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RESEARCH ARTICLE

Microplastics favor forbs over grasses in drylands: Opposing roles of particulates and chemical leachates on germination and plant traits

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Abstract

Background and aims Drylands face increasing microplastic pollution. We tested how plastic particulates and leachable chemicals affect key dryland plants (grasses and forbs).

Methods We performed two controlled experiments using dryland grasses and forbs, and evaluated the effect of plastic particulates and leachables on germination, plant morphological and physiological traits.

Results Plastic particulates reduced grasses germination velocity by ~ 17% compared to soils without particulates, likely by trapping seeds and impairing water uptake. Most forbs were marginally affected, although germination was inhibited in mucilage-producing species. Notably, leachates stimulated forbs germination through hormesis, contrasting with particulates physical inhibition. For instance, *E. vulgare* velocity increased by ~ 20% with leachates than without them. However, this stimulation was transient and faded in later development. Grasses shoot mass decreased by ~ 21% with particulates, likely from soil water loss via plastic-induced cracks, an effect exacerbated by their shallow root systems. Forbs avoided this stress through deeper rooting and benefited from improved soil aeration, which enhanced shoot growth by ~ 61% compared to control. Grasses allocated carbon to stress tolerance, increasing photosynthetic rates (+ 15%) and water-use efficiency (+ 7.2%). Forbs favored shoot growth despite lower photosynthetis (-8.1%) and water-use efficiency (-25%), using thinner leaves and higher transpiration rates. Root morphology also critically influence tolerance to microplastics. The divergent particulate effects on grasses and forbs, reveal a mechanistic trade-off between stress tolerance and growth investment.

Conclusion Microplastic particulates, more than leachates, drive plant responses, suggesting that plastic pollution may act as environmental filter by favoring stress-adapted forbs over grasses.

Keywords Environmental filter · Germination · Priming effects · Hormesis · Leachates · Pollution · Plant community traits · Toxicity

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Introduction

Drylands, which span approximately two-fifths of the planet's land area are home to 38% of the global population (Reynolds et al. 2007), are among the largest and most sensitive ecosystems to global change and human activities (Maestre et al. 2016). These ecosystems are increasingly threatened by a range of global change factors, among which a newly identified concern has emerged: microplastic pollution (Bernhardt et al. 2017). Microplastics, defined as plastic particulates smaller than 5 mm, enter soils via multiple routes, such as agricultural amendments, water irrigation, flood events, airborne particles deposition, and plastic mulch applications (Rochman et al. 2019). In dryland ecosystems, agricultural plastic films, such as mulches and temporary greenhouses, are particularly significant sources of microplastic pollution (FAO 2021). The high temperatures and intense solar radiation characteristic of drylands accelerate the breakdown of plastic debris into plastic particulates, leading to widespread ecosystem contamination.

Microplastics impact soil properties, germination processes, and plant development through multiple mechanisms. On one hand, plastic particulates may act as physical agents, potentially enhancing soil porosity and facilitating root system development, thereby improving nutrient uptake and plant growth (Lozano et al. 2024a). On the other hand, toxic chemicals can leach from microplastics, rapidly altering soil chemical and biological properties and negatively affecting plant development (Boots et al. 2023; Lozano et al. 2024a). Evidence suggests that plastic leachates have the strongest influence on soil properties, while plastic particulates primarily affect seed germination and individual plant performance (Lozano et al. 2024a, 2025). However, microplastic effects on seed germination of species from different plant functional groups and on plant communities performance remain poorly understood. Preliminary studies suggest that microplastics may favor certain species while may disadvantage others, potentially altering community evenness (Lozano and Rillig 2020; Lozano et al. 2025).

Critically, such shifts in plant community composition would mirror patterns observed under other global change drivers (Maestre et al. 2016; Speißer et al. 2022). For example, nitrogen deposition enhances biomass of grasses while reducing biomass of forbs (Li et al. 2014; You et al. 2017), and drought may select for grasses with finer root systems to optimize water and nutrient acquisition (Tjoelker et al. 2005; Comas et al. 2013; Lozano et al. 2020a), or for forbs with thicker root systems in deeper soil layers that depend on mycorrhiza fungi for nutrient and water uptake. Like these global change drivers, microplastics could act as an environmental filter shifting plant community composition by disrupting key soil properties. For example, they may modify soil pH levels and microbial activity (Zhao et al. 2021), reduce the diversity of mutualistic soil fungi (Lozano et al. 2024b), and disrupt soil-plant-water relations (de Souza Machado et al. 2019). Dryland plant communities are highly sensitive to changes in these specific factors (e.g., Maestre et al. 2015; Bradford et al. 2020; Gomez-Gomez et al. 2022; Zhou et al. 2024), suggesting that microplastic pollution could significantly alter their structure and function. Indeed, such alterations would likely be driven by divergent responses of key plant functional groups. Specifically, microplastics may act as a strong environmental filter by exacerbating water stress (Wan et al. 2019), a primary constraint in drylands. This would disproportionately impact shallow-rooted grasses, potentially reducing their biomass and survival. By contrast, deep-rooted forbs, which are often more stress-adapted, could avoid this water limitation and may even benefit from improved soil aeration caused by plastic particulates. Therefore, the interplay between microplastics and soil properties would be not uniform; it could shift competitive outcomes by favoring forb strategies (e.g., growth investment, deeper roots) over grass strategies (e.g., water-use efficiency, shallow roots), thereby restructuring the plant community.

Based on this, we hypothesized that microplastics would differentially affect the germination and performance of dryland grasses and forbs, through distinct physical (particulates), and chemical (leachates) pathways. Specifically, we aimed to i) identify the primary driver (particulates or leachates) of germination and performance responses in grass and forb species, and ii) determine key tolerance strategies of grasses and forbs to microplastic pollution. To test this, we exposed seeds and seedlings of three grass and three forb species to particulate plastic films and their chemical leachates in a controlled experiment. We measured seed germination, plant biomass,

shoot and root morphological traits, key physiological parameters, and relevant soil properties such as soil aggregation and respiration.

Materials and methods

Plant species selection

We chose three grasses (*Bromus rubens L.*, *Lagurus ovatus L.* and *Lolium rigidum Gaudin.*), and three forb species (*Echium vulgare L.*, *Malva sylvestris L. and Plantago lanceolata L.*) native from Eurasian drylands (Pugnaire and Lazaro 2000; Lozano et al. 2020b) which were used in the seed germination and plant community experiments. Seeds were procured from local commercial suppliers (Semillas Silvestres and Cantueso, Córdoba, Spain).

