectively), the Rodale Institute in Kutztown, PA, in 2008 (PA 2008), and the Russell E. Larson Agricultural Research Center in Rock Springs, PA, in 2009 (PA 2009). The experiment was conducted on a Matawan–Hammonton loam sand in MD 2008, a Codorus–Hatboro silt loam in MD 2009, a Berks shaley silt loam in PA 2008, and a Hagerstown silt loam in PA 2009. Across all sites, the soil pH was between 6.5 and 6.7.

### Experimental design

The experiment used a split-plot randomized complete block design with four blocks in each site-year. The main

plot factor was soybean density, and the split-plot factor was cereal rye mulch biomass. Cereal rye (cv. “Aroostook”) was seeded with a drill at 135–200 kg ha<sup>-1</sup> between October and December for each site-year. The following summer, the cover crop was terminated in early June using a haybine (New Holland 2450 in MD and John Deere 945 MoCo in PA) when the cereal rye was in the anthesis or early milk stage of development. Immediately after termination, cereal rye biomass was raked into windrows, and plots were demarcated between windrows using flags.

Mixtures of the common weeds collected in farms across Pennsylvania and Maryland were broadcast at a uniform rate to increase weed seedbank homogeneity and reduce within-site variation in the ambient weed seedbank, which could confound treatment effects. In MD 2008 and MD 2009, giant foxtail (*Setaria faberi* Herrm.) and smooth pigweed (*Amaranthus hybridus* L.) were broadcasted at 1000 seeds m<sup>-2</sup> species<sup>-1</sup>. The PA 2008 site received common ragweed (*Ambrosia artemisiifolia* L.), redroot pigweed (*Amaranthus retroflexus* L.), giant foxtail, and common lambsquarters (*Chenopodium album* L.) at 1000 seeds m<sup>-2</sup> species<sup>-1</sup>. In PA 2009, common ragweed, smooth pigweed, giant foxtail, common lambsquarters, and velvetleaf (*Abutilon theophrasti* Medik.) were broadcasted at 500, 350, 1000, 1000, and 150 seeds m<sup>-2</sup>, respectively.

Following weed seedbank supplementation, a drill seeder was calibrated to no-till plant at five rates (0, 19, 37, 56, and 74 seeds m<sup>-2</sup>) of rhizobium-inoculated feed-grade soybeans (Blue River 2A12, RM 1.9) into the rye stubble at a 19.05-cm row spacing. These seeding rates span recommendations for organic no-till planted feed-grade soybeans (52 seeds m<sup>-2</sup>; Menalled et al., 2021). After soybean planting, rye residue was manually spread back onto the plots to create a uniform mulch biomass gradient of 0, 0.5, 1, 1.5, and 2 times the ambient cereal rye biomass, which was between 600 and 1000 g of dried biomass m<sup>-2</sup> depending upon the site-year. Our experimental design resulted in 100 experimental units in each site-year (5 soybean density treatments × 5 mulch biomass treatments × 4 blocks). Experimental units were 3 × 4.6 m, except for in MD 2008, where the plot size was 3 × 3 m.

### Field data collection

Cereal rye biomass was quantified 1 week after soybean planting by removing cereal rye mulch in one 0.25-m<sup>2</sup> quadrat per experimental unit ( $n = 100$  site-year<sup>-1</sup>). Cereal rye biomass was dried at 50°C for 1 week before being weighed. Approximately 15 weeks after soybean planting, when most summer annual weeds were at physiological maturity, aboveground weed biomass was

clipped in one 0.5-m<sup>2</sup> quadrat per experimental unit. Soybean density was assessed concurrently by counting soybean plants in the quadrat. Weeds were sorted by individual species, oven-dried at 50°C for 1 week, and then weighed.

## Trait data collection and rationale

The life cycle (annual, biennial, or perennial), emergence timing (early spring, spring, or summer), seed weight (in milligrams), height at maturity (in centimeters), and specific leaf area (SLA; in square millimeters per milligram) of each weed species were used for the analysis of weed community functional structure. We extracted weed life cycle data from the BioFlor (Klotz et al., 2002) and USDA Plants databases (National Plant Data Team, 2021). Depending on regional observations, three emergence periods were considered: early spring, spring, and summer. Weeds classified as early spring emerging were those species that commonly emerged before mid-May; spring emergence was considered mid-May to mid-June; summer emerging weeds were exclusively warm-season annuals that emerged after mid-June. The majority of emergence data were collected from a weed field guide for the sampling region of this experiment (Uva et al., 1997). The emergence periods of 10 weed species were obtained from consultation with a weed botany expert (S. Morris, personal communication, 2021). Seed weight, height, and SLA were provided primarily by the TRY database (Kattge et al., 2011). All trait attribute data are accessible with source information in Appendix S1: Table S1.

