



# Microbiomes and glyphosate biodegradation in edaphic and aquatic environments: recent issues and trends

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## Abstract

Glyphosate (N-(phosphonomethyl)glycine) has emerged as the top-selling herbicide worldwide because of its versatility in controlling annual and perennial weeds and the extensive use of glyphosate-resistant crops. Concerns related to the widespread use of glyphosate and its ubiquitous presence in the environment has led to a large number of studies and reviews, which examined the toxicity and fate of glyphosate and its major metabolite, aminomethylphosphonic acid (AMPA) in the environment. Because the biological breakdown of glyphosate is most likely the main elimination process, the biodegradation of glyphosate has also been the object of abundant experimental work. Importantly, glyphosate biodegradation in aquatic and soil ecosystems is affected not only by the composition and the activity of microbial communities, but also by the physical environment. However, the interplay between microbiomes and glyphosate biodegradation in edaphic and aquatic environments has rarely been considered before. The proposed minireview aims at filling this gap. We summarize the most recent work exploring glyphosate biodegradation in natural aquatic biofilms, the biological, chemical and physical factors and processes playing on the adsorption, transport and biodegradation of glyphosate at different levels of organization and under different agricultural managements, and its impact on soil microbial communities.

**Keywords** Glyphosate · Soil microbial communities · Herbicide fate · Plant residues · Soil structure · Porosity · Aquatic environments

## Introduction

The present individual and societal environmental awareness demands that the increase in the efficiency of agricultural production systems does not come at the expense of soil sustainability and health of natural ecosystems. Since the

middle of the last century, the widespread intensification of industrial agriculture stemming from the so-called Green Revolution allowed major increases in crop yield required to keep pace with worldwide population growth. Yet the significant improvements in crop production have relied in part on the extensive use of fertilizers and pesticides (Pimentel

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1996). The herbicide glyphosate (N-(phosphonomethyl) glycine) was introduced in 1974 and has since been widely used due to its versatility in controlling annual and perennial weeds. It has subsequently been at the center of considerable controversy shortly after the introduction of transgenic, glyphosate-resistant crops and the increasing adoption of no-till farming worldwide. Concerns related to the widespread use of glyphosate has prompted many studies and reviews on the environmental fate of glyphosate and its major metabolite, aminomethylphosphonic acid (AMPA) (Singh and Walker 2006; Borggaard and Gimsing 2008; Padilla and Selim 2020; Chow et al. 2020).

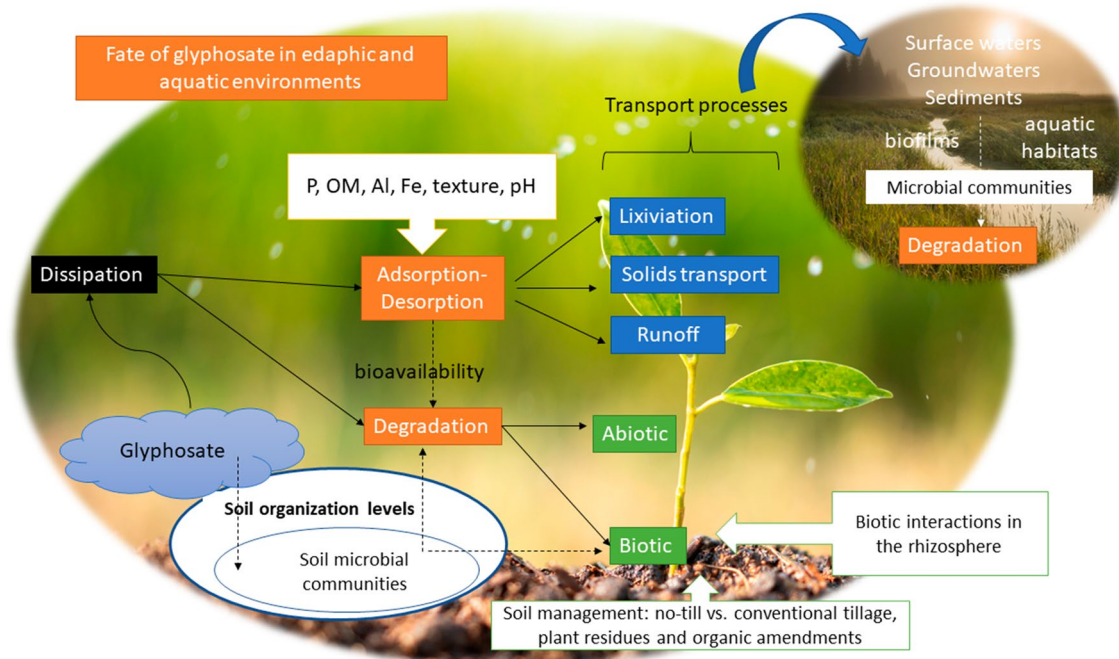
A major issue is that glyphosate also affects prokaryotes because it targets 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS; EC 2.5.1.19), also known as *aroA* enzyme, a central enzyme of the shikimate pathway involved in the synthesis of aromatic amino acids. Soil microorganisms are essential components for sustaining the multiple functions delivered by soils. Any environmental factor that affects microbial diversity and function could therefore potentially affect soil ecosystem services. In turn, the complex plant-associated microbial community, i.e. the rhizosphere microbiome, is critical for plant health and growth. Thus, the numerous research efforts addressing the effect of glyphosate on soil fungal and prokaryotic communities are well justified by the widespread agricultural use of glyphosate for weed control.

The biological breakdown of glyphosate is the main dissipation process in the environment, and is driven mainly

by microbial activity, in which bacteria have a predominant role. The microbial degrading capacity has been largely studied and reviewed and it is well established in *in vitro* experiments that they are able to use glyphosate as a source of inorganic P as well as N and C source under certain circumstances (Singh and Walker 2006; Ermakova et al. 2017; Zhan et al. 2018).

However, the fate of glyphosate and its effect on ecosystems will depend on microbial traits as well as on glyphosate application rate, soil characteristics, soil transport processes and soil management, among other factors. That is in part why the literature is characterized by seemingly contradictory findings. Microbiological processes, including glyphosate degradation, occur in physical environments where air, water and nutrients are further dependent on the organization of mineral and organic components. Thus, soil habitats must be considered as a key factor regulating, not only glyphosate biodegradation but also glyphosate adsorption and dissipation leading to an overall occurrence of this molecule in the environment (Fig. 1). Consequently, detailed description of soil characteristics, properties and structural arrangements are needed.

It follows that assessing the direct impact of herbicides on soil microbial communities is not straightforward: the factors and processes affecting glyphosate biodegradation must be identified and analyzed at the appropriate level of analysis. Soil type, farming system, crop sequence, agricultural management, climate, sampling season and other factors are



**Fig. 1** Overview of the main biological, chemical and physical processes responsible for the environmental fate of glyphosate

potentially confounding factors that must be accounted for before definite conclusions can be drawn.

Understanding the interplay between glyphosate biodegradation, soil and water microbiomes and soil physical and chemical properties is of crucial importance to ensure the maintenance of soil health and fertility. This mini-review aims at filling this gap. We have summarized research, with particular focus on the last 6 years, exploring the following issues: (i) Metabolic routes of microbial glyphosate biodegradation, (ii) The effect of glyphosate on soil microbial communities, (iii) The effect of soil chemical and physical characteristics on glyphosate availability and biodegradation, (iv) Glyphosate biodegradation in natural aquatic biofilms and the effect of aquatic habitat characteristics and (v) The impact of soil management, e.g. the presence of stubble, the fertilization regime, and other agronomic factors, on glyphosate biodegradation.

## Soil microorganisms: tolerance to glyphosate and degrading capacity

### Isolates

Two types of EPSP synthases have been described from various organisms on the basis of their intrinsic glyphosate sensitivities and their substantial sequence variations (Cao et al. 2012; Yi et al. 2016). While type I EPSP synthases, present mainly in plants and some bacteria, are naturally sensitive to glyphosate, the type II EPSP synthases exhibit significant activity under high glyphosate concentrations, so they are glyphosate-tolerant.

Glyphosate-degrading bacterial ability is widely distributed in the Bacteria domain and it is not restricted to particular taxonomic groups. On the contrary, most fungal strains isolated from glyphosate polluted environments are restricted to a few taxa and have relatively slow degrading activity with a predominance of the AMPA pathway, using glyphosate as a P source (Zhan et al. 2018; Singh et al. 2019; Correa et al. 2023).

Table 1 includes the most recent discoveries of bacterial and fungal degrading microbes, along with a minimum set of variables reported for the isolation. Research published before 2015 can be found in many previous reviews (Zhan et al. 2018; Padilla and Selim 2019; Singh et al. 2020). Most of the isolated bacteria were able to use glyphosate either as a sole source of P (Manogaran et al. 2017; Masotti et al. 2021) or both C and P source (Ermakova et al. 2017; González-Valenzuela and Dussán 2018; Firdous et al. 2020). Fewer studies reported the isolation of bacteria able to use glyphosate as sole source of C (Zhao et al. 2015). Fungal isolates belong to the Ascomycota division and were all able to use glyphosate as sole source of P (Zhan et al. 2018;

Singh et al. 2020; Correa et al. 2023) or either P and N sources (Carranza et al. 2019) (Table 1).

### Factors affecting microbial degradation in vitro

Many studies have focused on the optimization of batch culture conditions to achieve efficient microbial glyphosate degradation that would lead to a better understanding of the factors involved in its metabolism, e.g. (Yu et al. 2015; Ermakova et al. 2017; Manogaran et al. 2018; Firdous et al. 2020).

As mentioned before, glyphosate can bind to humic acids and metal ions at a range of pH conditions, leading to reduced availability for microbial degradation and thus, increasing its lifetime in aquatic and soil environments. Singh et al. (2019) reported that the addition in the culture medium of humic acids (HA, 10 ppm) had the most inhibitory effect on degradation rates of the isolates *Streptomyces* sp. GP1, *Bacillus* sp. GP2 and *R. leguminosarum* GP 3, followed by cupric (15 ppm) and ferric (25 ppm) ions. This resulted in up to 30% less glyphosate degrading at a slower rate, with half-life increasing about 50% in comparison to the control without ions or HA (Singh et al. 2019).

### Metabolic pathways that microbes follow in in vitro studies

Glyphosate is metabolized through either one of two known pathways, the C-P lyase pathway and the glyphosate oxidoreductase pathway, GOX (Borggaard and Gimsing 2008). The activation of the C-P lyase operon is downregulated by the external and endogenous levels of Pi and it is therefore rarely induced in the natural environments (Hove-Jensen et al. 2014; Zhan et al. 2018). However, glyphosate degradation under P starvation conditions has been analyzed in lab experimental studies. In the C-P lyase pathway, glyphosate is transported and cleaved by means of a set of about 14 proteins encoded in the *phn* operon, producing a P containing molecule (5-phosphoribosyl 1-diphosphate, PRPP) that subsequently releases inorganic P (Pi) and N-methylglycine (sarcosine), which can be further oxidized through sarcosine oxidase activity.

The GOX pathway results in the cleavage of the C-N bond with the formation of AMPA and release of glyoxylate that bacteria use as a C source. The ulterior fate of AMPA is less well-established. Some bacteria simply excrete it to the environment without further processing, while others metabolize it through acetylation, transamination, or methylation, probably rendering a less active compound (Zhan et al. 2018; Singh et al. 2020). As AMPA still retains the C-P bond, some bacteria ultimately channel this metabolite to the C-P lyase pathway for complete degradation (Jochimsen et al. 2011). Thus, the C-P lyase pathway is critical in the

**Table 1** Experiments performed with soil-borne glyphosate degrading microorganisms reported in papers published since 2015

Microorganisms	Source of isolation and location	Analytical method	Glyphosate concentration and formulation	Nutrient obtained	Time (duration of incubation, or to degradation)	Deducted metabolic pathway/enzymes	Observations	Reference
<i>Bacteria</i>								
<i>Pseudomonas</i> spp. strains GA07, GA09 and GC04	Polluted soil (China)	HPLC–UV	500 mg L <sup>-1</sup> (analytical grade, 95% purity)	C	5 days	AMPA pathway (GOX), GA09 may have C sarcosine pathway too	Cell free extracts were analyzed for metabolites	Zhao et al. (2015)
<i>Burkholderia vietnamiensis</i> AQ5-12	Glyphosate polluted soil (Malaysia)	Colorimetry	50 mg L <sup>-1</sup> (analytical grade, 99.5% purity)	P	48 h	N:D	C and N sources and concentrations, pH, glyphosate concentration, temperature, influenced degradation	Manogaran et al. (2018)
<i>Lysinibacillus sphaericus</i> CBAM5 and III(3)7	Polluted and oak forest soils (Colombia)	Colorimetry	144 mg L <sup>-1</sup> (n.a.)	C and P	72 h	Sarcosine pathway	Sporulation promoted degradation; sarcosine oxidase gene detected	Gonzalez Valenzuela and Dussan (2018)
<i>Bacillus subtilis</i> Bs-15	Rhizosphere soil	UV–Vis spectrophotometry	10 g L <sup>-1</sup> (analytical grade, 99.5% purity)	C and P	72 h	N:D	Glyphosate concentration, pH, aeration, temperature, mineral salts, C and N sources affected degradation	Yu et al. (2015)
<i>Agrobacterium tumefaciens</i> CHLDO; <i>Achromobacter denitrificans</i> SOS5; <i>Ochrobactrum haematophyllum</i> SR; <i>Pseudomonas nitroreducens</i> TR3	Soil, plant material and rhizosphere, in highly exposed field (Santa Fe, Argentina)	TLC+ H <sup>1</sup> NMR	1.5 mM (analytical grade, > 98% purity and Roundup Ultramax 74,7% isopropylamine salt)	P	96 h	Sarcosine pathway (C-P lyase genes cluster) and AMPA ( <i>thiO</i> ) in <i>A. tumefaciens</i>	AMPA was also used as P source, sometimes with higher degradation than GLY in vitro	Masotti et al. (2021)