Microplastic preparation

Low density polyethylene (PE) plastic film (silo film black, Folien-bernhardt, thickness: 0.07 mm) was ground into particulates with an upper size threshold of < 1.0 mm^2 and subjected to controlled UV-C degradation (254 nm) in a photodegradation chamber with an average incident irradiance of 20.98 W•m^{-2} (photometer; item number HD 2302.0, DeltaOHM). Microplastic films were photodegraded for 2 weeks and their positions were adjusted twice during the experiment (See details in Lozano et al. (2023)).

To extract water-soluble leachates (hereafter referred to as "leachates") from microplastic films, we followed a method outlined by Lozano et al. (2024a). Microplastics (0.84 g) were mixed with 50 ml of distilled water in a 60 ml syringe, ensuring that air pockets were eliminated. The syringes were sealed with parafilm, shaken up and down ten times, and then vortexed for five seconds. Syringes were incubated horizontally for 16 days at 40 °C. This temperature was selected because it is commonly achievable in dryland soils. Control samples containing only distilled water were incubated under identical conditions. Post-incubation, all solutions were filtered using sterile single-use syringe filters (pore size 0.45 µm, Carl Roth, GmbH, Germany) to collect the "microplastic leachates." The residual microplastic in the syringe was triple-rinsed with distilled water to ensure the removal of all water-extractable leachates, resulting in two microplastic treatments: "leachates (L)" and "particulates (P)". Given potential additive leaching during experimentation (Kim et al. 2020), our reported leachate effects may represent conservative estimates. Similarly, the observed impact of plastic particulates could potentially include minor toxic effects from leachates. Chemical characterization of leachates was performed using untargeted liquid chromatography-mass spectrometry (LC–MS) (Appendix 1). Further details on the LC–MS procedure, data processing, and detected levels of chemical compounds and heavy metals in microplastic leachates can be found in Lozano et al. (2025).

Soil preparation

Loamy soil from a dryland located in the Experimental Station “La Hoya” was collected in Almería, Spain (36° 50′ N, 2° 28′ O). Soil was air-dried, sieved (4 mm), homogenized, and autoclaved twice (121 °C, 20 min) with 24-h intervals to ensure seed bank elimination. Soil was mixed with sterile sand in a 1:1 volume ratio to prevent compaction (from now on, soil). For the seed germination experiment, a layer of 500 g of sterile sand (bottom) + 300 g of soil (top) was placed into pots (13 cm diameter × 11 cm height but filled up to 9 cm height, ca. 1500 ml) and watered until saturation. Then, an additional layer of 0.84 g of microplastic film mixed into 210 g of soil (0.4% w/w) was added for each pot. For the plant community experiment, a layer of 350 g of sterile sand (bottom) + 1000 g of soil (top) was placed into pots (ca. 17 cm diameter, 12.5 cm height, ca. 3000 ml) and watered until saturation. An additional layer of 1000 g soil mixed with 4 g microplastics (0.4% w/w) was added to each pot. Soil was prepared individually for each pot to ensure uniform microplastic distribution. Microplastics were mixed with soil for 1 min in a large container before potting. Control pots were prepared identically but without microplastic addition to account for soil disturbance effects.

Experimental design

In 2023, we established the seed germination and the plant community experiments under controlled conditions: 22 °C day/16 °C night temperatures, 60% relative humidity, and 12-h photoperiod. To disentangle the physical effects of microplastic particulates from

the chemical effects of their leachates on germination and growth performance of grasses and forbs, four microplastic treatments were established: soil mixed with films free of leachates was watered with i) distilled water (*plastic particulates treatment, (P)*); or ii) leachates (*leachates + plastic particulates treatment (L + P)*). Likewise, soil without added films was watered with iii) distilled water (*control treatment (C)*) or iv) leachates (*leachates treatment (L)*). Pots received 50 mL of either leachate solution or distilled water during the first watering event. For the plant community experiment, each pot received 235 ml in total of leachates solution or distilled water: 94 ml after transplanting, 94 ml during the first week, and 45 ml during the fourth week of growth. The seed germination experiment was structured with 4 microplastic treatments, 6 replicates per treatment (plus 6 additional control pots), and 6 plant species (3 grasses and 3 forbs), resulting in a total of 180 pots. Meanwhile, the plant community experiment included 4 microplastic treatments with 6 replicates each (plus 6 additional control pots), totaling 30 pots.

Seeds were surface-sterilized (4% NaOCl for 5 min, 75% ethanol for 2 min), rinsed with sterile water, and stratified at 4 °C for 5 days. For the germination experiment, seeds were randomly allocated (n = 50 per species per pot). Seeds were planted 1 cm from the pot edge to minimize border effects. All pots received 50 ml distilled water twice weekly via surface spraying, maintaining ~ 70% water holding capacity in control soils. Pre-test viability showed 80% germination potential. Germination (seedling emergence) was recorded every 48 h for 38 days; time when all pots showed no germination for three consecutive counting days. Seedlings were removed after emergence.

For the plant community experiment, seeds were germinated in sterile sand-filled trays. By doing so, we ensured that all plants started at a similar size across treatments before transplanting, and that their responses could be attributed to microplastic effects during the community phase, independent of prior effects of microplastics on seed germination. Therefore, three days after germination, uniformly sized seedlings were selected for transplantation. A grid of 24 equidistant planting holes was systematically arranged in each pot to minimize edge effects and ensure consistent spacing. Seedlings were randomly assigned to planting holes, with each pot receiving: 4 individuals × 6 species = 24 plants. Pots received 100 mL of water twice weekly for 40 days. Pots from both experiments were randomly distributed in the climatic chambers (germination experiment in two 600L chambers CH Equitec EGCS 941/3S AS LED HR, Spain, and the community experiment in a 1200L chamber, Aralab CH D1200PLH-LED −600 µE/m2, Portugal), and positions were rotated every 48 h to homogenize environmental conditions.

Seed germination measurements

To disentangle the effect of plastic particulates and leachates on germination success of grass and forb species, we quantified germination performance using three indices: (i) germination velocity (scaled 0–100), (ii) total germination percentage (0–100%), and (iii) germination synchrony (0 = asynchronous, 1 = perfectly synchronous (Aravind et al. 2021). Germination parameters were computed using the 'germinationmetrics' R package (Aravind et al. 2021), implementing three core functions: 'GermPercent', 'GermSpeed' and 'GermSynchrony', all of which incorporate both germination counts and observation intervals in their computations.

Plant morphological and physiological traits

At the end of the plant community experiment, the number of individuals per species was recorded, and the shoot mass was separated by species. Roots were gently rinsed to remove soil particles. Interspecies root separation was unfeasible due to extensive physical entanglement. Specific leaf area (SLA; $mm^2 \cdot mg^{-1}$) and leaf dry matter content (LDMC; $mg \cdot g^{-1}$) were measured following standard protocols.