Traits were selected to evaluate functional structure based on their importance for weed survival, growth, and reproduction in response to soybean density and cereal rye mulch biomass. Increased soybean density suppresses weeds through faster canopy closure (Schwinning & Weiner, 1998; Weiner, 1990) and greater light interception (Steckel & Sprague, 2004). Reduced light availability selects for increased leaf area (Colbach et al., 2020) and plant height (Colbach et al., 2020; Weinig, 2000). Short-lived annuals tend to display a greater ability to increase height in response to shading relative to longer-lived annuals and perennials, and might be promoted under dense soybean canopies (Colbach et al., 2020). Similarly, early-emerging weeds may be less affected by filtering from increased crop density because they can germinate and elongate before crop canopy closure. In a study of weed emergence with different mulches, physical interference was the primary mechanism by which mulches reduced weed emergence (Teasdale & Mohler, 2000). Weed emergence across several mulches increased with seed size (Bosy & Reader, 1995; Teasdale & Mohler, 2000), suggesting that greater seed

reserves may reduce the filtering effect of mulch biomass. Furthermore, weeds with larger seeds have more resources (Leishman & Westoby, 1994) and emergence force (Jensen et al., 1972), promoting higher emergence rates through mulches and justifying the analysis of seed weight.

## Weed suppression and diversity metrics

### Weed suppression

Total weed biomass, annual weed biomass, and perennial weed biomass across the soybean density and mulch biomass treatments were assessed to describe weed suppression.

### Taxonomic diversity

Pielou's evenness, Shannon's diversity, and species richness were calculated using the "vegan" package (Oksanen et al., 2020). Plant community evenness ( $J$ ) analyzes species relative abundance (Pielou, 1966) and describes community dominance (Ricotta & Avena, 2003). Pielou's evenness ( $J$ ) was calculated as:

$$J = \frac{H}{\ln s} \quad (1)$$

where  $H$  is the Shannon diversity index value, which quantifies the uncertainty of randomly sampling a given species in the community of interest, where  $s$  is the number of species or species richness (McCune & Grace, 2002). The Shannon diversity index was computed as:

$$H = - \sum_{i=1}^s p_i (\ln p_i) \quad (2)$$

where  $p_i$  is the relative biomass of species  $i$ , and  $s$  is the species richness.

### Functional structure

Community-weighted means (CWMs) and functional dispersion (FDis) were calculated with weighted species biomass and trait data using the "FD" package (Laliberté et al., 2014). Samples with no weed biomass ( $n = 73$  across all site-years) were excluded from CWM and FDis calculations because they contained no trait information.

Community-weighted means represent the expected trait value from a random sample within a community

and elucidate shifts in community functional composition (Garnier et al., 2004). In our analysis, the CWM of all traits were weighted by species biomass. The CWM of weed emergence was calculated by assessing the proportion of total weed biomass in each emergence group (i.e., early spring, spring, and summer) within each experimental unit.

Functional dispersion quantifies trait variability by assessing the mean distance of a trait or set of traits to the centroid of a plant community (Laliberté & Legendre, 2010). It accounts for species abundance by weighting trait distances and the plant community centroid by species biomass. For our analysis, the FDis of all traits and each individual trait was calculated from Gower dissimilarity matrices, which are a type of distance measure that accounts for continuous and categorical variables (Laliberté & Legendre, 2010).

## Statistical analysis

All analyses were conducted in R version 4.0.3 (R Core Team, 2020), and unless specified, all results were visualized with “ggplot2” (Wickham, 2016).

Weed suppression, taxonomic diversity, and functional structure metrics were described with generalized linear mixed-effects models fit with the “glmmTMB” package (Brooks et al., 2017). In each model, fixed effects were soybean density, cereal rye mulch biomass, and their interaction. Block was nested within site–year and modeled as a random intercept to account for the spatial variability between site–years and blocks. Differences in weed community composition arising from weed seedbank supplementation were also accounted for by treating site–year as a random intercept in all models. Furthermore, soybean seeding rate was nested within a block to account for the split-plot design. Each statistical model was fit with random slopes of differing complexities. In addition, the singular, additive, or interactive effect of soybean density and cereal rye mulch biomass was modeled as a random slope across site–years. The random slopes were considered to account for possible variation in soybean density and mulch biomass effects from differing growing conditions and soybean emergence across site–years.

Random slope models were compared by calculating their Akaike information criterion values and plotting their observed versus predicted values to select the best model. We only considered random slope models that converged to avoid model over-fitting and unstable results. Model assumptions were assessed by checking for multicollinearity with the “performance” package (Lüdtke et al., 2021) and plotting the simulated

residuals from the generalized linear mixed-effects models with the “DHARMA” package (Hartig, 2021). See the legend of Appendix S2: Figure S1 for a list of distribution families, link functions, and random slope terms used to model each response variable. After finding the best-fitting model, the effect of soybean density, mulch biomass, and their interaction was determined through type III likelihood-ratio tests using the “monet” package (Singmann, 2021). In all models, soybean density and mulch biomass values were scaled and centered.