Table 1 (continued)

Microorganisms	Source of isolation and location	Analytical method	Glyphosate concentration and formulation	Nutrient obtained	Time (duration of incubation, or to degradation)	Deducted metabolic pathway/enzymes	Observations	Reference
<i>Streptomyces</i> GP1, <i>Bacillus subtilis</i> GP2 and <i>Rhizobium leguminosarum</i> GP3	Croplands (Kaparthala, India)	ESI-MS	250 mg L <sup>-1</sup> (analytical grade, 98% purity)	C	14 days	AMPA, sarcosine pathways (GOX, C-P lyase)	> 86% degradation Humic acids > Cu (II) > Fe(III) reduced GLY degradation	Singh et al. (2019)
<i>Ochrobactrum anthropi</i> GPK and <i>Achromobacter</i> sp. Kg16, MPK7, mPS 12	Agricultural soil exposed to methylphosphonates and glyphosate for 15 years	HPLC-UV Colorimetry	500 mg L <sup>-1</sup> (analytical grade or commercial formulation GrounBio 36%)	C, N, P †	200 h	<i>O. anthropi</i> used AMPA (GOX) pathway; <i>Achromobacter</i> used AMPA pathway (GOX) or C-P lyase (MPK7 and MPS12)	Ermakova et al. (2017)	
<i>Comamonas odorotermittis</i> P2	Agricultural soil with glyphosate history (NSW, Australia)	HPLC-UV-Vis	500 mg L <sup>-1</sup> (n.a)	C, P	4 days	AMPA, sarcosine pathways	Factors affecting degradation were pH, temperature, inoculum density	Firdous et al. 2020
<i>Fungi</i>								
<i>Penicillium</i> 4A21	Amazonian forest soil (Manaus, Brazil)	LC-MS/MS	7.4 mM (Roundup WG)	P	14 days	AMPA, sarcosine pathways	50 GLY degrading isolates obtained 40% degradation	Correa et al. (2023)
<i>Aspergillus oryzae</i> AM1 and AM2	Agricultural soil (Argentina)	Reverse phase-HPLC/fluorescence detection system	1–10 mM (Roundup Con-trolmax)	N, P	15 days	N.D	> 50% degradation (up to 96%) A <sub>w</sub> influenced degradation at high concentration (10 mM)	Carranza et al. (2019)

N.D. not determined; n.a. not available; GLY glyphosate; A<sub>w</sub> water activity

†In different strains



mineralization of glyphosate as a connecting step in both metabolic pathways (Sviridov et al. 2015).

Besides the glyphosate oxidoreductase, the glycine oxidase enzymes, encoded by *thiO* gene, are also capable of catalyzing the oxidative deamination of glyphosate as well as other amines cleaving the C-N bond. Glyphosate degradation probably occurs as a result of low substrate specificity of these enzymes, which are widely distributed in many genera of bacteria such as *Ochrobactrum*, *Rhizobium*, *Pseudomonas*, *Bradyrhizobium* and others (Iyer et al. 2018; Guijarro et al. 2021).

Noteworthy, most of the isolates harbor more than one of the known degradation pathways (Zhao et al. 2015; Ermakova et al. 2017; González-Valenzuela and Dussán 2018; Singh et al. 2019; Firdous et al. 2020; Masotti et al. 2021).

The relevance of the previously discussed results goes beyond the intrinsic interest of disentangling microbial metabolism of the herbicide. It is particularly important to understand the multiplicity of metabolic strategies that these microbes may deploy in situ, where they interact with each other and with glyphosate-sensitive microorganisms. (Ermakova et al. 2017). For instance, three *Achromobacter* and one *Ochrobactrum* strains could complement each other's capacities in the degradation of glyphosate (Ermakova et al. 2017). The degradation metabolite AMPA or Pi could be excreted to the environment in *O. anthopi* GPK3 and support the growth of *Achromobacter* sp. MPK7 cells, which were unable to use glyphosate as source of P even under starvation conditions (Ermakova et al. 2017). These results give grounds to analyze how the interactions among glyphosate-degrading, glyphosate-sensitive and glyphosate "neutral" microbes in a microbial community may modulate the end-point response to glyphosate exposure in soils.

### Biodegradation in whole-soil studies

Most experimental studies of glyphosate degradation with whole soil were performed either in microcosms or soil columns, which present obvious limitations to reflect real conditions for soil degradation, yet they are clearly more representative than in vitro studies of isolated microbial degraders. The fundamental role of soil microbiota in glyphosate degradation and the influence of temperature and soil moisture in regulating their metabolic activities has been demonstrated in whole soil experiments by the use of abiotic controls (Bento et al. 2016; Tang et al. 2019; Sun et al. 2019; Muskus et al. 2020).

Table 2 shows studies reporting glyphosate degradation in soils in the period 2015–2021. They were conducted in a wide variety of soil types and textures as well as under different uses and management conditions, although most studies were performed on heavy soils (clayey to silty loam) and only a few were light soils (loam to sandy). All these

edaphic characteristics, as well as other soil properties (pH, organic carbon (OC), moisture, etc.), climatic conditions (temperature) and biota have been shown to affect glyphosate degradation at different degrees (Norgaard et al. 2015; Guijarro et al. 2018; Mercado and Mactal 2021).

Comparing the effect of the degradation rates between studies is difficult due to the large heterogeneity of formulations used and the limited information on the rationale for the chosen glyphosate doses. The informed doses ranged from 1 to > 100 mg kg<sup>-1</sup> (Table 2), while the average DT<sub>50</sub> in the microcosm's studies ranged from only 1.5 days (Bento et al. 2016) to almost 6 months (Padilla and Selim 2019), although under field conditions is probably short-lived (Guijarro et al. 2018; Carretta et al. 2021).

The vast majority of the studies were performed in agricultural soils. Therefore, a higher level of complexity is expected by the effect of agricultural management practices, such as fertilization, tillage, cover cropping, as well as by the previous glyphosate use history (Tang et al. 2019). Carretta et al (2021) analyzed the effects of tillage regime (no till, NT vs. conventional tillage, CT) on glyphosate degradation at two soil depths (0–5 and 5–20 cm) in a silt loam soil under maize-wheat/ soybean rotation. They suggested that, apart from influencing these soil properties, NT operation may also increase compaction and reduce the aeration necessary for microbial glyphosate degradation. P fertilizer added to glyphosate-treated microcosms resulted in mobilization of glyphosate in all soils, although a more marked effect was seen in a gray forest soil (Kulikova et al. 2020). This effect, however, did not increase the abundance of glyphosate-degrading bacteria that could use the herbicide as P source, nor affected the wheat growth in the exposed soils.

Glyphosate degradation in soils is thought to be driven by microbial co-metabolism, as the majority of glyphosate degrading microbes do not use it as source of C (Sviridov et al. 2015). It was recently shown that glyphosate degradation into AMPA was enhanced in microcosms amended with P and N sources and C limited, probably as a result of microbial use of the herbicide as a C source (Tang et al. 2019). The authors could not rule out, however, that co-metabolic degradation was taking place as a result of increased microbial activity. In another amendment experiment, soil plus C and N was P-limited and this promoted complete glyphosate degradation without any lag (Tang et al. 2019). In soil degradation experiments it has been demonstrated that the formation of AMPA through the GOX pathway is more frequently detected than the production of sarcosine resulting from the activity of the C-P lyase pathway. This may not necessarily represent the predominance of GOX pathway over C-P lyase pathway, but only the higher persistence of AMPA over sarcosine. Interestingly, a study that did not detect AMPA in any of the soils analyzed for glyphosate degradation suggested that the sarcosine pathway (C-P

**Table 2** Studies reporting glyphosate biodegradation in soils (2015–2021)

Study scale	Soil type <sup>a</sup>	Location	Soil management	Glyphosate dose and formulation <sup>b</sup>	Duration of experiment	DT <sub>50</sub>	Analytical method	Factors influencing degradation	Observations	Reference
Microcosms or soil columns	Ultisol	Agricultural Experiment Station in Newark, DE, USA	Corn/soybean rotation Chisel plowed P fertilization	1 $\mu\text{mol g}^{-1}$ (169 $\mu\text{g g}^{-1}$ soil)	175 days	28.9–31.5 days	LC–MS	Biota	AMPA half-life ranged 138.6 to 173.3 days Sarcosine pathway was absent	Sun et al. (2019)
	n.a	Hawkesbury-Napean River catchment area, NSW, Australia	Kikuyu grass pasture (LE), cereal-clover cropping field (ME), cleared field with GLY applications every 3 months	100 $\text{mg L}^{-1}$ (*)	180 days	n.a	HPLC–UV LC–MS	History of exposure, nutrients amendment (C, N, P)	Pre-exposure to GLY reduces lag time Both AMPA and sarcosine pathways are operative	Tang et al. (2019)
	Clayey, sandy	Uppsala, Sweden	Grassland since 2009, without pesticides	5 $\mu\text{g g}^{-1}$	31 days	n.a	radiorespirometry	Soil texture	Up to 30% Triton CG 110 used as coadjuvant had no effect on mineralization	Carretta et al. (2020)
	Stagnic Luvisol (clay loam)	Lamothe experimental station, Toulouse, France	Cover crops (avena, raygrass, mustard, vetch); wheat-sunflower rotation for 10 yrs previously, without GLY	2 $\text{L ha}^{-1}$ (**)	84 days	21 days	HPLC and radiorespirometry	Intercepting material	CC mulch residues vs. bare soil showed less degradation	Cassigneau et al. (2016)
	Silty loam loess	Nagelbeek, Netherlands	Harvested wheat field, no history of GLY available	16 $\text{mg a.i. kg}^{-1}$ soil (2.2 $\text{kg a.i. ha}^{-1}$ )	30 days	1.5 days to 53.5 days (non-sterile)	HPLC–MS/MS	Temperature, soil moisture, biota, light (minor)	No photodegradation AMPA dissipation behaves similar to GLY. At low temperatures (5 °C) AMPA pathway is predominant	Bento et al. (2016)

Table 2 (continued)

Study scale	Soil type <sup>a</sup>	Location	Soil management	Glyphosate dose and formulation <sup>b</sup>	Duration of experiment	DT <sub>50</sub>	Analytical method	Factors influencing degradation	Observations	Reference
	Humic Cambisols (sandy loam soil)	Piedecuesta, Santander Colombia	Andean raspberry cultivated area, with no history of GLY use available	50 mg a.i. kg <sup>-1</sup> soil	40 days	6–20 days	GC-C-irMS† LC-MS/MS‡	Temperature, TOC, pH	> 2.5% application rate of farmyard manure to soil increases non-extractable residues	Muskus et al. (2020)
	(Albic Retisol) Soddy-podzolic, Haplic Phaeozem (gray forest) and Luvisc Chernic Phaeozem (leached chernozem)	Solchnenogorsk, Tula and Danki, Russia	n.a	8 mg a.i. kg <sup>-1</sup> soil (6.7 L ha <sup>-1</sup> )	7 days + 14 days	n.a	HPLC-MS/MS	Phosphate application Soil type	GLY inactivated within 1–3 weeks in tested soils Wheat sprouts planted in the second stage in microcosms did not show phytotoxicity Sarcosine pathway suggested	Kulikova et al. (2020)
	Loam	Silstrup, Denmark	Danish Pesticide Leaching Assessment Programme, 5 GLY applications since 1983	1 mg kg <sup>-1</sup> soil	148 days	n. a	Microrespirometry coupled to autoradiography (radiolabeled GLY)	Ratio of clay to OC	First-order kinetics during 23 days > 6.6 × 10 <sup>4</sup> g <sup>-1</sup> degrader cells	Norgaard et al. (2015)
	Fluvaquentic Endoaquept (Silt loam) Chromic Epiaquept (clay)	Iberville Parish, LA, USA	Agricultural, cultivated soils	3 mg a.i. g <sup>-1</sup> soil	47 days	59–161 days	UPLC-MS/MS	Sorbed-phase degradation	Soil solution experiment (1:10 ratio) Lag time for onset of degradation 8–15 d AMPA pathway suggested	Padilla and Selim (2019)
	Aquic argiudoll (silty clay loam), Typic Argiudoll and Entic Haplustoll (silty loams)	Paraná, Pergamino and Manfredi (Argentina)	More than 16 yr under NT vs. CT, with maize/soybean or maize-wheat/soybean rotations. Annual applications of glyphosate (3–6 t ha <sup>-1</sup> )	6 L ha <sup>-1</sup> (4 mg a.i. kg <sup>-1</sup> soil)	62 days	9–38 days	UPLC-MS	Clay content, Adsorbed phosphate, CEC	Significant interactions for soil type and time; no differences between tillage type in the same soil Sarcosine pathway may predominate	Okada et al. (2019)