Fine roots (< 2 mm diameter) were analyzed for: length, surface area, volume and average diameter using a WinRhizo™ system (v.2007; Regent Instruments Inc., Canada) on fresh samples. Specific morphological root traits were then calculated from oven-dried (60 °C, 72 h) material: specific root length (SRL; $cm \cdot mg^{-1}$), specific root surface area (SRSA; $cm^2 \cdot mg^{-1}$) and root tissue density (RTD; $mg \cdot cm^{-3}$). Root and shoot dry mass were determined after drying at 60 °C for 72 h.

Physiological traits were measured in fully expanded, mature leaves with no apparent signs of aging or damage. We analyzed between 1–3 leaves

depending on the plant species. Chlorophyll fluorescence response was measured as the photochemical efficiency of photosystem II (Fv/Fm) with a MINI-PAM photosynthesis yield analyzer (Walz, Germany). Leaves were dark-adapted for 30 min before chlorophyll fluorescence measurements. Other physiological traits in leaves such as maximum leaf photosynthetic rate (A; µmol $CO_2 \bullet m^{-2} \bullet s^{-1}$), stomatal conductance (gsw; mol $H_2O \bullet m^{-2} \bullet s^{-1}$), and instantaneous water use efficiency (WUEi = A/E, µmol $CO_2 \bullet mol^{-1}$ H_2O) were measured with a LI-6800 Portable Photosynthesis System (LI-COR Biosciences, USA). Cuvette conditions were maintained at a constant photosynthetic active radiation (PAR) of 1500 $\mu mol \bullet m^{-2} \bullet s^{-1}$, a vapor pressure deficit (VPD) that ranged from 1.0 to < 2.0 kPa, a cuvette temperature of 20ºC and reference CO_2 concentration of 400 ppm.

Soil measurements

For the plant community experiment, soil respiration was quantified using a closed-chamber IRGA approach. Fresh soil aliquots (25 g) were sealed in 50 ml centrifuge tubes (Sarstedt AG & Co. KG, Nümbrecht Germany, item number 62.548.004) with septum-equipped lids. Following initial CO_2 equilibration (5 min flushing with CO_2-free air), samples were incubated (24 h, 20 °C). Headspace CO_2 was measured at T_0 and T_{24} using a LI-COR 6400XT system (1 ml injections, 2 s sampling interval). The difference between the maximum and the minimum value (peak) was calculated. Soil respiration was reported as the net CO_2 production (ppm) by using the equation: ppm = −467 + 195.18 peak.

We quantified water-stable aggregates (WSA) using a standardized wet-sieving approach, modified from Kemper and Rosenau (1986). Air-dried soil (4 g, < 4 mm) was capillary-rewetted and subjected to mechanical dispersion (250 µm mesh, 3 min, Agrisearch Equipment, Eijkelkamp, Giesbeek, Netherlands). Following wet sieving, we obtained two fractions: Water-stable aggregates (retained on 250 µm sieve), and coarse particulate matter (retained on the sieve after manual finger presssure). Both fractions were oven-dried at 60 °C for 24 h. Water-stable aggregate percentage (WSA) was calculated as: (dry matter—coarse matter)/(4.0 g—coarse matter).

Statistical analyses

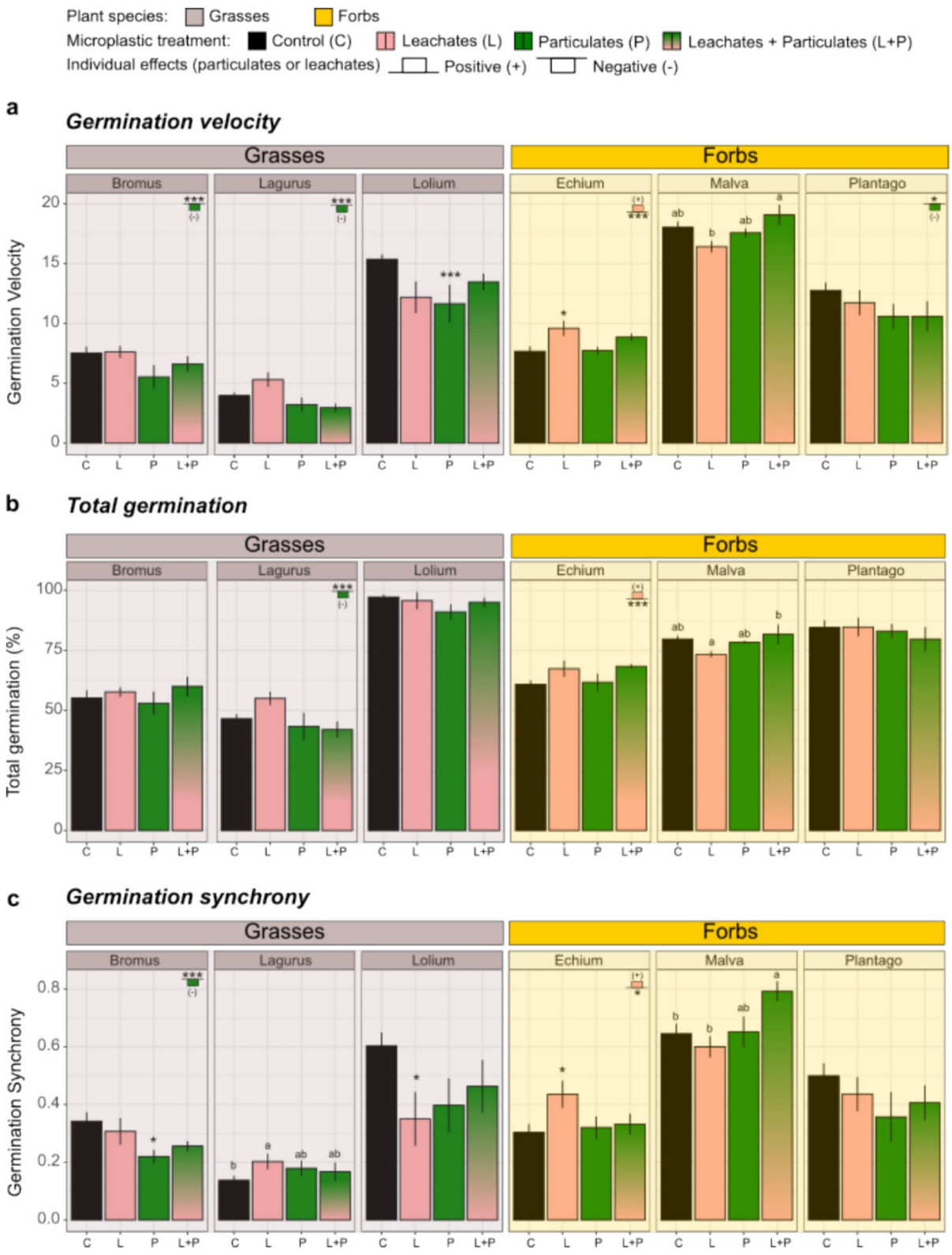
Seed germination experiment

Plastic particulates (absent, present), leachates (absent, present), functional group (grass, forb) and their interactions were treated as fixed effects in the model. Species (nested within functional group) was modeled as a random effect (Table S1). Afterwards, we conducted linear models for each functional group and/or individual species.