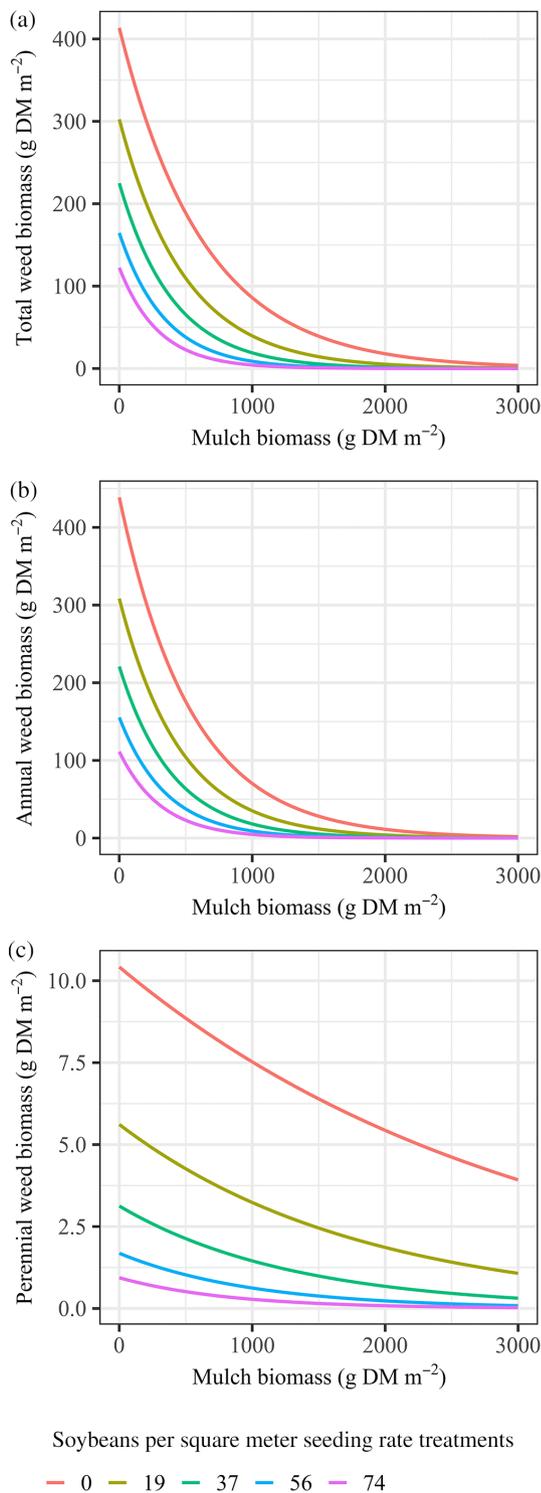
Analysis of weed community composition also included an assessment of weed species biomass across the experimental gradients, which was accomplished by partial redundancy analysis (pRDA). A pRDA is a multivariate analysis that depicts plant community responses to explanatory variables (McCune & Grace, 2002), showing which treatment gradients most affect species biomass. The pRDA models assessed log-transformed weed species biomass as a function of the additive and interactive effects of soybean density and cereal rye mulch biomass. Experimental site–years were modeled separately to account for local differences in weed seedbanks. Then, the pRDAs were tested through a permutation test where blocks and soybean seeding rates were constrained to account for the split-plot design of the experiment. All pRDAs were fit using the “vegan” package (Oksanen et al., 2020) and visualized with Canoco (ter Braak & Šmilauer, 2012).

## RESULTS

### Weed abundance and community composition

Total weed biomass was reduced by a positive interaction between increased soybean density and mulch biomass ( $p < 0.001$ ; Figure 1a), suggesting synergistic weed suppression when the two management practices were combined. However, soybean density and mulch biomass treatments had different effects on annual and perennial weed suppression (Figure 1b,c). Increased soybean density, greater mulch biomass, and the interaction between both treatments reduced annual weed biomass ( $p < 0.0001$ ,  $< 0.01$ , and  $< 0.05$ , respectively; Figure 1b), whereas perennial weed biomass was only reduced by increased soybean density ( $p < 0.0001$ ; Figure 1c).

A total of 59 weed species were identified across the four site–years. Soybean density only affected weed community composition in MD and PA during 2008 ( $p < 0.01$ ; Figure 2a). In contrast, mulch biomass affected weed community composition in all site–years ( $p < 0.005$ ; Figure 2). In all site–years, annuals often accounted for the most



**FIGURE 1** (a) Total, (b) annual, and (c) perennial weed dry matter (DM) biomass across cereal rye mulch biomass and soybean density gradients. All weed abundance models were Tweedie family generalized linear mixed-effects models with log link functions and had random slopes that allowed the relationship between mulch biomass and weed biomass to be different for each site-year (Appendix S2: Figure S1 panels a–c for observed vs. predicted values of the models; Appendix S2: Table S1 for  $p$ -values).

variability in weed community composition across treatment gradients (Figure 2). *Cyperus esculentus* L. in MD 2008 and *Taraxacum officinale* (L.) Weber ex F.H.Wigg. in PA 2009 were the only perennial weeds to be in the five species that accounted for the largest percentage of variation in weed biomass across treatments (Figure 2a,d).