Table 2 (continued)

Study scale	Soil type <sup>a</sup>	Location	Soil management	Glyphosate dose and formulation <sup>b</sup>	Duration of experiment	DT <sub>50</sub>	Analytical method	Factors influencing degradation	Observations	Reference
Plot or field-scale	Luvic Phaeozem	INTA Balcarce, Argentina	Pristine soil (PO) and agricultural sites with 5 to 10 yr of glyphosate use (A5, A10), under CT and soybean/maize-wheat rotation	Commercial glyphosate formulation 48% 3 mg a.i. kg <sup>-1</sup> soil	72 days	8.6–16.1 days	UPLC-MS/MS	Kd and Kf which are proxies of sorption capacity of soils (and dependent on OM, CEC, clay)	Soils with higher sorption capacity of Glyphosate showed slower degradation due to limited bio-availability	Guijarro et al. (2018)
	San Manuel series, clay and clay loam	San Manuel, Taclac, Philippines	RR Corn fields cultivated since 2007, irrigation and NPK fertilization	1-gallon ha <sup>-1</sup> (0.96 mg kg <sup>-1</sup> soil)	90 days	n.a	GC	OM, clay, CEC, pH	> 90% degradation 15 days after application. Glyphosate residues were below I.o.d at 30 and 90 d.a.a	Mercado and Mactal (2021)
	Silt loam	Padova University Experimental Farm in the Po valley (Italy)	CT soil under maize-wheat soybean rotation NT included cover crops in the rotation, for 6 yr. Both had history of glyphosate	Roundup Power 2.0 4 L ha <sup>-1</sup> (1.44 kg a.i. ha <sup>-1</sup> )	182 day	8.3–17.7 days	UHPLC-MS/MS	Soil depth and tillage treatment	No lag phase for degradation in any treatment	Carretta et al. (2021)

n.a. not available; *GLY* glyphosate; *TOC* total organic carbon, *OC* organic carbon OM organic matter; *CEC* cation exchange capacity; *NT* no till; *CT* conventional tillage

\*Soil slurries were used

\*\*No calculation of concentration of a.i per kg possible

†Gas chromatography combustion isotope ratio mass spectrometer

‡Liquid chromatography tandem mass- mass spectrometry

<sup>a</sup>Soil type or texture as reported in the original article

<sup>b</sup>Dose and/or formulation as reported in the original article; when possible, concentration of a.i. per kg soil was also performed

lyase pathway) was predominant under their experimental conditions (Kulikova et al. 2020). Similarly, it was observed that glyphosate degradation did not result in a concomitant increase in AMPA levels, attributing this result to preferred herbicide degradation via C-P lyase pathway generating sarcosine (Okada et al. 2019). The authors highlighted that this pathway is usually underestimated because the labile nature of sarcosine and its production from many different natural sources makes it difficult to link its concentration to glyphosate degradation. In contrast, it was reported that, on average, 20 to 43% of the  $^{14}\text{C}$ -glyphosate applied to microcosms of two different soils was mineralized to  $^{14}\text{CO}_2$  while most  $^{14}\text{C}$  remained associated to the phosphonic acid moiety in AMPA, which is indicative of degradation via the GOX pathway (Padilla and Selim 2019). They showed that 18 to 40% of the adsorbed  $^{14}\text{C}$ -glyphosate was degraded to AMPA in the silt loam soil while 56 to 74% of it was converted in the clay soil, which despite a higher affinity to adsorb glyphosate may harbor a more active microbial community and/or degrading species. The non-significant relationship between sorption and degradation was previously postulated by Norgaard et al. (2015) when degraders are very numerous in a soil.

The composition of the glyphosate commercial formulation is also relevant with regards to the degradation rates and potential detrimental effects observed in soil experiments. The studies that have explored this aspect of glyphosate degradation are rather scarce, mainly because it is difficult to obtain proprietary information of commercial products so as to conduct appropriately controlled experiments that allow distinguishing between the active ingredient's effects from the surfactants and adjuvants' effects (Carretta et al. 2020). After the European Union banned the use of polyethoxylated tallow amine (POEA) adjuvant, most glyphosate-based products contain a blend of non-ionic alkyl polyglucoside (APG) and nitroaryl (Mesnage et al. 2019). Carretta and coworkers (2020) investigated the effect of different concentrations of the APG-based surfactant Triton CG-110, on the adsorption and mineralization of glyphosate when used in realistic doses in two soils of contrasting texture and inert sand. Triton CG-110 reduced glyphosate adsorption more strongly in the inert sand, followed by the sandy soil and only slightly in the clay soil, while no significant differences were observed among surfactant concentrations in the herbicide mineralization based on  $^{14}\text{C}$ - $\text{CO}_2$  evolution. This study showed that the presence of up to 30% Triton CG-110 in the formulations would have negligible effects in glyphosate degradation in soils (Carretta et al. 2020).

## Impact of glyphosate on soil microbial communities

### Soil bulk and rhizosphere microbiomes

A review published almost a decade ago already highlighted the role played by soil type and soil physicochemical properties on glyphosate biodegradation and on the inhibitory or stimulatory effects of glyphosate on soil microbiota (Wolmarans and Swart 2014). A later meta-analysis identified pH, glyphosate concentration, OC and time after application as moderator variables that significantly affected microbial biomass and its activity (Nguyen et al. 2016), and concluded that at recommended field application rates (i.e.  $< 10 \text{ mg kg}^{-1}$ ) glyphosate application had no significant effect on soil microbial respiration and soil microbial biomass. Using a range of enzyme activities and C substrates in three contrasting agricultural soils, Nguyen et al (2018) confirmed that soil type and formulation of the herbicide are important factors when assessing potential impacts on soil, although the effects on soil functions were negligible at application rates below  $2.9 \text{ mg kg}^{-1}$ .

Earlier investigations about glyphosate's effect on soil microbial communities were based on culture-dependent techniques, phospholipid fatty acid (PLFA) profiles, molecular fingerprinting analysis of 16S rRNA genes, such as denaturing gradient gel electrophoresis (DGGE) and terminal-restriction fragment length polymorphism (T-RFLP). Most of those studies showed minor or no effects on microbial community structure (see (Dennis et al. 2018) and references therein). The use of more advanced sequencing techniques for the study of microbial community structure allows for a more integrative analysis of the communities and a better understanding of the network of complex interactions present in soils. Yet even with the use of more sophisticated techniques, studies may still lack the needed statistical power to discern small differences between treatment and controls. Table 3 lists more recent published studies about the effects of the application of glyphosate on soil and rhizosphere microbiota.

Several studies have investigated the structure, diversity, and functions of microbial communities in short term experiments under controlled conditions in greenhouse and microcosm experiments and fewer have been conducted at field scale. Among the latter studies, three multi-site, multi-year field experiments did not find any impact caused by glyphosate on the whole populations of bacteria, archaea and fungi associated with the roots of glyphosate-resistant crops across diverse farming systems, regardless the previous history of herbicide use (Allegrini et al. 2015; Schlatter et al. 2018; Kepler et al. 2020). Similarly, only small effects on the wheat rhizosphere bacterial communities were found

**Table 3** Studies reporting effect if glyphosate on soil microbial communities (2015–2021)

Study scale	Type of soil <sup>a</sup>	Crops/plants	Glyphosate concentration	GLY use history	Taxa targeted	Analysis tool	Study length	Community changes	Pathogens fate	Country	Reference
Field	Silt loam Ultisols and silt loam typic Alfisol (ST)	Corn and soybean	0.87 kg ha <sup>-1</sup> twice at 4 weeks after planting	15 years	Bacteria, archaea and fungi	16S rRNA gene and fungal ribosomal ITS sequencing	2 years	No effects	No effects on <i>Fusarium</i>	USA	Kepler et al. (2020)
	Alluvial soils of sandy, brown primary material and rounded pebble stones	White grape variety Gewürztraminer ( <i>Vitis vinifera</i> L.)	Roundup® (200 g L <sup>-1</sup> ) applied at 3.75 L ha <sup>-1</sup>	None	Bacteria and fungi	16S rRNA gene sequencing	77 days	Non-significant increase of the relative abundance of cultivable and not-cultivable soil bacteria. Absence of fungus <i>Mucor</i>	Suppression of <i>Clonostachys rosea</i> , stimulation of <i>Colletotrichum</i> sp and mold <i>Striatibotrys</i> sp	Austria	Mandl et al. (2018)
	Luvic Phaeozem (WRB)	Maize-wheat/soybean	3 mg of active ingredient/kg soil	0, 5 and 10 years	Bacteria	16S rRNA gene sequencing	72 days	Small changes in relative abundance, especially in soil with no previous application history	N/A	Argentina	Gujjarro et al. (2018)
	Vertic Argiudolls, Typic Haplustolls (ST)	soybean, wheat, olives	N/A	8–20 years	Bacteria	CLPP, qPCR and DGGE	19 years	Non-significant changes in bacterial composition and abundance	N/A	Argentina	Allegrini et al. (2015)
	Clay loam Brown Chernozem (WRB)	Wheat ( <i>Triticum turgidum</i> var. durum Desf.)	450 g ae ha <sup>-1</sup>	N/A	Bacteria	Pyrosequencing	6–7 years	Few effects on the soil bacterial communities in wheat rhizosphere	N/A	Canada	Lupwayi et al. (2021)
	Silty clay loam Typic Natraquoll (ST)	Perennial grass <i>Lolium arundinaceum</i>	Glacoxan®, 3 L ha <sup>-1</sup> and 1.44 kg active ingredient ha <sup>-1</sup>	None	Pseudomonads	culturable pseudomonads and PCR-RFLP	4 years	Significant reduction of fluorescent pseudomonads	N/A	Argentina	Lorch et al. (2021)
	Sand (12 m3) and peat (12 m3) mixed with existing clay soil (pH 7.1)	short-lived perennial weed Lupinus polyphyllus	Roundup Gold (450 g L <sup>-1</sup> , equivalent to the recommended maximum dose of 3 kg ha <sup>-1</sup> )	> 10 years	Endophytic microbiota bacteria and fungi	HTS	59 days	Shifts in community structure of weeds endophytic microbiota	N/A	Finland	Ramula et al. (2021)
	Sandy clay soil Stagnosol (WRB)	Festuca pratensis	Roundup®Gold (450 g L <sup>-1</sup> ) 5 L ha <sup>-1</sup>	N/A	Arbuscular mycorrhizal fungal (AMF)	AMF root colonization	8 months	Decreased arbuscular mycorrhizal colonization, depending on tilling and soil history	N/A	Finland	Helander et al. (2018)

Table 3 (continued)

Study scale	Type of soil <sup>a</sup>	Crops/plants	Glyphosate concentration	GLY use history	Taxa targeted	Analysis tool	Study length	Community changes	Pathogens fate	Country	Reference
Field pot	typic Natraquoll (ST)	<i>Lolium arundinaceum</i>	3 L ha <sup>-1</sup> , (0, 384 and 1440 g active ingredient ha <sup>-1</sup> , respectively) applied in late summer	None	arbuscular mycorrhizal fungi (AMF), dark septate endophytes and (DSE) and free-living diazotrophs	AMF spore number and viability; AMF root colonization	4 years	AMF viable spores density reduced by 56%; total AMF root colonization not affected; reduced arbuscules percentage	N/A	Argentina	Druille et al. (2016)
	Silty-loamy Haplic Chernozem (WRB)	white clover seedlings ( <i>Trifolium repens</i> L.)	177.48 mL Roundup/m2	None	Bacteria and fungi	PLFA, MSIR	14 days	30% increase in microbial respiration, no effects on PLFA profile	N/A	Austria	Bruckner et al. (2019)
	Silt loam	wheat/canolas, wheat/fallow	2 times 1.68 kg ha <sup>-1</sup>	> 30 years	Bacteria	16S rRNA gene sequencing	2 years	Less than 1% of wheat rhizobacterial taxa impacted by glyphosate	N/A	USA	Schlatter et al. (2017)

Table 3 (continued)