Linear models were performed to test the effect of microplastic leachates (L), plastic particulates (P) and their combined effect (L + P) on germination parameters. Residuals were inspected to verify normality and homogeneity of variances. When violations occurred, heteroscedasticity was addressed using the 'varIdent' function. We used the function "joint_tests" from the "emmeans" R package (Lenth 2024) to perform the analyses of variance, as we had an unbalanced design (more replicates in the control treatment). We performed the Dunnett test using the "lsmeans" function from the eponymous R package (Lenth 2024), to compare all microplastic treatments against the control group (no microplastics). Comparisons among treatments were done using the "Tukey" test. When the particulate × leachate interaction was significant, we focused our interpretation on the interaction effects rather than individual main effects.

Plant community experiment

Community weighted means (CWM) of shoot mass, SLA, LDMC, and photosynthetic traits were calculated by weighting the trait values by species abundance, as some individuals died during the experiment. These calculations were performed for the entire plant community as well as separately for each functional group (forbs and grasses). Tables and figures for these traits displayed community-weighted means (CWM) at the plant functional group and community level. On the other hand, mean values were used for species-level traits, as well as for root traits and soil properties which were analyzed at the community level. To calculate CWM, we used the function "weighted.mean" from the "stats" R package. After that, linear models were performed as described above, using microplastic leachates (L), plastic particulates (P) and their combined effect (L + P) as fixed


Plant species: Grasses Forbs
Microplastic treatment: Control (C) Leachates (L) Particulates (P) Leachates + Particulates (L+P)
Individual effects (particulates or leachates) Positive (+) Negative (-)
a
Germination velocity
Grasses
Forbs
Bromus
Lagurus
Lolium
Echium
Malva
Plantago
Germination Velocity
b
Total germination
Total germination (%)
c
Germination synchrony
Germination Synchrony
C L P L+P

◂**Fig. 1** Plastic particulates and leachates effects on seed germination. Microplastic leachates (L), particulates (P) and their combined effect (L + P) on germination velocity, total germination and germination synchrony of grasses and forbs. Control (C). Microplastic individual (main) effects of leachates or particulates, being positive or negative, indicate higher or lower germination when leachates (pink) or particulates (green) were present compared to their absence; in such cases, interactions among factors (particulates, leachates) were not significant (Tukey test). Mean and standard error are represented. Significant interactions among factors were assessed using the Tukey test (letters above the bars). Differences between microplastic treatments and the control were assessed using the Dunnett test (asterisks above the bars). Bromus (*B. rubens*), Lagurus (*L. ovatus*), Lolium (*L. rigidum*), Echium (*E. vulgare*), Malva (*M. sylvestris*), Plantago (*P. lanceolata*). Significance was established at ***$p < 0.05$; *$p < 0.1$. $N = 6$ for microplastic treatment, $N = 12$ for control samples

factors. We also employed the "Tukey" and the "Dunnett" post-hoc tests to compare differences among treatments and between each microplastic treatment and the control, respectively.

Community evenness quantifies the uniformity of shoot mass distribution among species. We calculated it using the function "diversity" from the "vegan" R package (Oksanen et al. 2024). Greater interspecific shoot mass variation indicates lower community uniformity, reflecting dominance by one or few species (Smith and Wilson 1996). Curves of cumulative germination (Figure S1) and the other figures were made up using the "ggplot2" R package (Wickham, 2016). Results are presented as mean values ± 1 SE throughout the text. All statistical analyses were performed using R version 4.2.3 (R Core Team 2023).

Results

Water extractable leachates

Untargeted LC–MS analysis of water-extractable leachates from polyethylene films was conducted in positive and negative ion modes. The analysis detected 13 features in positive mode and 10 in negative mode that were absent in the solvent blank. Tentative annotation revealed compounds such as bis[2-(4-aminoanilino)ethyl]-methyl-prop-2-enylazanium-methane (positive mode) and (1-methylcyclohexyl) 2-morpholin-4-ium-4-ylacetate (negative mode). However, no functional information for these compounds was available in PubChem, the largest open-access chemical database, indicating they are potentially novel or poorly characterized (Data from Lozano et al. 2025, Appendix 1).

Plastic particulates reduced germination in all grasses, with a minor but notable effect on the forb *P. lanceolata*

Overall, our results showed that plastic particulates mostly tended to affect the germination velocity of grass species (Fig. 1, S2, Table 1, S1-S3). Specifically, germination velocity of the grasses *B. rubens* and *L. ovatus*, decreased by ~ 19.6% and ~ 30.3%, respectively, in soils with plastic particulates (P, L + P) than in their counterpart soils without them (L, C) (Fig. 1a, Table S3). Germination velocity of the grass *L. rigidum* also decreased by ~ 24.2% in soils with plastic particulates (P) compared to control soils (C). Similarly, particulates mostly explained the total germination of the grass *L. ovatus* and the germination synchrony of the grass *B. rubens* which decreased by ~ 13.6% and ~ 30%, respectively, in soils with plastic particulates (P, L + P), than in their counterpart soils without them (L, C) (Fig. 1b, c). Finally, germination velocity of the forb *P. lanceolata* was marginally affected ($p = 0.1$) and decreased by ~ 14.7% with plastic particulates (P, L + P) than without them (L, C) (Fig. 1a).