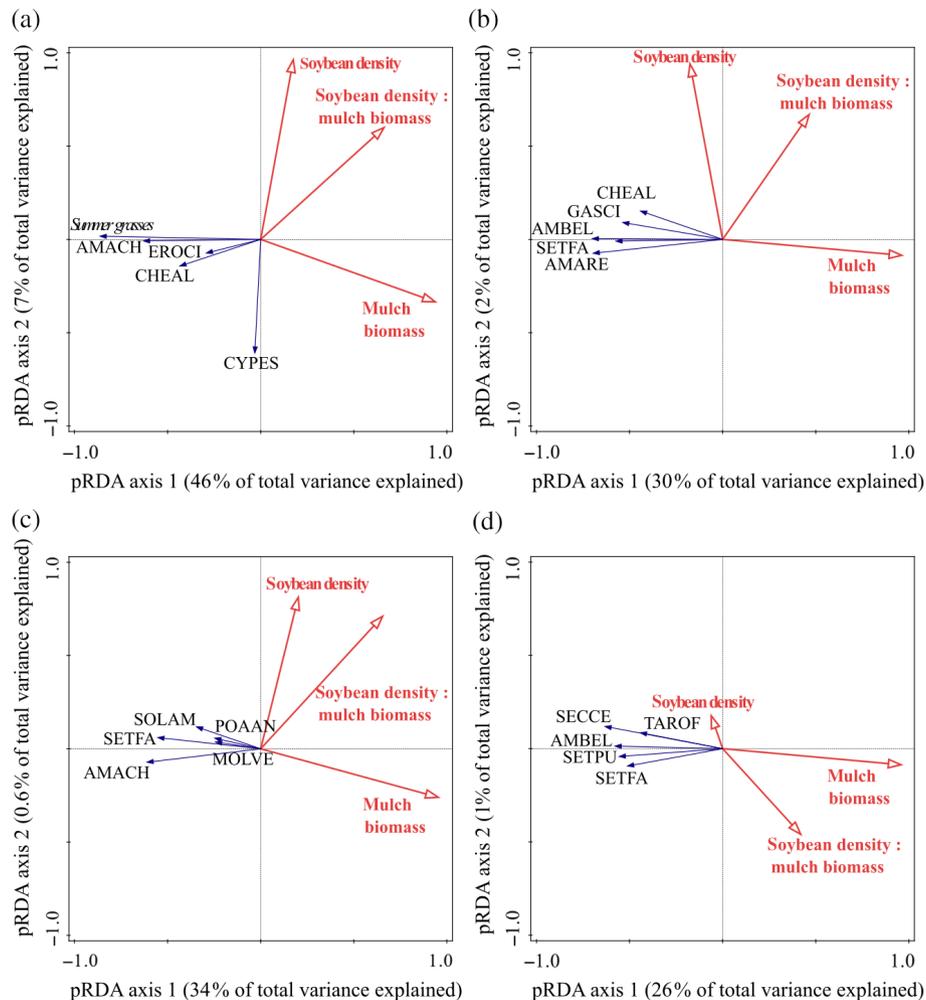
## Taxonomic diversity

Taxonomic diversity metrics were affected by the two cultural management treatments. Increasing soybean density, greater mulch biomass, and a positive interaction between treatments reduced weed community evenness ( $p < 0.005$ , 0.0001, and 0.01, respectively; Figure 3a). Species richness was also reduced by increased soybean density ( $p < 0.005$ ; Figure 3b) and cereal rye mulch biomass ( $p < 0.0001$ ). However, there were no interactive effects of the two treatments on species richness ( $p = 0.10$ ). When changes in species richness across 2 SD above and below mean soybean density and mulch biomass were compared, mulch biomass variation resulted in an 86% greater reduction in species richness than soybean density. The larger impact of mulch biomass, compared with soybean density, on species richness was even clearer in the case of the Shannon diversity of weed communities, which was only reduced by mulch biomass ( $p < 0.0001$ ; Figure 3c).

## Functional structure

The FDis of all traits, when considered together, was reduced by increased soybean density and cereal rye mulch biomass ( $p < 0.005$  and 0.0001, respectively; Table 1). Soybean density and mulch biomass effects on FDis were not mediated by an interaction between the two treatments ( $p = 0.09$ ). Compared with soybean density, 2 SD of mulch biomass variation above and below the treatment mean resulted in a 68% greater reduction in the FDis of all traits taken together, indicating that mulch biomass had a greater effect on weed trait dispersion than soybean density.