Study scale	Type of soil <sup>a</sup>	Crops/plants	Glyphosate concentration	GLY use history	Taxa targeted	Analysis tool	Study length	Community changes	Pathogens fate	Country	Reference
Green-house	Silt loam Epiaqualf (ST)	corn and soybean	300.79 mL ha <sup>-1</sup>	None	Rhizosphere bacteria	16S rRNA gene sequencing	3 years	No significant impact on bacterial communities in the rhizosphere of corn and soybean	N/A	USA	Newman et al. (2016)
	Sandy haplic arenosol (WRB)	Soybean	Pots arranged in 1 m <sup>2</sup> and for each area a dilution of 0.3 mL glyphosate (360 g L <sup>-1</sup> ) in 40 mL distilled water was applied	None	Rhizosphere bacteria	T-RFLP profiles	14 days	Higher rhizosphere bacterial diversity compared to controls. <i>Burkholderia</i> sp significantly inhibited, Gemmatimonadetes significantly increased	N/A	Germany	Arango et al. (2014)
	Silt loam soil Vertic Epiaqualfs (ST)	soybean	800, 1200 and 2400 g a.e. ha <sup>-1</sup>	N/A	<i>Fusarium</i> , fluorescent pseudomonads, Mn-oxidizing and Mn-reducing bacteria	Plate cultivation	4 months	Suppression of fluorescent pseudomonads and Mn-reducing rhizobacteria	High root colonization by <i>Fusarium</i> spp.	Brazil/USA	Zobiole et al. (2011)
	dryland	wheat	2× recommended field rate, 1.68 kg ha <sup>-1</sup>	> 30 years	Fungi; bulk soil and rhizosphere	Fungal ribosomal ITS sequencing	2 years	Small impacts on fungal community composition or diversity. Most fungi influenced by glyphosate are saprophytes that likely feed on dying roots	Increase of <i>Fusarium</i> species in bulk soil, but not in the rhizosphere	USA	Schlatter et al. (2018)
	Vertic Argiudoll (ST)	<i>Avena sativa</i> L. var. Cristal	4 L ha <sup>-1</sup> , 662 g L <sup>-1</sup> , monopotassium salt	20 years	Bacteria	16S rRNA gene sequencing, CLPP	67 days	No differences in taxonomic diversity. Shifts in specific taxa, such as Betaproteobacteria, Verrucomicrobia, Mesorhizobium, Gaiella	N/A	Argentina	Allegrini et al. (2019)
	Vertic Argiudolls, Typic Haplustolls (ST)	continuous soybean/maize crop; Olive	3 applications separated by 14 days at a rate of 49 µg g <sup>-1</sup> soil	9–20 years	Ammonium oxidizing bacteria (AOB)	QPCR, DGGE		Abundance of Eubacteria and AOB was not affected by glyphosate. Shifts in the abundance of AOB relative to Eubacteria were observed. DGGE profiles of AOB were different between control and treated microcosms	N/A	Argentina	Allegrini et al. (2017)

Table 3 (continued)

Study scale	Type of soil <sup>a</sup>	Crops/plants	Glyphosate concentration	GLY use history	Taxa targeted	Analysis tool	Study length	Community changes	Pathogens fate	Country	Reference
Micro-cosms	Sandy loam Petrocalcic Paleustoll (ST)	none	1.9 kg ha <sup>-1</sup>	N/A	AOA, AOB	qPCR, DGGE	32 days	Glyphosate + N fertilizer amendment had no effect compared to fertilizer alone	N/A	Argentina	Zabalay et al. (2017)
	Sandy loam	Barley	2.4 mL of RoundUp (9.6 g L <sup>-1</sup> glyphosate)	N/A	Bacteria, flagellates and protists	DGGE, MPN, qPCR	30 days	Increase in protist abundance and in bacterial abundance and diversity	N/A	Denmark	Imparato et al. (2016)

<sup>a</sup>Type of Soil denotes soil texture and taxonomy when available. *ST* Soil Taxonomy, *WRB* World Reference Base

in a wheat monoculture or pea–wheat rotation in two tillage systems after 7 years of continuous glyphosate application in the field (Lupwayi et al. 2021), in different soil types with different herbicide application history in the field (Guijarro et al. 2018) or under laboratory conditions (Dennis et al. 2018). Likewise, glyphosate residues did not affect plant–microbe interactions or plant growth, despite shifts in the endophytic microbiota community structure (Ramula et al. 2021).

In contrast, after repeated application of glyphosate during 4 consecutive years, there was a reduction in the abundance of total culturable pseudomonads and enrichment in glyphosate-degrading lineages (Lorch et al. 2021). Suppression of rhizosphere fluorescent pseudomonads by glyphosate had been observed before in a greenhouse experiment (Zobilole et al. 2011). Whole cell metabolome studies suggested that the disruption of the de novo biosynthesis of aromatic amino acids, notably tryptophan, was responsible for the adverse effects of glyphosate on sensitive soil *Pseudomonas* species (Lorch et al. 2021). Indirect and confounding factors originate from the selective action of plant root exudates, which may influence or mask the effects of glyphosate on microbial communities, and reciprocally, the buildup of residues resulting from the effect of glyphosate on plants, which may alter the chemical composition of the rhizosphere and have subsequent impacts on rhizosphere communities. Since plant root exudates are key determinants of rhizosphere microbiota composition, glyphosate deleterious effect on rhizosphere pseudomonads may derive from the elimination of vegetation, which takes away substrates that they utilize for growth.

Whereas the consequences of the reduction of beneficial microorganisms on plant health cannot be ruled out, root microbiome contains a diverse number of bacterial and fungal genera. Several reports indicated shifts in microbial structures and functions, which can be attributed to release of organic matter from the dying roots following glyphosate application. These included the increase in soil microbial respiration (Bruckner et al. 2019), the contrasting changes in bacterial abundance of copiotrophs, such as Proteobacteria and oligotrophs, such as Acidobacteria (Newman et al. 2016; Schlatter et al. 2017), the response of saprophytic fungi (Schlatter et al. 2018), the increase in the abundance of rhizosphere culturable bacteria and protists (Imparato et al. 2016), and the increase in bacterial diversity (Arango et al. 2014; Schlatter et al. 2017). The influence that decaying root material may have on rhizosphere microbial communities following glyphosate desiccation call attention to the need of using proper controls of herbicide-free mechanical suppression (Allegrini et al. 2019).

Rhizospheric communities appear to play a role in the well-known ability of low doses of glyphosate to increase growth in a variety of plant species (Cedergreen et al. 2009).



**Table 4** Glyphosate fate in soil when arriving in plant residues or when applied to a soil surface covered with vegetal material (1997–2021)

	Mamy et al. (2016)	Cassaigne et al. (2016)	Doublet et al. (2009)	Von Wiren-Lehr et al. (1997)	Carretta et al. (2021)
Number of studied sites	1	1	1	4	2
Soil	Clay loam calcareous	Clay loam	Clay loam calcareous	NA	Silt loam
Soil history	NA	No glyphosate in the last 10 years	NA	<b>Org<sup>a</sup></b>	<b>Conventional tillage (CT)</b>
Plant material	Oilseed rape	<b>Vetch + oat, Vetch, White mustard, Ryegrass</b>	Oilseed rape	Soybean	Maize
Part of plants	Leaves	Aerial parts (not specified)	<b>Aerial parts: lamina, petiole, apex and stem</b>	Sterile plant cell culture suspension	Residues after maize harvest
Amount plant residues	plant:soil ratio = 3 g kg <sup>-1</sup>	8 t ha <sup>-1</sup>	plant:soil ratio = 3 g kg <sup>-1</sup>	0.28% w/w	1.48 t ha <sup>-1</sup>
Residue fragmentation	<b>Variable (entire, 3 mm, crushed)</b>	1 cm <sup>2</sup> /pieces	NA	Pulverized	Field conditions
Incorporation	<b>Yes<sup>b</sup></b>	No	Yes	Yes	No
Glyphosate interception	Applied to leaves (laboratory)	Applied to soil covered with mulch (laboratory)	Applied to leaves (laboratory)	Applied to soil	Applied to soil covered with 1-month old maize residues
Glyphosate rate	Active ingredient: 0.018 mg / leaf = 0.54 kg ha <sup>-1 c</sup>	Active ingredient: 2 L ha <sup>-1</sup>	Active ingredient or commercial formulation: 0.36 mg/leaf	Commercial formulation: 7.6 nmol glyphosate g <sup>-1</sup> dry weight vegetal residues <sup>-1 d</sup>	Commercial formulation: 1.44 kg ha <sup>-1</sup>
Labelled herbicide	Yes	Yes	Yes	Yes	No
Glyphosate half-life (DT50)	Up to 26.2 days (in plant)	7.1 days (bare soil)	28–47 days (in plant) (bare soil)	NA	NT: 17.7 days CT: 8.3 days
Incubation	80 days	84 days	35 days	26 days	182 days

Table 4 (continued)

	Mamy et al. (2016)	Cassigneul et al. (2016)	Doublet et al. (2009)	Von Wiren-Lehr et al. (1997)	Carretta et al. (2021)
Main reported effects of plant residues on glyphosate fate	<b>Protective effect</b> reduced mineralization, higher quantities of NER and extractable residues relative to soil with no vegetal residues	<b>Protective effect:</b> Lower cumulative mineralization relative to bare soil, increasing NER during incubation in the mulch compartment, increasing or constant NER in soil below mulch compartment	<b>Protective effect:</b> reduced mineralization, increased NER, extractable residues relative to soil with no vegetal residues	<b>Non-protective effect:</b> bioavailability of the plant-associated residues not reduced compared to free herbicide	<b>Protective effect</b> (relative to CT): significant increase in persistence in the 5–20 cm layer under NT
Other effects of plant residues on glyphosate fate	NA	Higher cumulative mineralization of soil organic carbon	NA	Higher microbial biomass C	NA
Other relevant observations	Availability for mineralization depends on size and distribution of plant residues	Higher NER in white mustard mulch than other cover crops, positive correlation between NER formation and mineralization in mulch and in soil below mulch	Significantly higher quantity of glyphosate in roots than stem or leaves (maize)	No correlation between microbial biomass C and mineralized C from glyphosate	Glyphosate concentration at day 182 was higher under NT relative to CT

Text in bold letter indicates properties that were considered as experimental factors in the corresponding studies. NA indicates no information available

<sup>a</sup>Org: organic cropping with no pesticide and mineral fertilizer for 15 years. Conv: Close to Org site treated regularly with pesticides and mineral fertilizers. Conv to org: Conventional to organic farming, organic farming in the last 2 years. Hop: regular fungicide applications, hop plantation

<sup>b</sup>Degrees of incorporation: surface, middle or homogeneous distribution depending on the leaf fragmentation

<sup>c</sup>The equivalence is based on an application volume of 150 L ha<sup>-1</sup> in agreement with the dose usually used for weed control in oilseed rape

<sup>d</sup>140 mg vegetal residues 50 g<sup>-1</sup> soil

Ramirez-Villacis demonstrated that even though low doses of glyphosate produced only small changes in the composition of the root microbiome of *Arabidopsis*, there is a complex interplay between the plant associated bacteria and the plant's hormesis response to the herbicide, which depends on the presence or absence of root growth inhibitors and other bacterial strains in the rhizosphere (Ramirez-Villacis et al. 2020).

### Emerging concerns on glyphosate-exposed microbial communities

A growing number of studies in the last three years have begun to raise concerns about the effects of glyphosate in one of the major strategies of bacterial communities to adapt to environmental changes and generate genetic diversity: the horizontal gene transfer (HGT) process and its role in antibiotic resistance proliferation. The implications of these effects acquire a special relevance in agroecosystems, where the release of antibiotics of veterinary use through direct deposition of animal feces and urine, treated waste and liquid effluents from intensive animal husbandry and soil application of manure and organic amendments, contributes to the spread of antibiotic resistant bacteria and the transmission of antibiotic resistance genes (ARGs). Shifts in mobile genetics elements (MGEs) and bacterial conjugation of broad host-range plasmids have all been reported in glyphosate-exposed soils. Exposure of bacterial communities in bulk soil to pure glyphosate ( $10 \text{ mg kg}^{-1}$ ) significantly raised the number and the relative abundance of MGEs and ARGs and higher conjugation frequency compared to the controls (Liao et al. 2021). Interestingly, these changes were observed even in the absence of large shifts in taxonomic composition, suggesting a cryptic herbicide-mediated selection acting on genetic composition rather than on species abundances. A stimulation of conjugative transfer rates in a concentration-dependent manner was also reported in aqueous medium, at concentrations between  $0.1\text{--}0.6 \text{ mg L}^{-1}$  in the culture medium (Zhang et al. 2021). Shifts in broad host range plasmids (Allegrini et al. 2019) or transposons genes (Zeng et al. 2021) have also been reported in rhizospheric soil of common oat (*Avena sativa* L.) and cassava (*Manihot esculenta*), respectively. Allegrini et al (2019) reported changes in the occurrence of broad host range plasmids (IncP-1 plasmids from  $\epsilon$  and  $\beta$  subgroups) in the rhizosphere of a cover crop under glyphosate desiccation without clear changes in the structure of bacterial communities. IncP-1 plasmids from the  $\epsilon$  and  $\beta$  subgroups have been suggested as important vectors in agricultural systems for HGT of antibiotic resistance genes (Heuer et al. 2012).