Microplastic leachates affected seed germination with divergent effects on grasses and forbs

Our results showed that microplastic leachates rather than particulates better explained total germination, germination velocity and synchrony of the forb *E. vulgare,* which increased by ~ 11.1%, ~ 20% and ~ 22.6% respectively, in soils with leachates (L, L + P) than in their counterpart soils without them (P, C) (Fig. 1). Similarly, there was a significant interaction effect of leachates and particulates on all germination parameters of the forb *M. sylvestris* (Table S3). Total germination, germination velocity and synchrony increased by ~ 11.4%, ~ 16.2% and ~ 31.8%, respectively, in soils with leachates and particulates (L + P) in comparison with soils with only leachates (L) (Fig. 1). Microplastic leachates did not affect germination velocity or total germination of grasses (Fig. 1a, b). However, some changes were observed in germination synchrony. Specifically, *L. ovatus* exhibited

Table 1 Summary of the plastic particulates (P) and leachates (L) effects on the germination parameters and plant traits of grasses (*B. rubens*, *L. ovatus*, *L. rigidum*) and forbs (*E. vulgare*, *M. sylvestris*, *P. lanceolata*). Information extracted from Figs. 1 and 2. Symbols denote positive (+), negative (–), and non-significant effects. Note that ± denote the direction of change relative to the control, not necessarily a value judgment. Other interactions between treatments (int) are indicated. See figures for detailed results

Germination parameter	*B.rubens*	*L.ovatus*	*L.rigidum*	*E.vulgare*	*M.sylvestris*	*P.lanceolata*
Velocity	P (-)	P (-)	P (-)	L (+)	int	P (-)
Total	n.s	P (-)	n.s	L (+)	int	n.s
Synchrony	P (-)	L (+), int	L (-)	L (+)	P (+), int	n.s
Plant traits		Grasses			Forbs	
Shoot mass		P (-), int			P (+)	
Specific leaf area (SLA)		L (+)			P (+), int	
Leaf dry matter content (LDMC)		L (+)			L (+)	
Photochemical efficiency (Fv/Fm)		n.s			n.s	
Photosynthetic rate (A)		P (+)			P (-)	
Stomatal conductance (gsw),		n.s			P (+), L (+)	
Water use efficiency (WUEi)		P (+)			P (-), int	

a ~ 47.2% increase while *L. rigidum* showed a ~ 41.9% decrease in germination synchrony when exposed to microplastic leachates (L) compared to control soils (Fig. 1c).

Plastic particulates mostly affect shoot mass and physiological traits with contrasting effects between grasses and forbs

Plastic particulates, rather than leachates, played the primary role in influencing shoot mass and physiological responses of grasses and forbs. These effects were generally opposite between the two functional groups: when the effect was positive for grasses, it tended to be negative for forbs, and vice versa. Furthermore, forbs exhibited greater sensitivity to microplastics than grasses, as evidenced by the number of traits significantly affected (Fig. 2). Our results showed that shoot mass of grasses decreased by ~ 21% with plastic particulates (P), while shoot mass of forbs increased with particulates (P) by ~ 61.2% compared to control soils (Fig. 2, Table S4). Specific leaf area (SLA) of grasses increased with leachates (L) by ~ 10% compared to control, while SLA of forbs rather increased with particle treatments (P, L + P) by ~ 12.6% compared to controls (Fig. 2, Table S4). Such a pattern was followed by each grass and forb species analyzed (Fig. S3). Leaf dry matter content (LDMC) of both forbs (~ 5.4%) and grasses (~ 2.7%) increased with leachates (L, L + P) than without them (C, P). Overall, plants of both plant functional groups showed optima values of photochemical efficiency of PSII (Fv/Fm; ~ 0.80, Fig. 2). However, Fv/Fm values of the grass *L. ovatus* decreased with leachates (L, L + P) than without them (P, C) (Fig. 3). Meanwhile, Fv/Fm of the forbs *E. vulgare* and *M. sylvestris* decreased with particulates, while the forb *P. lanceolata* showed an opposite pattern (Fig. 2, Table S5). Maximum photosynthetic rate (A) of grasses increased by ~ 15% with plastic particulates (P, L + P) than without them (L, C), while photosynthetic rate of forbs decreased by ~ 8.1% with particulates (P, L + P). Such patterns were specifically followed by the grass *L. ovatus* and the forb *M. sylvestris* (Fig. 2, S3). The stomatal conductance (gsw) of grasses was unaffected by microplastics (Fig. 2) as within this functional group, plant species showed divergent patterns (Figure S3). However, gsw of forbs increased with both particulates and leachates compared to plants in control soils. Water use efficiency (WUEi) of grasses increased by ~ 7.2% with particulates (P, L + P) than without them (L,C), while that of forbs showed an opposite pattern decreasing by ~ 25% with plastic particulates (Fig. 2).

Microplastic leachates primarily affect root morphological traits and soil respiration, while particulates predominantly affect root mass

Root traits and soil properties were analyzed at the whole-plant-community level. Overall, plastic