Gradients of soybean seeding density and mulch biomass had differing effects on the FDis and composition of individual traits. Mulch biomass reduced weed seed weight FDis ( $p < 0.0005$ ; Table 1), increasing the prevalence of heavier seeds at higher mulch biomass ( $p < 0.0001$ ; Figure 4a). Similarly, increased mulch biomass reduced the FDis of weed emergence ( $p < 0.0001$ ; Table 1). However, across the three emergence groups, mulch biomass only affected the CWM of early-emerging weeds (Appendix S2: Table S1), which



**FIGURE 2** Partial redundancy analysis (pRDA) highlighting weed community response to soybean density, mulch biomass, and their interaction in (a) MD 2008, (b) PA 2008, (c) MD 2009, and (d) PA 2009, after parsing out the effect of experimental blocks. All weeds were used for the pRDAs; the weeds labeled in the ordinations are the five species that accounted for the largest percentage of variation in weed biomass across treatments (Appendix S2: Table S2 for  $p$ -values). Species are named by their EPPO codes (EPPO, 2022). In MD 2008, *Digitaria sanguinalis* (L.) Scop., *Echinochola crus-galli* (L.) Beauv., *Setaria viridis* (L.) Beauv., and *Setaria faberi* Herrm. were not separated during sampling and were analyzed as “summer grasses” in this site-year.

decreased at greater mulch biomass ( $p < 0.0005$ ; Figure 4b). While weed height FDis was only affected by mulch biomass ( $p < 0.0001$ ; Table 1), only soybean density affected the CWM of weed height ( $p < 0.05$ ; Figure 4c). Conversely, while increased mulch biomass reduced the FDis of weed SLA ( $p < 0.0001$ ; Table 1), neither treatment affected the CWM of weed SLA (Figure 4d).

## DISCUSSION

### Cultural management effects on weed abundance and taxonomic diversity

While high soybean density and cereal rye mulch biomass reduced total weed biomass, the two treatments had a

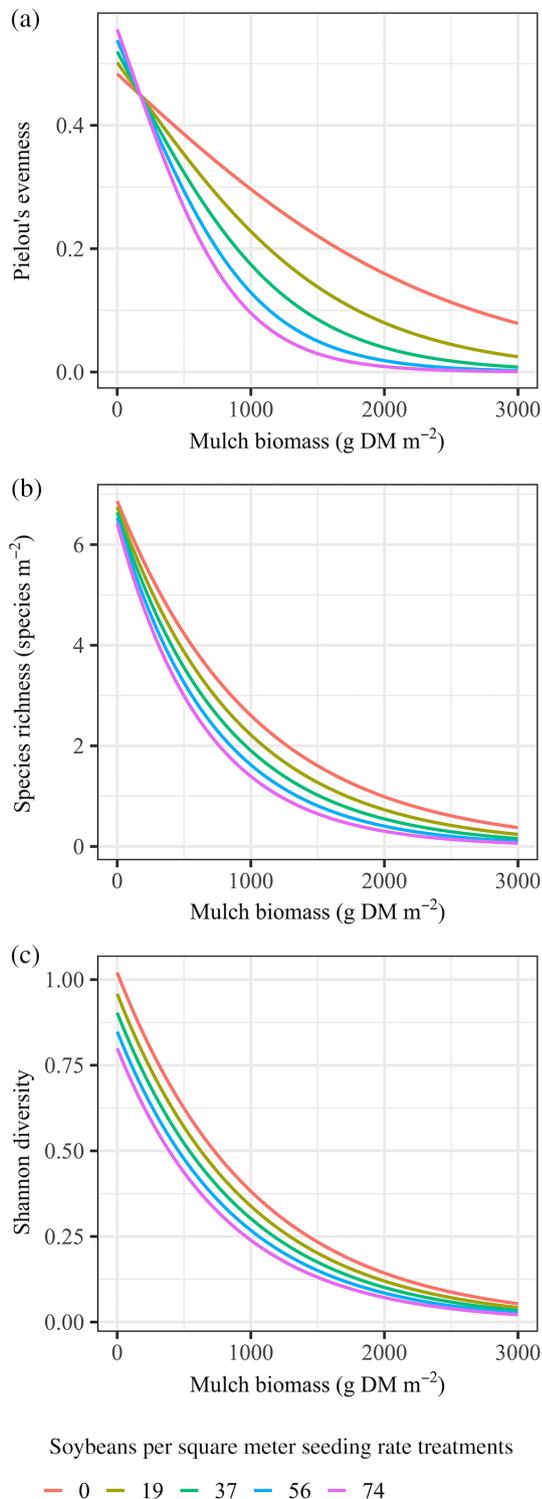
differing impact on annual and perennial weeds. As reported in Ryan et al. (2011), there was a positive interaction between the two management practices, suggesting synergistic weed suppression (Figure 1a). However, while both treatments suppressed annual weeds (Figure 1b), only soybean density affected perennial weed biomass (Figure 1c). The primary mechanism by which mulches reduce weed emergence is physical interference (Teasdale & Mohler, 2000), selecting species with more emergence resources (Bosy & Reader, 1995; Teasdale & Mohler, 2000). The lack of a mulch biomass effect on perennial weed abundance may have stemmed from the fact that perennial weeds can emerge from vegetative structures with high amounts of stored resources (Figure 1c). Conversely, increased crop planting density promotes weed suppression through more intense crop resource interference (Jordan, 1993; Steckel & Sprague, 2004; Weiner et al., 2001)

and may suppress weeds regardless of their emergence ability through mulches.