A higher relative abundance of whole MGEs was detected in the rhizosphere metagenome of glyphosate-treated plants as well as a higher relative abundance of *istA* and *istB* genes,

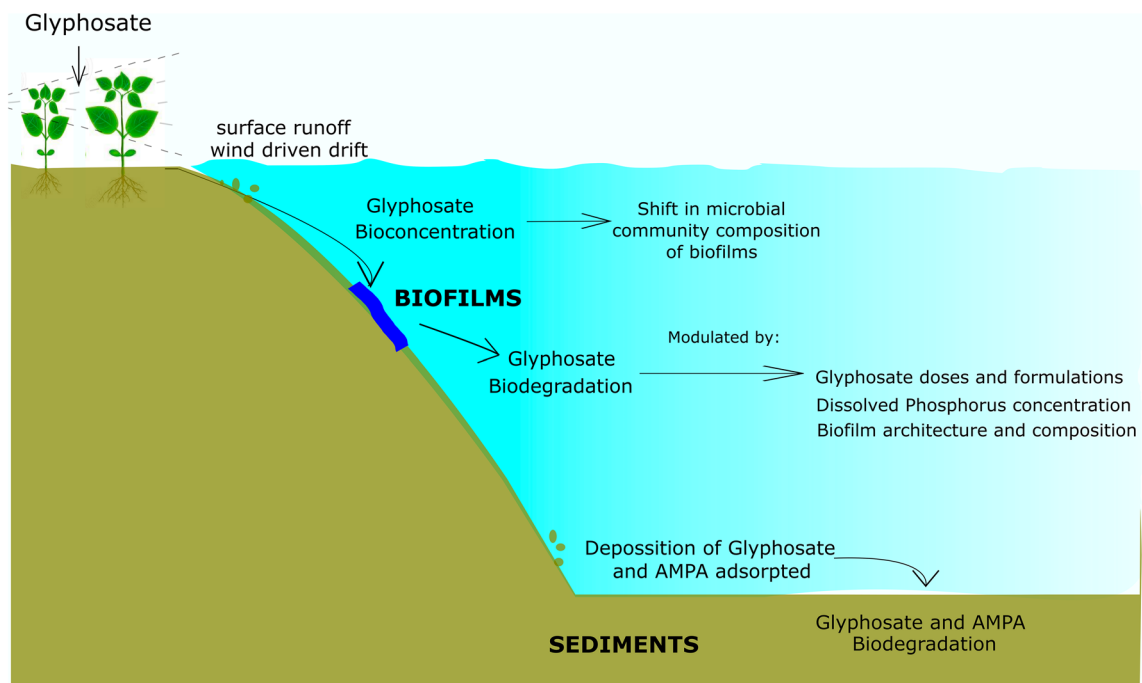
related with IS21 family of transposons (Zeng et al. 2021). This family can modulate the expression of several flanked genes, including genes encoding efflux pumps for antimicrobial and xenobiotics compounds (Vandecraen et al. 2017). Interestingly, degradative genes have also been reported to be flanked by members of IS21 family, such as the organophosphorus degradation gene *opd* (Singh and Walker 2006). Whether a potential relationship exists between MGEs in complex soil microbial communities and the spread of degradative genes among several taxa of known degraders remains unclear (Table 1). Nevertheless, genomic analyses have indicated that *phn* genes for phosphonate degradation are frequently located close to genes encoding transposases or inactivated transposases and phylogenetic analyses suggest an extensive lateral gene transfer during evolution of phosphonate degradative pathways (Huang et al. 2005). Also, for some rhizobacteria such as *Mesorhizobium loti*, *phn* genes have been detected in conjugative plasmids close to genes for transposases and may have evolved separately from its chromosomal counterpart (Huang et al. 2005).

The exact biological mechanism triggered by glyphosate to increase the transfer rates of MGEs through conjugation has not been completely elucidated (Zhang et al. 2021; Liao et al. 2021). Beyond the biological mechanisms that mediate higher conjugation frequencies, it should be highlighted that a well-described inducer of HGT is the exposure to subinhibitory environmental levels of several antibiotics (Bernier and Surette 2013; Iavicoli et al. 2021) and pesticides (Xing et al. 2020), as well as mixtures of pesticides and antibiotics (Xing et al. 2020). Thus, from a microbial ecology perspective, future concerns about the effects of glyphosate in microbial communities should be based on subinhibitory levels rather than focusing only on residual glyphosate levels above the minimum inhibitory concentration values for the different bacterial taxa. This consideration is particularly relevant because specific environments, like the rhizosphere, the high microbial activity stimulates a fast dissipation of xenobiotics, e.g. antibiotics (Jechalke et al. 2014) and root exudates lead to an acidification, which stimulates glyphosate sorption.

Water bodies, impacted by agricultural anthropic activities, are scenarios that incorporate a wide variety of chemical contaminants, including antibiotics, which makes them propitious for the acquisition and dissemination of ARGs. Yet information related to exposure to glyphosate as a possible booster of the HTG in aquatic environments is lacking.

### Arbuscular mycorrhizal fungi

Even though glyphosate targets plant's EPSPS, the presence of the enzyme homologues in non-target organisms creates concerns about its potential effects on beneficial soil microorganisms. Arbuscular mycorrhizal fungi (AMF)



**Fig. 2** Fate of glyphosate in aquatic environments

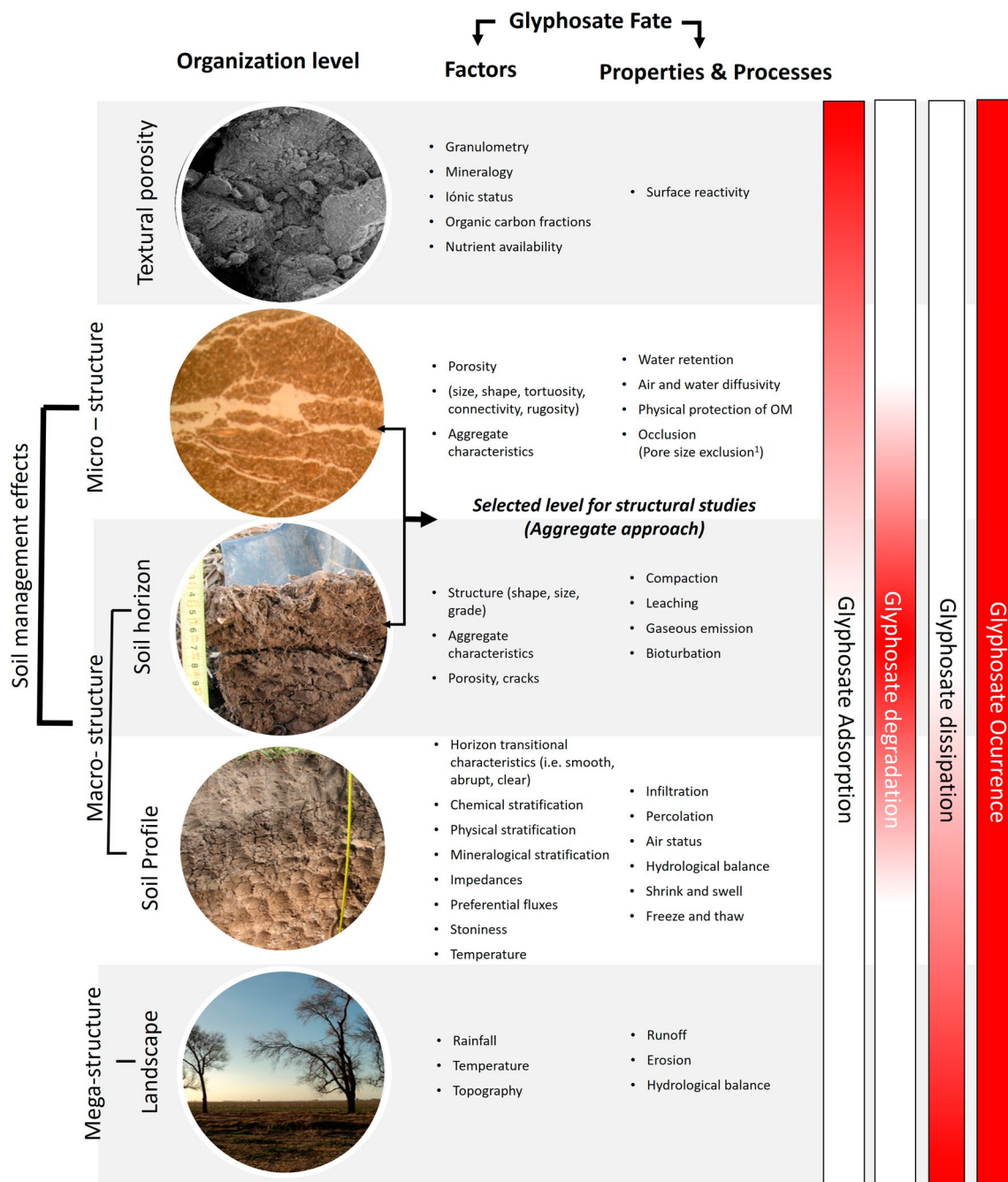
establish symbiotic associations with plant roots, contributing to plant nutrition and growth. Wilkes et al. (2020) did observe decreased mycorrhizal colonization of wheat roots under no-till conditions following glyphosate application. However, they also noted that the consequences on AM fungal growth were less marked than the physical damage of the AM fungi hyphal structures caused by the soil inversion in conventional tillage. More pronounced effects of residual glyphosate on mycorrhizal colonization of crop plants and forage grasses were observed in cold climatic conditions, where the rate of glyphosate degradation is slower (Helander et al. 2018).

It was also observed that two years of glyphosate application to a glyphosate residue-free soil caused a shift in the relative abundance of AM species without affecting the root colonization level (Sheng et al. 2012), whereas total AMF root colonization was neither affected, although arbuscules percentage and AMF viable spores were reduced (Druille et al. 2016). Similarly, the decreased growth of AMF caused by the combined effects of glyphosate and nitrogen fertilization, did not translate into any detectable effect on below-ground and above-ground interactions, or crop productivity (Nivelle et al. 2018).

## The influence of plant residues on the fate of glyphosate in soil

### The effects of plant residues on bioavailability and biodegradation

The fraction of glyphosate released into the soil via translocation to the roots and exudation has been thoroughly investigated (e.g. Rodrigues et al. 1982; Martinez et al. 2018). A comparatively less studied aspect is the fraction that reaches the soil environment with plant residues, which is associated with the decomposition of treated vegetal residues (aerial/root biomass). Earlier studies found no significant differences in the mineralized fraction, nor in the bioavailability of glyphosate from plant residues among soils with different histories of herbicide application (Von Wiren-Lehr et al. 1997). An increase in the non-extractable residues (NER) in soil and a decrease in the mineralization of  $^{14}\text{C}$ -labeled glyphosate was reported for the first time in incorporated oilseed rape (*Brassica napus* L.) residues (Doublet et al. 2009) (Table 4). Later studies using  $^{14}\text{C}$ -labeled glyphosate supported these observations, namely an increase in NER in soil and a higher glyphosate persistence associated to the vegetal tissue, i.e. protective effect, even with different plant materials and different modes of exposure to the herbicide (Cassigneul et al. 2016; Mamy et al. 2016). The negative correlation between NER and soluble glyphosate fraction in mulch, together with a weak mineralization and a steady sorbed fraction suggested that NER formation is one of the



**Fig. 3** Main factors, properties, and processes related to glyphosate fate at different levels of observation. Colored bars indicate high (red) to low (white) relationship of glyphosate adsorption, degradation, dissipation, and overall relationship to each one of observation levels

main dissipation pathways in cover crop mulch (Cassigneul et al. 2016). NER formation can involve different processes including retention in the nanopores, diffusion to sites with low accessibility or chemical stabilization by bonding (Cassigneul et al. 2016). Similar processes have been described for antibiotics in the soil environment, reducing the bioavailability with increasing contact time (Jechalke et al. 2014). However, in contrast to many antibiotics for which

mineralization represents less than 2% of the initial quantity, the fate of glyphosate is strongly influenced by its rapid degradation in soil. Thus, NER formation is not only related with a physical entrapment but also with biogenic NER formation from the degradation products (Muskus et al. 2019). Agricultural management favoring mineralization and biogenic NER formation by endogenous microorganisms in soil constitute a promising area of research (Muskus et al. 2019).



The fate of glyphosate in entire roots buried within the soil profile warrants a special consideration, as mineralization rates are lower for glyphosate in entire plant residues than those homogeneously mixed in soil (Mamy et al. 2016). This is a particularly relevant field of research for glyphosate sensitive crops, in which glyphosate applications are followed by a turnover period of necrotic root tissues (Imparato et al. 2016). Knowledge in this area will contribute to predict potential effects on crops sown immediately after application of glyphosate, as expected on cash crops after cover crop desiccation. Similarly, for perennial forest plants, recent studies have demonstrated that residual glyphosate can be detected for up to 12 years post-treatment in the roots of fireweed (*Chamaenerion angustifolium* L. Scop), with a retention of more glyphosate and for a longer period than shoots (Botten et al. 2021).