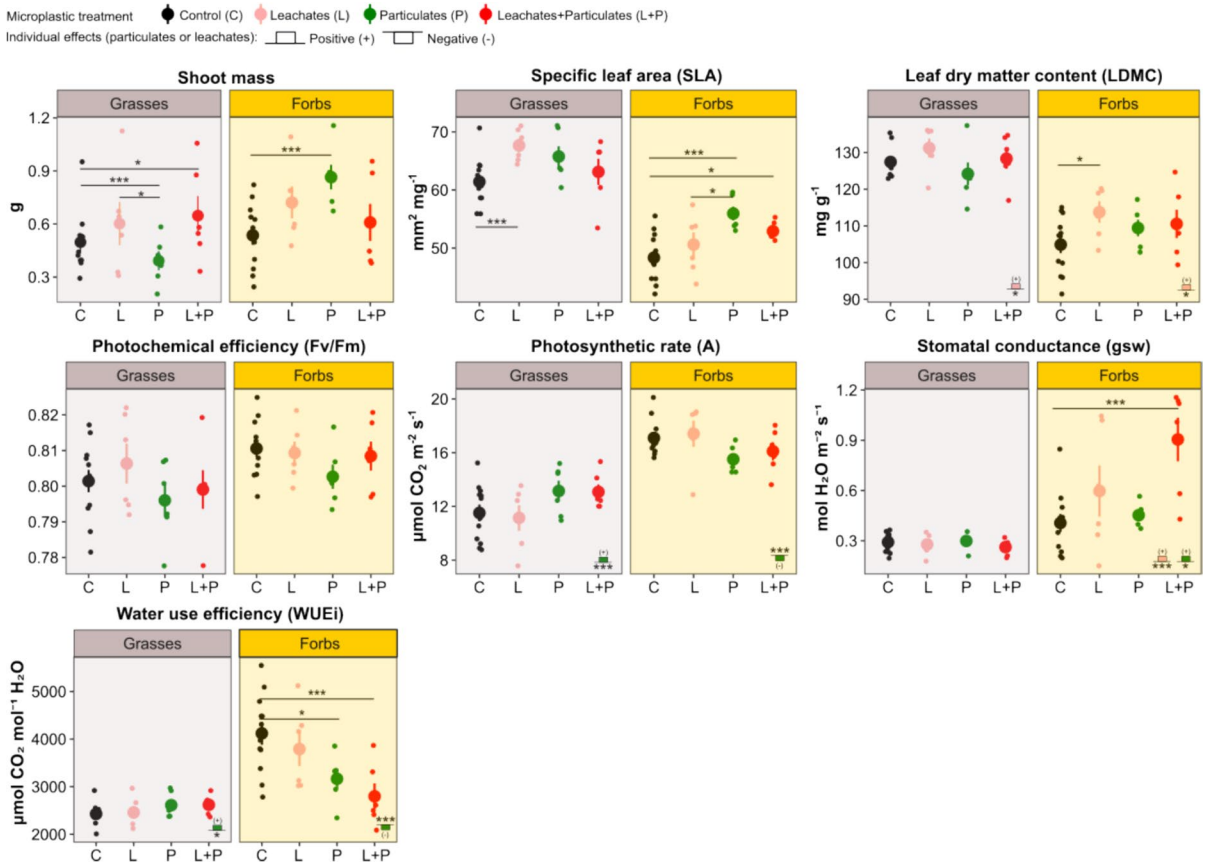


Fig. 2 Shoot morphological and physiological traits at the plant functional group level. Microplastic leachates (L), plastic particulates (P) and their combined effect on the community weighted means (CWM) of shoot mass, shoot morphological traits: specific leaf area (SLA), leaf dry matter content (LDMC), and shoot physiological traits: photochemical efficiency of photosystem II (Fv/Fm), photosynthetic rate (A), stomatal conductance (gsw), and instantaneous water use efficiency (WUEi) of both plant functional groups (grasses and forbs). Mean and standard error are represented. Data points are shown as circles. Significance was established at 0.05 (***) and 0.1 (*) for both Tukey and Dunnett test. N = 6 for microplastics treatments, N = 12 for control samples

leachates influenced root morphological traits and soil respiration, whereas plastic particulates primarily affected root mass (Fig. 3). Specifically, specific root length (SRL) decreased by ~ 27% and ~ 23.9%, in soils with leachates (L) and particulates (P) compared to control soils (C). Specific root surface area (SRSA) showed a similar pattern, while root tissue density (RTD) increased by ~ 37.7% with leachates (L) compared to control soils (Fig. 3, Table S6). Root mass decreased by ~ 28.7% with plastic particulates (P, L + P) compared to soils without them (L, C) (Table S6). Soil respiration increased by ~ 65.1% with leachates (L, L + P) compared to soils without them (P, C), while soil aggregation (WSA) was not affected by leachates or plastic particulates (Fig. 3, Table S6). Finally, shoot mass evenness decreased by ~ 15.4% and ~ 13.7% with leachates (L) and particulates (P) compared to control soils (C) (Fig. 3).

Discussion

Plastic particulates negatively affected seed germination of all grasses with marginal effects on forbs

Plastic particulates negatively affected germination velocity of all grass species examined, with similar

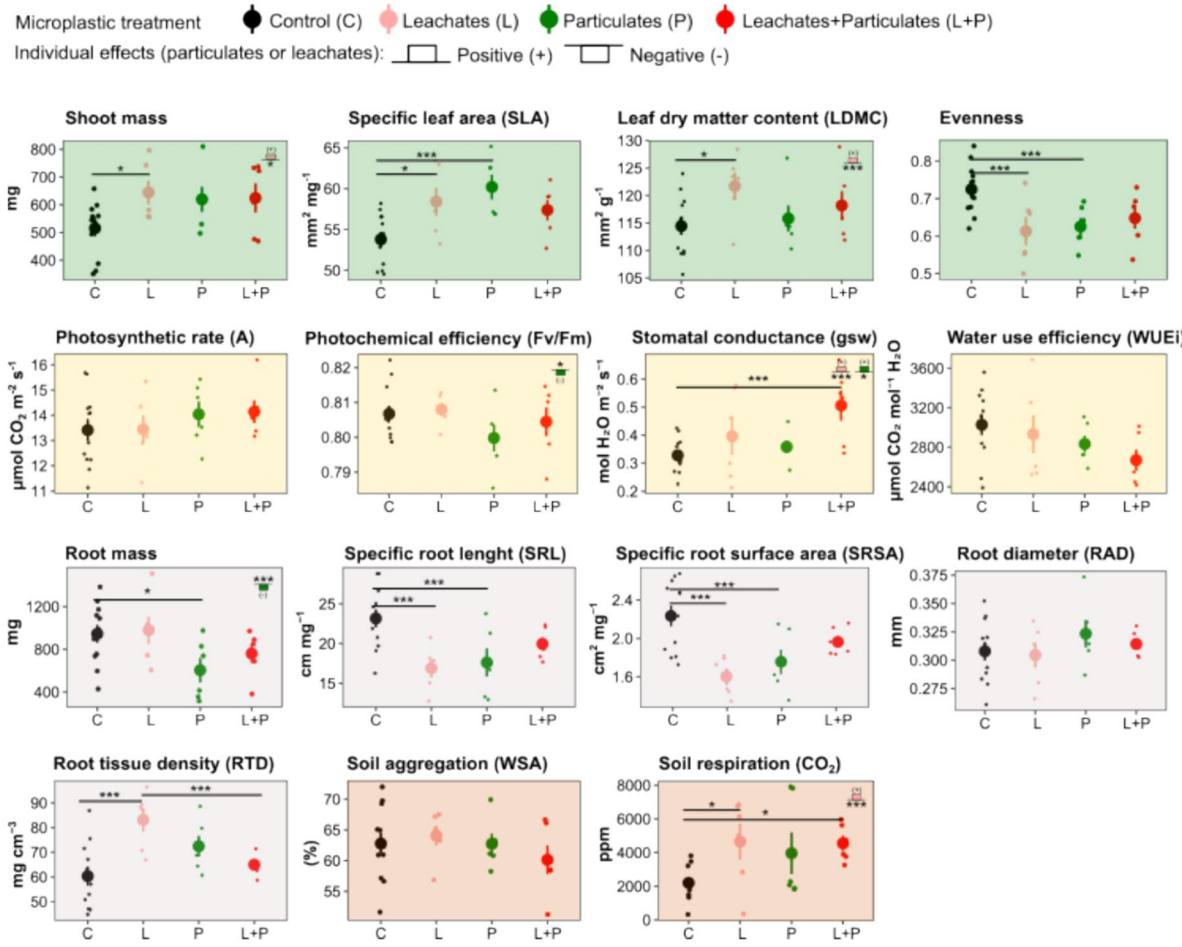


Fig. 3 Plant traits and soil properties at the community level. Microplastic leachates (L), plastic particulates (P) and their combined effect on the community weighted means (CWM) of shoot mass, shoot morphological traits: specific leaf area (SLA), leaf dry matter content (LDMC); and shoot physiological traits: photosynthetic rate (A), stomatal conductance (gsw), instantaneous water use efficiency (WUEi), and photochemical efficiency of photosystem II (Fv/Fm). Control (C). Community evenness, root traits and soil properties correspond to the average value in the pot. Mean and standard error are represented. Data points are shown as circles. Microplastic individual (main) effects of leachates or particulates—being positive or negative— indicate higher or lower value when leachates (pink) or particulates (green) were present compared to their absence; in such cases, interactions among factors (particulates, leachates) were not significant (Tukey test). Significant interactions among factors were assessed using the Tukey test while differences between microplastic treatments and the control were assessed using the Dunnett test. Significance was established at ***$p < 0.05$; *$p < 0.1$. $N = 6$ for microplastic treatment, $N = 12$ for control samples