Focusing on the dominant perennial weed at each site–year illustrates the differing effects of mulch biomass and soybean density on perennial weed suppression. The dominant perennial weed was *C. esculentus* ( $60.6 \text{ g m}^{-2}$ ), *Trifolium pratense* L. and *Trifolium repens* L. (combined average biomass of  $0.245 \text{ g m}^{-2}$ ),

*Calystegia sepium* (L.) R.Br. ( $15.5 \text{ g m}^{-2}$ ), and *T. officinale* ( $0.747 \text{ g m}^{-2}$ ) at MD 2008, MD 2009, PA 2008, and PA 2009, respectively. The *Trifolium* spp. in MD 2009 was unaffected by mulch biomass or soybean density. However, of the three other dominant perennials, increased mulch biomass only suppressed *T. officinale*. Specifically, between the lowest ( $0 \times$  ambient) and highest ( $2 \times$  ambient) mulch biomass treatment levels, *C. esculentus* and *C. sepium* experienced a threefold increase in mean biomass, and *T. officinale* was completely suppressed. The suppression of *T. officinale* but not *C. esculentus* or *C. sepium* may be due to the reproductive strategy of these species. Of the three perennials, *T. officinale* is the only species that reproduces mainly by seed (Uva et al., 1997) and, consequently, has a higher probability of being susceptible to physical weed suppression from mulches. Conversely, between the lowest ( $0 \text{ seeds m}^{-2}$ ) and highest ( $74 \text{ seeds m}^{-2}$ ) soybean density treatments, *C. esculentus*, *C. sepium*, and *T. officinale* experienced a 4-, 1-, and 10-fold reduction in average biomass in MD 2008, PA 2008, and PA 2009, respectively. Thus, while high mulch biomass is an effective tool to reduce annual weeds, increasing crop density may be a more consistent driver of perennial weed suppression—particularly when these weeds can reproduce through vegetative structures.

While both management treatments exerted suppressive effects on total weed biomass (Figure 1), soybean density affected weed community composition in only two site–years (Figure 2a,b). Inconsistent soybean density effects on weed communities suggest that cereal rye mulch biomass, which affected pRDAs at all site–years, is a stronger driver of weed community composition. Differences in weed community composition across the management gradients were primarily associated with the effect of mulch biomass and soybean density on annual weed species (Figure 2). Weed species that responded to the mulch biomass and soybean



**FIGURE 3** (a) Pielou's evenness, (b) weed species richness (in number of species per square meter), and (c) Shannon's diversity of weed communities across cereal rye mulch dry matter (DM) biomass and soybean density treatments. Pielou's evenness was modeled with a beta distribution and a log link function. The species richness model had a Poisson distribution, accounted for zero inflation in the fixed effects, and had a logit link function. Shannon's diversity was modeled with a log-linked Gaussian distribution. All three of these diversity metrics were modeled without random slope terms (Appendix S2: Figure S1 panels d–f for an assessment of model fit; Appendix S2: Table S1 for  $p$ -values).

**TABLE 1** Functional dispersion of weed traits.

Effect	Scaled parameter	$\chi^2$	<i>p</i>
All traits			
Soybean density	−0.21	9.94	0.002
Mulch biomass	−0.60	51.38	<0.0001
Soybean density × Mulch biomass	−0.16	2.92	0.09
Life cycle			
Soybean density	−0.33	2.7	0.1
Mulch biomass	−0.28	1.12	0.29
Soybean density × Mulch biomass	−0.26	0.81	0.37
Seed weight			
Soybean density	−0.21	2.26	0.13
Mulch biomass	−0.58	14.35	0.0002
Soybean density × Mulch biomass	−0.23	2.35	0.13
Emergence			
Soybean density	−0.17	1.23	0.27
Mulch biomass	−0.99	30.58	<0.0001
Soybean density × Mulch biomass	−0.05	0.05	0.82
Height at maturity			
Soybean density	−0.11	1.67	0.2
Mulch biomass	−0.47	20.62	<0.0001
Soybean density × Mulch biomass	−0.07	0.37	0.55
Specific leaf area			
Soybean density	−0.13	2.77	0.1
Mulch biomass	−0.68	49.94	<0.0001
Soybean density × Mulch biomass	−0.02	0.02	0.88

Note: No models had random slope terms, and except for seed weight, all variables were modeled with a log-linked Tweedie distribution. The functional dispersion of seed weight was modeled with a Gaussian distribution. For an assessment of model fit, observed versus predicted values were plotted (Appendix S2: Figure S1 panels g–l).

density gradients varied across site–years (Figure 2), likely due to differences in local weed seedbanks.