### The effects of organic amendments on glyphosate fate

Recent studies have demonstrated that glyphosate in animal feed can accumulate in excretion products and spread via organic fertilizers, decreasing the growth of a forage grass (*Festuca pratensis*) and of the strawberry *Fragaria x vesca* (Muola et al. 2021). Mineralization of  $^{13}\text{C}_3$ -glyphosate was higher in microcosms amended with cow farmyard manure relative to the control microcosms (Muskus et al. 2019). Similarly, extractability of glyphosate was also higher, consistent with a raise in soil pH due to manure additions (higher pH is a known cause of lower glyphosate adsorption). Microbial metabolism was also consistent with a higher percentage of biogenic NER (between 70 and 87%) than xenobiotic NER in manure-treated microcosms (Muskus et al. 2019).

### Fate of glyphosate in aquatic environments

Glyphosate and AMPA contaminate aquatic environments mainly as a consequence of direct overspray or wind driven drift during herbicide applications. Molecules sorbed to soil particles, can also be transported by lixiviation—preferential flow through soil macropores- and surface runoff when heavy rains occur shortly after herbicide applications (Borggaard and Gimsing 2008). As a result, both glyphosate and AMPA were often detected in surface water, groundwater and sediments in several parts of North and South America, Europe, Asia and Oceania. Glyphosate measures in aquatic environments were mostly in ppb levels, with values ranging from 0.2 to 45  $\mu\text{g L}^{-1}$  in surface waters, 0.1 to 9.7  $\mu\text{g L}^{-1}$  in ground waters and 0.5  $\mu\text{g kg}^{-1}$  to 1  $\text{mg kg}^{-1}$  in sediments (Okada et al. 2018, 2020; Gunarathna et al. 2018; Pires et al. 2020; Geng et al. 2021). The fate of glyphosate

biodegradation in aquatic environments is schematized in Fig. 2. The average half-life of glyphosate in water bodies may vary from a few days to 3 months (Tomlin 2006). The evidence indicates that, similar to soil, the herbicide degradation in water bodies is carried out by microorganisms of multiple genera and by different and complementary metabolic pathways (Huntscha et al. 2018; Rossi et al. 2021). This process is mainly associated to sessile communities (biofilms, sediments) rather than to free-living microorganisms (Wang et al. 2016; Lozano et al. 2018). Accordingly, periphyton is more resistant than phytoplankton to glyphosate, both in single formulations as in mixture with other herbicides (Lozano et al. 2018). Microbial resilience, both at structural and taxonomic levels, depends on the initial glyphosate concentration (Vera and Trinelli 2021).

Several cyanobacterial strains have tolerance to glyphosate (Forlani et al. 2008), and many have the capacity to use it as a sole source of P or N (Lipok et al. 2007; Lozano et al. 2018). Strains evaluated in laboratory assays included the genera *Arthrospira*, *Anabaena*, *Leptolyngbya*, *Microcystis*, *Nostoc*, *Synechocystis* and *Spirulina* (Lipok et al. 2007; Forlani et al. 2008; Lozano et al. 2018). Bacteria belonging to genera such as *Acidovorax*, *Agrobacterium*, *Ensifer*, *Novosphingobium* and *Ochrobactrum*, co-existing in stream biofilms, have metabolized glyphosate and AMPA by different and complementary pathways (Rossi et al. 2021).

Mineralization in sediments, the matrix with the highest concentration of glyphosate (Ronco et al. 2016; Wang et al. 2016), occurs through the sarcosine and the AMPA degradation pathways (Wang et al. 2016). Organic matter, total phosphorus (P), copper (Cu) and sulfides are related with the dissipation rates of glyphosate and AMPA on sediments (Ronco et al. 2016). The rates of glyphosate degradation are much higher and have shorter lag phases at lower glyphosate concentrations (Wang et al. 2016) and are not influenced by the level of glyphosate pre-exposure (Tang et al. 2019). In turn, the high frequencies of AMPA detection in sediments could indicate that this molecule is persistent and more resistant to biodegradation than glyphosate (Tang et al. 2019).

Biofilms play an important role in the bioconcentration and biodegradation of glyphosate. The herbicide concentration in biofilms is almost 2 to 4 orders of magnitude higher than those found in the surrounding water (Beecraft and Rooney 2021). These dynamic and complex communities, composed by diverse groups of bacteria, archaea, fungi, viruses, algae and protists, are embedded in a protective polymer matrix that facilitate glyphosate bioconcentration (Klátyik et al. 2017; Carles et al. 2019). The presence of glyphosate is accompanied by an increase in the rate and extent of glyphosate metabolism (Klátyik et al. 2017), along with changes in biofilm microbial communities (Gonzalez et al. 2019; Carles and Artigas 2020). Glyphosate uptake by



biofilms could be influenced by periphyton total biomass, which increases during submersion periods and is modulated by water velocity in streams and lakes. The periphyton thickness and its microarchitecture are additional factors that contribute to the sensitivity to glyphosate (Khadra et al. 2018). Microalgal photosynthetic organisms- diatoms- and eukaryotes in general are more susceptible to increasing glyphosate concentrations (Corrales et al. 2021), whereas shifts in the structure of prokaryotes are associated with glyphosate transformation (Artigas et al. 2020; Carles and Artigas 2020). The eutrophication by P favors the incomplete degradation of glyphosate in aquatic systems and the formation of AMPA. In natural river biofilms, the rate of glyphosate biodegradation is modulated by the concentration of P and is not related to the previous exposure to the herbicide (Carles et al. 2019). Yet, a higher frequency of detection of a *phnD* gene involved in the metabolism of glyphosate, as well as an increase of picocyanobacteria communities, were reported in lakes impacted by glyphosate use for almost 3 decades (Berman et al. 2020). The amount of the dissolved organic matter (DOM) contributed by photoautotrophic organisms does not enhance the glyphosate degradation rate in aquatic biofilms (Artigas et al. 2020).

### Factors and processes that affect glyphosate fate at different levels of soil organization

Soils are characterized by a complex organization, which derives both from the physical arrangement -or structuring- of its components at different spatial scales, as well as from the dynamic nature of these structures in time and space. Numerous factors and mechanisms play in those different levels of organization influencing different functional parameters, particularly the retention and movement of water and, therefore, of soluble elements and colloidal particles. Consequently, processes related to the fate of glyphosate can be analyzed at different levels of observation, ranging from the nanoscale in soils and sedimentary materials to megastructures at the landscape level, and thus through a multiplicity of analytical techniques (Fig. 3).

### Soil components and herbicides behavior

Most of the studies on the behavior, interactions and fate of glyphosate in soil are related to surface processes that occur at the nano-scale level of organization and are evaluated using ground and sieved samples. It has been shown that high sorption and low desorption kinetics affected glyphosate bioavailability (Gómez Ortiz et al. 2017). As shown in Tables 1 and 2 the main glyphosate degradation determinants are soil texture, clay mineralogy (content and composition), organic carbon fractions (source and concentration),

clay/organic carbon ratio, salinity, pH, cation exchange capacity (CEC), phosphates and Fe-oxides (Ololade et al. 2014; Sidoli et al. 2016). Most of these variables express the ionic charges of the soil exchangeable complex and surface reactivity, and thus the affinity or adsorption of glyphosate molecule in soils. Glyphosate is an anion that can be sorbed onto variable-charge surfaces and there is a consensus that it has a high affinity to soil and organic carbon fractions (organic carbon–water partition coefficient,  $K_{oc}$ , in units of  $L\ kg^{-1}$ : 884–60000). In terms of location and charge density of soil minerals, edge sites and external surfaces of the clay minerals have been described as relevant sites for glyphosate degradation (Maqueda et al. 2017). Thus, the main sorption surfaces are those of Fe and Al oxides and poorly ordered aluminum silicates, whereas soils dominated by permanent charge minerals such as illite and other 2/1 clay minerals sorb less glyphosate (Borggaard and Gimsing 2008; Maqueda et al. 2017). Several authors agreed that this process is governed by the mineral phase rather than by the organic phase (Rampazzo et al. 2013). However, there is evidence that suggests that mineral-organic complexes may have higher glyphosate adsorption rates (Albers et al. 2009). In a recent study, kaolinite bound with humic acids showed higher adsorption compared to clean kaolinite (Guo et al. 2021). Hence, at this level of analysis, surface reactivity is a key process modulating glyphosate affinity through adsorption on the mineral fraction and on the organic carbon fraction and its subsequent degradation (Yang et al. 2018; la Cecilia and Maggi 2018).

The reactivity of mineral and organic fractions have been synthesized in affinity measurements (*i.e.* the linear sorption coefficient,  $K_d$ ), which are derived from some readily available soil variables as clay content, pH, CEC and OC. Thus, affinity coefficients estimated from these and other soil variables have been used in pedotransfer functions and modeling to predict the adsorption and degradation of different herbicides, including glyphosate, in soil profiles and at landscape level (De Gerónimo et al. 2018; Giannini Kurina et al. 2019).

### Soil architecture, soil biology and herbicide fate

Although most studies relate degradation process of herbicides to soil characteristics measured on bulk soil samples, the values obtained poorly reflect local environmental conditions and the spatial heterogeneity of microorganisms (Vieublé Gonod et al. 2006). Clearly, studies on homogenized samples do not take into account the physical and chemical anisotropy of the soil, which increases as the scale of soil organization increases. For instance, lower CEC values have been obtained using undisturbed compared to sieved soil samples and different soil moisture and critical density limits (*i.e.* Proctor tests) were obtained from disturbed and undisturbed samples (Hartmann et al. 1998). This implies that the

ionic state together with the actual biological habitats cannot be derived from disturbed soil samples. In this sense, Chaplain suggested that “to improve the understanding of the fate of pesticides in soils, there is a need to better take into account the soils heterogeneity and variability. Thus, studies have to consider relevant integrative parameters describing the soil structure and interfacial properties” (Chaplain et al. 2011).

Microbiological processes including glyphosate degradation, occurs in physical environments where air, water and nutrients are further dependent on the organization of mineral and organic components. Thus, soil habitats must be considered as a key factor regulating not only glyphosate biodegradation but also glyphosate adsorption and dissipation, leading to an overall occurrence of this molecule in the environment. The interaction between soil type and its management, defining soil structure, surface reactivity and therefore soil habitats, are main factors controlling biological composition and activity (Rosa et al. 2014; Morriën et al. 2017). Hence, detailed description of soil characteristics, properties and structural arrangements is highly relevant.

### Textural porosities

Physical habitats and their influence on microbial behavior can be characterized at different levels of organization (Fig. 3). A first level of soil organization is what has been called “basic microstructure” (Stoops 2021) and corresponds to what is commonly called “textural porosity” and is the result of the random packing of soil particles. The characteristics of the pores thus formed depend on the size, morphology and crystallo-chemical composition of the particles involved. At this level of organization, porosity is given by micro- and nanopores (pores < 2  $\mu\text{m}$ ).

The sorption of several pesticides in micro-nanopores have been studied in natural soils and sediments as well as in different model solids (Hatzinger and Alexander 1995). Nanometer-scale pores have dimensions comparable to the sizes of organic molecules and biological molecules and they can cause significant preservation of degradable organic contaminants. Physical shielding of organic molecules and exclusion of microorganisms from micro-nanopores are mechanisms causing preservation of pesticides (Cheng et al. 2012). Thus, protection of glyphosate in textural pores can inhibit their abiotic and biotic transformations and reduce their bioavailability, playing a key role on its long-term fate in the environment.

### Structural porosities

The characterization of higher levels of soil structural organization is framed by the joint evaluation of aggregation and porosity. Several parameters are considered to describe soil

aggregates and pores, including the surface to pore volume ratio that indicates the level of interaction between soil and biological entities. Aggregate and pore characteristics control the hydrological connectivity of soils (Behrends Kraemer and Morrás 2018a), biogeochemical processes (Horn and Kutilek 2009) and microbial habitats (Nunan et al. 2006), which in turn are influenced by both soil inherent properties and soil management. Conversely, soil structural cohesion, strength and stability as well as pore features are strongly influenced by the interactions between microorganism and soil groundmass. In opposition to textural porosity, structural porosity resulting in the development of soil aggregates offers a wider diversity of pore sizes and thus of physical habitats (Chenu and Cosentino 2011) and the geochemical cycles most relevant for soil microbiome appear to occur within and between soil aggregates (Wilpiseski et al. 2019). These facts support the conception that soil aggregates represent a suitable organization level and an appropriate transition scale between laboratory studies on disturbed and homogenized samples and field measurements.