negative effects observed on germination synchrony and total germination. By contrast, forbs remained largely unaffected, with only *P. lanceolata* showing marginal sensitivity to plastic particulates. Grass species often possess awns (bristle-like appendages) and hair-like structures on the lemma, which aid in dispersal through epizoochory (Petersen and Kellogg 2022). However, these awns and dense hairs can easily trap or accumulate plastic particulates, potentially obstructing seed pores, limiting water absorption, and delaying germination (Bosker et al. 2019; Lozano et al. 2022). Additionally, plastic particulates may potentially cause physical damage to the seed coat or embryo, further negatively affecting seed germination in grasses. Visual inspection revealed microplastic particulates adhering to the surfaces and lodged into the hairs of seeds and radicles of grasses. By contrast, the smoother surfaces of forb seeds might make

them less likely to trap plastic particulates compared to the textured seeds of grasses (Baskin and Baskin 2014), which helps explain the reduced effect of plastic particulates on forb species. Nevertheless, our results indicate that the forb *P. lanceolata* was still affected by plastic particulates. This is likely due to the mucilage these seeds release upon contact with water (Kreitschitz et al. 2016), which can attract surrounding plastic particulates, blocking the seeds and impairing germination.

Microplastic leachates affected seed germination with divergent effects on grasses and forbs

Microplastic leachates positively influenced all germination parameters of the forb *E. vulgare*, and the combined effect of leachates and particulates had a similar positive effect on the forb *M. sylvestris.* By contrast, leachates affected grasses in divergent ways: *L. ovatus* increased its germination synchrony, while *L. rigidum* showed the opposite response.

The majority of chemical substances released by microplastics are toxic to seed germination (Lithner et al. 2011; Lozano et al. 2025). However, at low doses, these toxicants may exert positive effects on germination through hormetic responses. Specifically, low concentrations of toxic substances can induce a moderate upregulation of reactive chemical species, stress hormones, antioxidant systems, and protective proteins (Agathokleous et al. 2020). Through hormesis, these mechanisms can ultimately lead to beneficial effects of microplastic leachates on seed germination. Certain chemical leachates may even act as hormone analogs at low concentrations (Vandenberg et al. 2012), potentially stimulating germination in forbs. The positive effect observed in the forb *E. vulgare* may result from the activation of stress-response pathways that promote germination under suboptimal conditions, a phenomenon known as seed priming (Jatana et al. 2024). Forbs like *E. vulgare* may have evolved to respond positively to low levels of environmental stressors, as they often thrive in disturbed or nutrient-poor soils (Pugnaire and Lazaro 2000). This adaptability allows them to exploit low concentrations of microplastic leachates as a resource or signal for germination. In addition, forbs frequently exhibit high phenotypic plasticity (Lipowsky et al. 2015), enabling them to tolerate diverse environmental stressors, including the presence of novel chemicals such as those from microplastics. As a pioneer species commonly found in disturbed habitats, *E. vulgare* may have evolved mechanisms to capitalize on such novel chemicals at early life stages of seed germination, suggesting an adaptive trait for colonizing new or degraded environments. Research has shown that hormesis can be particularly pronounced in slow-growing species (e.g., forbs), whereas fast-growing plants (e.g., grasses) rarely exhibit such responses (Belz and Sinkkonen 2019). Thus, the divergent germination synchrony among grasses (e.g., *L. ovatus* vs. *L. rigidum*) could be better attributed to differences in seed coat thickness, dormancy mechanisms, or species-specific sensitivity to certain chemicals. Although we observed a hormetic effect on seed germination, it is crucial to emphasize that this positive response is transient and does not compensate for the long-term detrimental effects of plastic pollution. For instance, in *E. vulgare*, the early benefit of microplastics on germination was overshadowed by a detriment in shoot mass and photochemical efficiency (Fv/Fm) during later growth stages, demonstrating the overall negative impact of plastic leachates. Therefore, this finding should not be misinterpreted as a beneficial effect; instead, it underscores the complex and insidious nature of plastic pollution and reinforces the critical need to combat it at its source.

Plastic particulates mostly affect shoot mass and physiological traits with opposite effects between grasses and forbs

Plastic particulates play the primary role affecting shoot mass and physiological traits of grasses and forbs within the community, with these effects generally being opposite between the two functional groups. Microplastic leachates instead showed a negligible effect on shoot mass and physiological traits.

Shoot mass of grasses decreased with plastic particulates, while forbs exhibited the opposite response. Although plastic particulates are generally known to enhance soil aeration, thereby improving root penetration and shoot mass (Lozano et al. 2024a), our results demonstrate that their effects are strongly dependent on plant functional group. Grasses, which typically develop thinner and shallower root systems (Weaver 1958; Roumet et al. 2008), are more vulnerable to reduced water and nutrient availability. The increased soil aeration caused by plastic particulates

may accelerate water flow and loss (Wan et al. 2019), which could have increased water stress in the upper soil layers where grass roots are concentrated. This may explain the observed decline in shoot mass for grasses. Despite this, grasses showed an improvement in photosynthetic rate (A) and water use efficiency (WUEi) with plastic particulates, suggesting a shift in resource allocation. Rather than investing in shoot growth, grasses may allocate more fixed carbon to stress tolerance mechanisms (Lozano et al. 2020a). For instance, under water scarcity induced by microplastics, instantaneous water use efficiency becomes particularly critical as water is a limiting resource (Hatfield and Dold 2019), highlighting the adaptive strategies grasses employ to cope with microplastic pollution.