In contrast to species composition, both soybean density and mulch biomass decreased weed community evenness and species richness (Figure 3a,b). Thus, while weed community composition was more responsive to the mulch gradient, both high soybean density and mulch biomass increased weed species dominance. Increased dominance in the weed communities along treatment gradients indicates that high soybean density and mulch biomass filtered weed

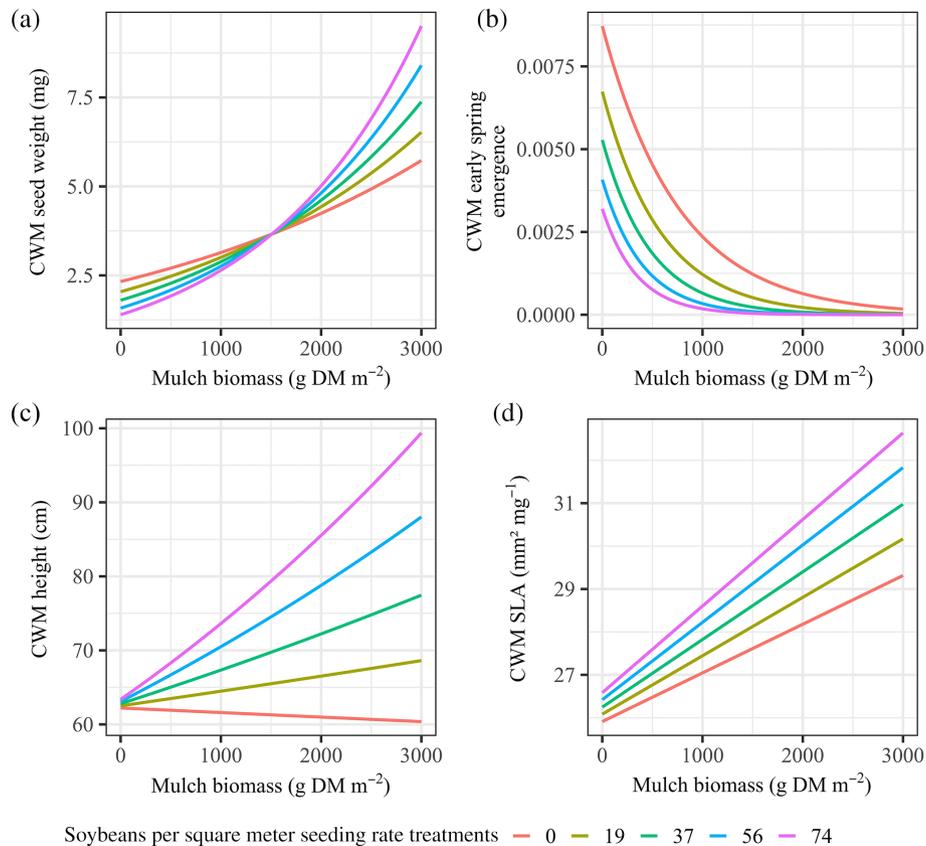
species with unfavorable traits during community assembly. Analysis of weed functional structure across the soybean density and mulch biomass gradients further elaborates upon changes in weed community dominance by elucidating how the two weed management practices affected weed traits.

## Cultural management effects on weed community functional structure

Increased soybean density and mulch biomass constrained trait dispersion and shifted weed community functional composition. A reduction in FDis implies a reduction in trait variability between species in a community and hence the selection of weed species with adapted trait values. For instance, similar to our finding that soybean density and mulch biomass constrained weed community FDis, pesticides can reduce the FDis of multiple traits within weed seedbanks (Rotchés-Ribalta et al., 2020). The reduction in weed trait FDis from both ecological and conventional practices indicates that weed management can filter weed communities by constraining trait variability. Changes in the CWM of plant community are another sign of trait filtering. Past CWM analyses have found that reducing tillage can lower weed seed weight (Armengot et al., 2016; Hernández Plaza et al., 2015), and increase time until germination (Alarcón Villora et al., 2019) and flowering (Armengot et al., 2016). Shifts in the CWM of weed trait suggest that the efficacy of management practices varies across weed functional groups as some weeds are filtered out of the community, while others are resistant to the management.

In this experiment, mulch biomass had a greater effect on the FDis of all weed traits assessed together compared with soybean density (Table 1). Likewise, soybean density did not affect the FDis of any trait, when considered individually. The greater effect of mulch biomass on weed community trait dispersion aligns with past research, suggesting that management practices vary in their strength as community assembly filters (Légère et al., 2005; Ryan et al., 2010). Our work builds upon this knowledge because it shows that management practices filter weed trait FDis to differing extents during community assembly.