The relationship between aggregate and pore characteristics and biological process have been studied using different techniques, including micromorphology and micromorphometry on soil thin sections, mercury intrusion porosimetry, scanning electron microscopy, X-ray computed tomography, electron and atom probe tomography, small-angle neutron scattering. A complete description of benefits and limitations and spatial resolution of these techniques are discussed in (Wilpiseski et al. 2019). Soil structure and porosity are complex and difficult to quantify, yet such information is essential to predict soil transport properties. The advent of 3D imaging technology as X-ray computed tomography as well as the development of mathematical models to construct 3D images based on the 2D measurements can bridge the gap. On the other hand, the spatial organization of bacterial cells in soil pore space can be described and quantified using a combination of thin sections with image analysis and mathematical modeling (Wu and Zhang 2011).

### Micro-structure

Several researchers have suggested that sub-millimeter spatial scale and aggregate-based approaches are the most relevant to study microbial communities and their interaction with bio-geochemical processes (e.g. Wilpiseski et al. 2019). Microscale spatial patterns may have a regulatory effect on bacterial density (Nunan et al. 2003) and activity (Grundmann et al. 2001), and on microbial functional expression (Vos et al. 2013).

The microscopic architecture of the edaphic habitat can influence the degradation of glyphosate through different processes. Firstly, oxygen diffusivity as well as water and organic carbon availability play a major role on glyphosate

degradation metabolic pathways (Ia Cecilia and Maggi 2018). Circulation of fluids and their availability in soil are regulated by the characteristics of the structure (*i.e.* size, morphology, and degree of development of aggregates) and by pore geometry (*i.e.* shape, orientation, continuity, tortuosity and rugosity features) (Morrás 2015; Stoops 2021). In turn, soil structure and pore characteristics depend both on the type of soil and the agricultural management (Woignier et al. 2011; Behrends Kraemer et al. 2022b). In Mollisols under no-till, platy structures with horizontal pore orientation decreased the saturated hydraulic conductivity (Behrends Kraemer and Morrás 2018a) or restricted infiltration and increased runoff process (Sasal et al. 2017; Behrends Kraemer et al. 2022b), highlighting the importance of processes occurring in the pores and on their surfaces. The stability of aggregates must also be considered, given the strong dependence of soil biology on both morphology and pore stability (Carrizo et al. 2015).

Secondly, the physical entrapment of organic molecules in small pores conditions their bioavailability and reduces the degradation by bacteria and fungi. This is in agreement with the “pore size exclusion” theory, where the interaction between different molecules, soil particles and biological entities depends on the size of the neck of pores. Sorption in micropores prevents contaminants from being accessed by microorganisms and their extracellular enzymes, and can also inhibit abiotic degradation by protecting them in confined spaces with little reactive water, slowing down hydrolysis and other water-mediated transformations (Cheng et al. 2012). Woignier showed that transport of agrochemicals depended on soil microstructure, mesopores and tortuosity (Woignier et al. 2018).

In summary, soil microstructure has a profound effect on water and air dynamics controlling the accessibility and activity of microorganisms, and therefore on the occurrence and degradation of glyphosate.

### Macro-structure: soil horizon

Although natural processes define the macro-structural arrangement of the soil, any agricultural management produces a strong modification of the morphology of aggregates and the geometry of pores, influencing the circulation of fluids and thus soil physical, chemical and biological processes. Agricultural management may affect glyphosate degradation rates by producing compaction and by lowering oxygen diffusivity, water transmission and retention (Villarreal et al. 2020). On the other hand, glyphosate availability in topsoil is related to the residence time in the soil matrix, which could be affected by a high proportion of large vertical macropores, enhancing leaching (Medalie et al. 2020), or by dense and platy structures (Sasal et al. 2017) enhancing runoff and superficial redistribution. The cultural profile

methodology focusing on macro-structural features and their spatial heterogeneity has been useful to explain water flux and pesticides fate (Filipović et al. 2014). Management treatments differing in tillage and crop intensities affect the balance between mechanical densification and bioturbation processes, with great impact on structural quality and pore geometry, general anisotropy and thus air and water fluxes related to soil biological habitats (Behrends Kraemer and Morrás 2018a).

### Macro-structure: soil profile

Although most glyphosate transformations and dynamics occur in the surface horizon of the soil, the soil as a whole plays a meaningful role. The solubility, mobility and bioavailability of organic pollutants, together with the differences in soil permeability, regulate the fate of agrochemicals. Numerous studies indicate that glyphosate could be transported through preferential flow, losing its bioavailability (Caprile et al. 2017). Thus, horizon sequences, characteristics, limits (*i.e.* smooth, abrupt) and impedances governing water balance and aeration must be considered when adsorption of herbicides is analyzed.

However, when densified structures are present in the upper part of the soil, which are also frequent under no-till management (Behrends Kraemer and Morrás 2018b; Castiglioni et al. 2018; Behrends Kraemer et al. 2022a), superficial or sub-epidermal lateral flow occurs, rather than deep preferential fluxes. Infiltration and hydraulic conductivity, and thus movement of glyphosate, are highly dependent on soil management. Soracco found higher temporal variation and vertical transport of glyphosate and AMPA in a Mollisol under conventional tillage than under no-tillage (Soracco et al. 2018). In turn, platy structure resulting from no-tillage also restricts water entry into the soil and favors surface runoff (Sasal et al. 2017). Usually, the degradation of soil structure limits leaching, increasing the concentration of glyphosate and its metabolites in the topsoil, as well as its surface dispersion (Silva et al. 2018; Andrade et al. 2021; Mac Loughlin et al. 2022). Thus, superficial and sub-superficial processes linked to agricultural managements appear to be the main drivers that modulate glyphosate availability for microbial degradation.

### Mega-structure: landscape

Landscape scale integrates all previously discussed levels of organization that should be considered to evaluate the fate of pesticides in the environment. At this level, the occurrence of a high complexity of adsorption, degradation and dissipation processes are synthesized in the quantity and distribution of residues finally found in soil and water.

The complexity at the landscape level relates to their interaction with different agricultural practices, making the behavior of pesticides varied and difficult to decipher (Morás et al. 2022). For instance, glyphosate fate is controlled by the interaction between tillage, crop phenology, product application timing and climate conditions (Stenrød et al. 2006; Yang et al. 2015; Silva et al. 2018; Andrade et al. 2021; Mac Loughlin et al. 2022). Dissipation processes, including sorption and desorption, are strongly related to the main factors playing at this level: climate, topography, vegetation and soil type (Fig. 3). Rainfall intensity, frequency and regime are main factors affecting glyphosate leaching and degradation (Borggaard and Gimsing 2008; Lefrancq et al. 2017; Andrade et al. 2021; Mac Loughlin et al. 2022). Temperature is also a factor that directly affects biological and biogeochemical reactions (Chow et al. 2020), affecting water status due to evapo-transpiration mechanisms. Glyphosate persists when inadequate biological habitats constrain biological activity, as in dry soils and at very low temperatures (Bento et al. 2016).

Factors at the megastructure level modulate runoff, hydric and wind erosion and thus soil water balance. These external factors may interact with pesticides in soil, affecting their occurrence in different environmental matrices (Stenrød et al. 2006; Yang et al. 2015). The risk of ground and surface water pollution by glyphosate has been considered limited because of sorption onto variable-charge soil minerals and because of microbial degradation (Borggaard and Gimsing 2008). However, water erosion may be an important pathway driving glyphosate towards water bodies (Todorovic et al. 2014; Yang et al. 2015; Caprile et al. 2019). Wind erosion process is also considered an important driver of glyphosate transport (Bento et al. 2016; Mendez et al. 2017; Silva et al. 2018; Ramirez Haberkon et al. 2020).

In summary, the adsorption and the clear tendency of accumulation of glyphosate and its metabolites in the first centimeters of soil, explain the magnitude of erosion-driven transport and therefore their occurrence in the environment. Given the relevance of climate, erosion and water balance in the fate of glyphosate, other additional uncertainties appear on the horizon regarding its behavior in a climate change scenario.

## Concluding remarks

Biological, chemical and physical factors and processes playing on the adsorption, transport, degradation and in the overall fate of glyphosate and its metabolites occur at different levels of soil organization and must be studied through a combination of different methods of analysis. Transformation of pesticides depends on soil structure and basically soil

porosity that regulate glyphosate bioavailability. The evaluation of soil structural variables from undisturbed samples is an inevitable path to fully understand pesticide degradation mechanisms.

We argue that the debate should focus the attention on the functional consequences of glyphosate exposure on soil ecosystem services, especially in agroecosystems, as well as their impact on other environmental matrices—surface water bodies and sediments—related with the herbicide application. Further research of effects at subinhibitory levels, including the complex and dynamic environment of the rhizosphere, will permit assessment of the potential implications of environmental long-term persistence of glyphosate.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

## References

- Albers CN, Banta GT, Hansen PE, Jacobsen OS (2009) The influence of organic matter on sorption and fate of glyphosate in soil—comparing different soils and humic substances. *Environ Pollut* 157:2865–2870. <https://doi.org/10.1016/j.envpol.2009.04.004>
- Allegrini M, Zabaloy MC, Gómez EdV (2015) Ecotoxicological assessment of soil microbial community tolerance to glyphosate. *Sci Total Environ* 533:60–68. <https://doi.org/10.1016/j.scitotenv.2015.06.096>
- Allegrini M, Gomez EDV, Zabaloy MC (2017) Repeated glyphosate exposure induces shifts in nitrifying communities and metabolism of phenylpropanoids. *Soil Biol Biochem* 105:206–215. <https://doi.org/10.1016/j.soilbio.2016.11.024>
- Allegrini M, Gomez EdV, Smalla K, Zabaloy MC (2019) Suppression treatment differentially influences the microbial community and the occurrence of broad host range plasmids in the rhizosphere of the model cover crop *Avena sativa* L. *PLoS ONE* 14:e0223600. <https://doi.org/10.1371/journal.pone.0223600>
- Andrade VS, Gutierrez MF, Regalado L et al (2021) Influence of rainfall and seasonal crop practices on nutrient and pesticide runoff from soybean dominated agricultural areas in Pampean streams, Argentina. *Sci Total Environ* 788:147676. <https://doi.org/10.1016/j.scitotenv.2021.147676>
- Arango L, Buddrus-Schiemann K, Opelt K et al (2014) Effects of glyphosate on the bacterial community associated with roots of transgenic Roundup Ready® soybean. *Eur J Soil Biol* 63:41–48. <https://doi.org/10.1016/j.ejsobi.2014.05.005>
- Artigas J, Batisson I, Carles L (2020) Dissolved organic matter does not promote glyphosate degradation in auto-heterotrophic aquatic