Conversely, forbs increased shoot mass with plastic particulates in soil and decreased photosynthetic rate (A) and water use efficiency (WUEi). Contrary to grasses, forbs usually present thicker roots in deeper soil layers (Roumet et al. 2008; Rojas-Botero et al. 2023). This characteristic may make them less susceptible to the rapid water flow and loss induced by plastic particulates. In addition, plastic particulates can increase soil aeration, which favors forb root systems by improving root penetration, water uptake, and nutrient acquisition, ultimately promoting shoot growth (Lozano et al. 2024a). As a result, forbs may allocate a larger proportion of fixed carbon to shoot growth rather than to stress tolerance or root development. However, the presence of plastic particulates also led to a decrease in photosynthetic rate (A) and water use efficiency (WUEi) in forbs. These declines are likely linked to the observed increase in specific leaf area (SLA) and stomatal conductance (gsw). Thinner and/or broader leaves (i.e., 2076 mm^2 in plastic-exposed plants (P) vs. 1754 mm^2 in controls) and higher stomatal conductance result in greater transpiration rates, which, combined with a lack of stress-induced water conservation mechanisms, reduce water use efficiency. Additionally, the increase in leaf area may not be accompanied by proportional increases in chlorophyll content or Rubisco activity. This is because nitrogen resources can become diluted across larger leaf surfaces, limiting the concentrations of chlorophyll and Rubisco and ultimately reducing the photosynthetic rate (Hikosaka 2004).

Microplastic leachates primarily affect root morphological traits and soil respiration

At the community level, root fineness (specific root length, SRL and specific root surface area, SRSA) decreased with microplastic leachates, while root tissue density (RTD) followed the opposite pattern. Microplastic leachates had a negligible effect on shoot mass and physiological traits but a significant effect on root traits and soil respiration. This could be attributed to the soil substrate and roots, which are the first point of contact with the soil, functioning as a buffer by absorbing microplastic leachates, thereby avoiding the exposure of aboveground tissues to potential toxicants.

Overall, soil has the capacity to store, filter, buffer, degrade, and inactivate pollutants such as pesticides, largely due to the turnover of soil organic matter (Burauel and Baßmann 2005). At the community level, microplastic leachates increased soil respiration, potentially linked to hormetic responses, as discussed earlier. This increase in respiration may also result from the degradation of microplastics, during which many potentially hazardous leachates could be eliminated (Lozano et al. 2024c) and soil biota could be favored. Additionally, microplastic leachates could trigger a "priming" effect, enhancing microbial activity (Rillig et al. 2021), which further explains the increase in soil respiration. However, in single-species experiments, leachates were found to negatively affect soil respiration (Lozano et al. 2024a), which suggests that at the community level, compensatory dynamics (Gonzalez and Loreau 2009) may counteract the negative effects of microplastic leachates.

Similarly, plant roots have the potential to significantly mitigate the negative effects of microplastic leachates through rhizofiltration, a key strategy in phytoremediation. In this process, plant roots either adsorb or absorb pollutants from the soil (Kafle et al. 2022). These pollutants can react with organic compounds released by roots through exudates, leading to the precipitation of toxic substances such as heavy metals (Kafle et al. 2022). The rhizosphere, as a critical interface between soil and roots, plays a vital role in the phytoremediation of polluted soils. Microbial populations within the rhizosphere influence heavy metal mobility and availability to plants through mechanisms such as the release of chelating agents, acidification, and other biochemical processes

(Jing et al. 2007). Additionally, heavy metal ions can be transported into root cells and immobilized within vacuoles (Jing et al. 2007). These processes collectively help explain how microplastic leachates influence root traits response and their ability to counteract the pollutant effect of microplastic leachates.

The decrease in root fineness (specific root length, SRL; specific root surface area, SRSA) and the increase in root tissue density can be attributed to plant strategies for coping with stress. These root morphological changes, induced by microplastic leachates, align with responses observed under other environmental stressors (Lozano et al. 2020a). Finer and longer roots are more prone to absorbing pollutants like cadmium (Cd), whereas thicker roots can retain more Cd, reducing its translocation to shoots and improving shoot tolerance (Zhang et al. 2022). Similarly, under aluminum (Al) toxicity, roots inhibit cell division mechanisms, leading to brittle and stunted roots (Rahman et al. 2024), which ultimately reduces root fineness. Thus, in response to microplastic toxicity plants may sacrifice fine roots to prevent the spread of pollutants to aboveground tissues. Also, roots with a high tissue density often develop thicker cell walls and more suberized layers (Taiz et al. 2018), which can act as barriers to block the uptake of toxic elements into the cytoplasm (Chen et al. 2022). All of which helps explain why microplastic leachates strongly influence root traits while having a practically negligible effect on aboveground tissues. Our results showed that root morphology may play a critical role in plant tolerance to microplastic pollution.

Future directions and research opportunities

Our research advances the understanding of how plastic particulates and their leachates affect plant species. Plastic particulates reduced seed germination across all grass species, while also diminishing shoot mass and altering physiological traits. These negative effects may stem from nutrient immobilization due to carbon input from plastics (Rillig et al. 2019), though this hypothesis requires further testing. Interestingly, microplastic leachates appeared to have positive effects on seed germination in forbs and enhanced soil respiration within the plant community. These effects may be attributed to hormetic responses, where low doses of stressors stimulate biological processes. However, hormesis is often a transient phenomenon that can lead to trade-offs over time. For instance, plants stimulated by microplastic leachates may experience accumulating disadvantages in the long term (e.g., seed production, offspring viability). To investigate this possibility, long-term experiments are required, in which plants are exposed to microplastic leachates over extended periods. Our study provides a foundational understanding of the effects of plastic particulates and leachates on grass and forb species. However, generalizing these findings and deepening insights into these complex interactions will require both a broader diversity of species within each plant functional group and the use of microplastic mixtures, including a variety of polymer types, sizes and shapes, that better reflect their non-uniformity under field conditions. Finally, seed germination in grasses and forbs plays a critical role in supporting diverse restoration programs. Understanding how these plant groups respond to microplastics in soil is essential for optimizing restoration strategies and ensuring their long-term success.

Conclusions

Our study demonstrates that microplastic pollution can act as a significant environmental filter in drylands, with the potential to shift plant community composition by favoring forbs over grasses. The primary driver of these changes is the physical presence of plastic particulates, which directly inhibit grass germination, potentially by exacerbating water stress for shallow-rooted grasses, reducing their shoot mass. By contrast, forbs largely avoid these negative effects likely through deeper rooting and probably by benefiting from improved soil aeration. Chemical leachates triggered a transient, hormetic stimulation of forb germination. The divergent responses, where grasses invested in stress tolerance (higher photosynthesis and water-use efficiency) and forbs prioritized growth, reveal a fundamental trade-off induced by microplastics. By altering plant-soil-water dynamics, microplastic particulates can thus disadvantage the dominant grass component of dryland communities, predicting a potential shift towards forb-dominated systems with consequences for ecosystem structure and function.

Author contributions Yudi M. Lozano conceived the ideas and designed methodology with the help of Cristina Armas. Leonie S. Kuhlmann, Julian W. Zeller and Alejandro Terrones established the experiment and collected the data with the help of Cristina Armas. Yudi M. Lozano analyzed the data and led the writing of manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Data will be available in the Dryad Digital Repository upon publication.

Declarations

Competing interests We have no conflict of interest to declare.

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