When soybean density or mulch biomass affected both FDis and CWM of single traits, FDis and composition shifted across the treatment gradient. Increased mulch biomass reduced the FDis of seed weight but increased this trait's CWM value. The reduction in seed weight FDis (Table 1) suggests that increased mulch biomass resulted in less seed weight variability. Subsequently, larger seed weight CWM values at higher mulch biomass (Figure 4a) show that increased mulch biomass filters species with



**FIGURE 4** Community-weighted means of weed (a) seed weight, (b) early spring emergence probability, (c) height, and (d) specific leaf area (SLA) across cereal rye mulch dry matter (DM) biomass and soybean density. The seed weight model had a Gaussian distribution, a log link function, and no random slopes. The proportion of weeds with early spring emergence was also modeled without random slopes but had a log-linked Tweedie distribution. In the weed height and SLA models, mulch biomass was a random slope within site-years. The weed height model had a gamma distribution and a log link function, and the SLA model had a Gaussian distribution without a link function. All community-weighted mean (CWM) models were assessed by plotting fitted and observed values (Appendix S2: Figure S1 panels m–r; Appendix S2: Table S1 for *p*-values).

light seeds out of weed communities. Species with heavy seeds may be resistant to high mulch biomass because they have more resources (Leishman & Westoby, 1994), greater emergence force (Jensen et al., 1972), and lower susceptibility to allelopathy (Putnam & DeFrank, 1983) than lighter-seeded species. Increased mulch biomass also constrained the FDis of weed emergence (Table 1) and reduced the proportion of early-emerging weeds in the sampled communities (Figure 4b). Suppression of early-emerging weeds is essential for successful weed management in summer annual crops (Nord et al., 2012) because weeds that establish before crops can be aggressive competitors (Swanton et al., 2015). The absence of a mulch effect on the CWM of later emerging weeds (Appendix S2: Table S1) may have resulted from the degradation of the mulch, which is supported by past research that reports diminishing mulch effects on weed emergence across the growing season (Jodaugienė et al., 2006). Furthermore, mulches lower soil temperature and increase soil moisture

(Gauer et al., 1982; Teasdale & Mohler, 1993). Under the mulched treatments, soil conditions during the early spring may have been too cold for many early-emerging weeds.

Weed management can also filter plant functional structure through distinct effects on FDis and CWM (Schellenberger Costa et al., 2017). In our study, the FDis but not CWM of weed SLA (Table 1) was affected by mulch biomass (Figure 4d). A mulch biomass effect on the FDis but not CWM of weed community SLA indicates trait filtering toward the same CWM value along the mulch biomass gradient. Conversely, soybean density affected the CWM of weed height (Figure 4c) but not FDis (Table 1). Therefore, greater soybean density increased mean weed height but did not affect the dispersion of weed height values. The increase in the CWM of weed height along the soybean density gradient suggests that tall weeds are more likely to escape the filtering effect of shading from a dense crop canopy. Broadly, opposing FDis and CWM trends indicate that

management filters can have differing effects on trait dispersion and composition during weed community assembly.

## CONCLUSIONS

Reduced resource availability and increased physical interference from high soybean density and mulch biomass decreased the biomass and taxonomic diversity of agronomic weeds. The FDis of all weed traits, when considered together, was also reduced by increased soybean density and mulch biomass. However, the two management gradients had differing effects on the FDis and composition of individual traits. Often, mulch biomass had larger effects on the FDis and CWM of individual traits than soybean density, confirming that management practices are unique filters of differing importance during weed community assembly. Yet, change in a trait's FDis did not always correspond to shifts in its CWM value, suggesting that cultural weed management has variable effects on the functional structure of a weed community.

In an applied context, our results show that the combination of two cultural weed management practices led to a synergistic interaction and suppressed weeds with differing functional attributes. Increasing mulch biomass had a larger effect on annual weed suppression and weed community composition than soybean density. However, increased mulch biomass did not suppress perennial weeds and selected later emerging species with heavier seeds and shorter stature. On the contrary, increased soybean density reduced perennial weed biomass. Used as part of an integrated weed management approach, increasing soybean density can complement the use of high mulch biomass and decrease the probability of perennial species dominance, which is particularly important for successful organic no-till production. Future research should test the effects of additional combinations of cultural practices on weed suppression and community assembly. Furthermore, predictive power may be enhanced by collecting trait data rather than relying on trait databases (Chen et al., 2019; Siefert, 2012). Considering that trait-based analyses are generalizable beyond the ecological species pool in their underlying experiment (Booth & Swanton, 2002; Garnier & Navas, 2012), the information from this research and the proposed work is relevant to farmers in varied locations and production systems.

## AUTHOR CONTRIBUTIONS

Uriel D. Menalled, Guillaume Adeux, Stéphane Cordeau, Richard G. Smith, and Matthew R. Ryan conceived the ideas. Steven B. Mirsky and Matthew R. Ryan collected the

data. Uriel D. Menalled, Guillaume Adeux, and Stéphane Cordeau analyzed the data. Uriel D. Menalled led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Menalled et al., 2022) are available at the Cornell University eCommons Repository: <https://doi.org/10.7298/6s0s-gq43>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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