- microbial communities. *Environ Pollut* 259:113951. <https://doi.org/10.1016/j.envpol.2020.113951>
- Beecraft L, Rooney R (2021) Bioconcentration of glyphosate in wetland biofilms. *Sci Total Environ* 756:143993. <https://doi.org/10.1016/j.scitotenv.2020.143993>
- Behrends Kraemer F, Morrás HJM (2018a) Macroporosity of a typical argiudoll with different cropping intensity under no-tillage. *Span J Soil Sci* 8:214–235. <https://doi.org/10.3232/SJSS.2018.V8.N2.06>
- Behrends Kraemer F, Morrás HJM (2018b) Compactación e intensificación agrícola en siembra directa. Escalas de estudio. In: Imbellone P, Álvarez C (eds) *Compactaciones Naturales y Antrópicas en Suelos Argentinos*. Argentina de la Ciencia del Suelo, Buenos Aires, pp 179–212
- Behrends Kraemer F, Castiglioni M, Morrás H et al (2022a) Pores size distribution and pores volume density of Mollisols and Vertisols under different cropping intensity managements with no-tillage. *Geoderma* 405:115398. <https://doi.org/10.1016/j.geoderma.2021.115398>
- Behrends Kraemer F, Sainz D, Morrás H, et al (2022b) Soil structure and glyphosate fate under no-till management in the Pampa region. I. Soil structural anisotropy and hydro-physical behavior. *Soil Till Res* in press
- Bento CPM, Yang X, Gort G et al (2016) Persistence of glyphosate and aminomethylphosphonic acid in loess soil under different combinations of temperature, soil moisture and light/darkness. *Sci Total Environ* 572:301–311. <https://doi.org/10.1016/j.scitotenv.2016.07.215>
- Berman MC, Llamas ME, Minotti P et al (2020) Field evidence supports former experimental claims on the stimulatory effect of glyphosate on picocyanobacteria communities. *Sci Total Environ* 701:134601. <https://doi.org/10.1016/j.scitotenv.2019.134601>
- Bernier SP, Surette MG (2013) Concentration-dependent activity of antibiotics in natural environments. *Front Microbiol* 4:20. <https://doi.org/10.3389/fmicb.2013.00020>
- Borggaard OK, Gimsing AL (2008) Fate of glyphosate in soil and the possibility of leaching to ground and surface waters: a review. *Pest Manag Sci* 64:441–456. <https://doi.org/10.1002/ps.1512>
- Botten N, Wood LJ, Werner JR (2021) Glyphosate remains in forest plant tissues for a decade or more. *For Ecol Manag* 493:119259. <https://doi.org/10.1016/j.foreco.2021.119259>
- Bruckner A, Schmerbauch A, Ruess L et al (2019) Foliar Roundup application has minor effects on the compositional and functional diversity of soil microorganisms in a short-term greenhouse experiment. *Ecotoxicol Environ Saf* 174:506–513. <https://doi.org/10.1016/j.ecoenv.2019.02.073>
- Cao G, Liu Y, Zhang S et al (2012) A novel 5-enolpyruvylshikimate-3-phosphate synthase shows high glyphosate tolerance in *Escherichia coli* and tobacco plants. *PLoS ONE* 7:e38718. <https://doi.org/10.1371/journal.pone.0038718>
- Caprile AC, Aparicio VC, Portela SI et al (2017) Drenaje y transporte vertical de herbicidas en dos molisoles de La Pampa ondulada Argentina. *Cienc Del Suelo* 35:147–159
- Caprile A, Sasal M, Repetti M, Andriulo A (2019) Plaguicidas retenidos en el suelo y perdidos por escurrimiento en dos secuencias de cultivo bajo siembra directa. *Asoc Argentina Ciencias Del Suelo AACCS* 37:338–354
- Carles L, Artigas J (2020) Interaction between glyphosate and dissolved phosphorus on bacterial and eukaryotic communities from river biofilms. *Sci Total Environ* 719:137463. <https://doi.org/10.1016/j.scitotenv.2020.137463>
- Carles L, Gardon H, Joseph L et al (2019) Meta-analysis of glyphosate contamination in surface waters and dissipation by biofilms. *Environ Int* 124:284–293. <https://doi.org/10.1016/j.envint.2018.12.064>
- Carranza CS, Regñicoli JP, Aluffi ME et al (2019) Glyphosate in vitro removal and tolerance by *Aspergillus oryzae* in soil microcosms. *Int J Environ Sci Technol* 16:7673–7682. <https://doi.org/10.1007/s13762-019-02347-x>
- Carretta L, Cardinali A, Masin R et al (2020) Decyl glucoside surfactant triton CG-110 does not significantly affect the environmental fate of glyphosate in the soil at environmentally relevant concentrations. *J Hazard Mater* 388:122111. <https://doi.org/10.1016/j.jhazmat.2020.122111>
- Carretta L, Cardinali A, Onofri A et al (2021) Dynamics of glyphosate and aminomethylphosphonic acid in soil under conventional and conservation tillage. *Int J Environ Res* 15:1037–1055. <https://doi.org/10.1007/s41742-021-00369-3>
- Carrizo ME, Alesso CA, Cosentino D, Imhoff S (2015) Aggregation agents and structural stability in soils with different texture and organic carbon contents. *Sci Agric*. <https://doi.org/10.1590/0103-9016-2014-0026>
- Cassigneuil A, Benoit P, Bergheaud V et al (2016) Fate of glyphosate and degradates in cover crop residues and underlying soil: a laboratory study. *Sci Total Environ* 545–546:582–590. <https://doi.org/10.1016/j.scitotenv.2015.12.052>
- Castiglioni MG, Behrends-Kraemer F, Marquez-Molina JJ (2018) Conductividad hidráulica saturada determinada por distintos procedimientos en suelos con alta humedad inicial. *Asoc Argentina Cienc Del Suelo* 36:158–169
- Cedergreen N, Felby C, Porter JR, Streibig JC (2009) Chemical stress can increase crop yield. *Field Crops Res* 114:54–57. <https://doi.org/10.1016/j.fcr.2009.07.003>
- Chaplain V, Mamy L, Vieublé L, et al (2011) Fate of pesticides in soils: toward an integrated approach of influential factors. In: *Pesticides in the modern world—risks and benefits*. InTech, pp 535–560
- Cheng H, Hu E, Hu Y (2012) Impact of mineral micropores on transport and fate of organic contaminants: a review. *J Contam Hydrol* 129–130:80–90. <https://doi.org/10.1016/j.jconhyd.2011.09.008>
- Chenu C, Cosentino D (2011) Microbial regulation of soil structure dynamics. In: Ritz K, Young I (eds) *The architecture and biology of soils: life in inner space*. CABI, Wallingford, Oxfordshire
- Chow R, Scheidegger R, Doppler T et al (2020) A review of long-term pesticide monitoring studies to assess surface water quality trends. *Water Res* X 9:100064. <https://doi.org/10.1016/j.wroa.2020.100064>
- Corrales N, Meerhoff M, Antoniadis D (2021) Glyphosate-based herbicide exposure affects diatom community development in natural biofilms. *Environ Pollut* 284:117354. <https://doi.org/10.1016/j.envpol.2021.117354>
- Correa LO, Bezerra AFM, Honorato LRS et al (2023) Amazonian soil fungi are efficient degraders of glyphosate herbicide; novel isolates of *Penicillium*, *Aspergillus*, and *Trichoderma*. *Braz J Biol* 83:e242830. <https://doi.org/10.1590/1519-6984.242830>
- De Gerónimo E, Aparicio VC, Costa JL (2018) Glyphosate sorption to soils of Argentina. Estimation of affinity coefficient by pedotransfer function. *Geoderma* 322:140–148. <https://doi.org/10.1016/j.geoderma.2018.02.037>
- Dennis PG, Kukulies T, Forstner C et al (2018) The effects of glyphosate, glufosinate, paraquat and paraquat-diquat on soil microbial activity and bacterial, archaeal and nematode diversity. *Sci Rep* 8:2119. <https://doi.org/10.1038/s41598-018-20589-6>
- Doublet J, Mamy L, Barriuso E (2009) Delayed degradation in soil of foliar herbicides glyphosate and sulcotrione previously absorbed by plants: consequences on herbicide fate and risk assessment. *Chemosphere* 77:582–589. <https://doi.org/10.1016/j.chemosphere.2009.06.044>
- Druille M, García-Parisi PA, Golluscio RA et al (2016) Repeated annual glyphosate applications may impair beneficial soil microorganisms in temperate grassland. *Agric Ecosyst Environ* 230:184–190. <https://doi.org/10.1016/j.agee.2016.06.011>

- Ermakova IT, Shushkova TV, Sviridov AV et al (2017) Organophosphonates utilization by soil strains of *Ochrobactrum anthropi* and *Achromobacter* sp. Arch Microbiol 199:665–675. <https://doi.org/10.1007/s00203-017-1343-8>
- Filipović V, Coquet Y, Pot V et al (2014) Modeling the effect of soil structure on water flow and isoproturon dynamics in an agricultural field receiving repeated urban waste compost application. Sci Total Environ 499:546–559. <https://doi.org/10.1016/j.scitotenv.2014.06.010>
- Firdous S, Iqbal S, Anwar S (2020) Optimization and modeling of glyphosate biodegradation by a novel *Comamonas odontotermitis* P2 through response surface methodology. Pedosphere 30:618–627. [https://doi.org/10.1016/S1002-0160\(17\)60381-3](https://doi.org/10.1016/S1002-0160(17)60381-3)
- Forlani G, Pavan M, Gramek M et al (2008) Biochemical bases for a widespread tolerance of cyanobacteria to the phosphonate herbicide glyphosate. Plant Cell Physiol 49:443–456. <https://doi.org/10.1093/pcp/pcn021>
- Geng Y, Jiang L, Zhang D et al (2021) Glyphosate, aminomethylphosphonic acid, and glufosinate ammonium in agricultural groundwater and surface water in China from 2017 to 2018: occurrence, main drivers, and environmental risk assessment. Sci Total Environ 769:144396. <https://doi.org/10.1016/j.scitotenv.2020.144396>
- Giannini Kurina F, Hang S, Macchiavelli R, Balzarini M (2019) Spatial predictive modelling essential to assess the environmental impacts of herbicides. Geoderma 354:113874. <https://doi.org/10.1016/j.geoderma.2019.07.032>
- Gómez Ortiz AM, Okada E, Bedmar F, Costa JL (2017) Sorption and desorption of glyphosate in Mollisols and Ultisols soils of Argentina. Environ Toxicol Chem 36:2587–2592. <https://doi.org/10.1002/etc.3851>
- Gonzalez D, Juarez AB, Krug CP et al (2019) Freshwater periphyton response to technical-grade and two commercial formulations of glyphosate. Ecol Austral 29:020–027. <https://doi.org/10.25260/EA.19.29.1.0.816>
- González-Valenzuela LE, Dussán J (2018) Molecular assessment of glyphosate-degradation pathway via sarcosine intermediate in *Lysinibacillus sphaericus*. Environ Sci Pollut Res 25:22790–22796. <https://doi.org/10.1007/s11356-018-2364-9>
- Grundmann GL, Dechesne A, Bartoli F et al (2001) Spatial modeling of nitrifier microhabitats in soil. Soil Sci Soc Am J 65:1709–1716. <https://doi.org/10.2136/sssaj2001.1709>
- Guijarro KH, Aparicio V, De Gerónimo E et al (2018) Soil microbial communities and glyphosate decay in soils with different herbicide application history. Sci Total Environ 634:974–982. <https://doi.org/10.1016/j.scitotenv.2018.03.393>
- Guijarro KH, De Gerónimo E, Erijman L (2021) Glyphosate biodegradation potential in soil based on glycine oxidase gene (thiO) from *Bradyrhizobium*. Curr Microbiol 78:1991–2000. <https://doi.org/10.1007/s00284-021-02467-z>
- Gunarathna S, Gunawardana B, Jayaweera M et al (2018) Glyphosate and AMPA of agricultural soil, surface water, groundwater and sediments in areas prevalent with chronic kidney disease of unknown etiology, Sri Lanka. J Environ Sci Health B 53:729–737. <https://doi.org/10.1080/03601234.2018.1480157>
- Guo F, Zhou M, Xu J et al (2021) Glyphosate adsorption onto kaolinite and kaolinite-humic acid composites: experimental and molecular dynamics studies. Chemosphere 263:127979. <https://doi.org/10.1016/j.chemosphere.2020.127979>
- Hartmann A, Gräsele W, Horn R (1998) Cation exchange processes in structured soils at various hydraulic properties. Soil Tillage Res 47:67–72. [https://doi.org/10.1016/S0167-1987\(98\)00074-9](https://doi.org/10.1016/S0167-1987(98)00074-9)
- Hatzinger PB, Alexander M (1995) Effect of aging of chemicals in soil on their biodegradability and extractability. Environ Sci Technol 29:537–545. <https://doi.org/10.1021/es00002a033>
- Helander M, Saloniemi I, Omacini M et al (2018) Decreases mycorrhizal colonization and affects plant-soil feedback. Sci Total Environ 642:285–291. <https://doi.org/10.1016/j.scitotenv.2018.05.377>
- Heuer H, Binh CTT, Jechalke S et al (2012) IncP-1e plasmids are important vectors of antibiotic resistance genes in agricultural systems: diversification driven by class I integron gene cassettes. Front Microbiol 3:2. <https://doi.org/10.3389/fmicb.2012.00002>
- Horn R, Kutilek M (2009) The intensity-capacity concept—how far is it possible to predict intensity values with capacity parameters. Soil Tillage Res 103:1. <https://doi.org/10.1016/j.still.2008.10.007>
- Hove-Jensen B, Zechel DL, Jochimsen B (2014) Utilization of glyphosate as phosphate source: biochemistry and genetics of bacterial carbon-phosphorus lyase. Microbiol Mol Biol Rev 78:176–197. <https://doi.org/10.1128/mmb.00040-13>
- Huang J, Su Z, Xu Y (2005) The evolution of microbial phosphonate degradative pathways. J Mol Evol 61:682–690. <https://doi.org/10.1007/s00239-004-0349-4>
- Huntscha S, Stravs MA, Bühlmann A et al (2018) Seasonal dynamics of glyphosate and AMPA in lake Greifensee: rapid microbial degradation in the epilimnion during summer. Environ Sci Technol 52:4641–4649. <https://doi.org/10.1021/acs.est.8b00314>
- Iavicoli I, Fontana L, Agathokleous E et al (2021) Hormetic dose responses induced by antibiotics in bacteria: a phantom menace to be thoroughly evaluated to address the environmental risk and tackle the antibiotic resistance phenomenon. Sci Total Environ 798:149255. <https://doi.org/10.1016/j.scitotenv.2021.149255>
- Imparato V, Santos SS, Johansen A et al (2016) Stimulation of bacteria and protists in rhizosphere of glyphosate-treated barley. Appl Soil Ecol 98:47–55. <https://doi.org/10.1016/j.apsoil.2015.09.007>
- Iyer R, Iken B, Damania A, Krieger J (2018) Whole genome analysis of six organophosphate-degrading rhizobacteria reveals putative agrochemical degradation enzymes with broad substrate specificity. Environ Sci Pollut Res 25:13660–13675. <https://doi.org/10.1007/s11356-018-1435-2>
- Jechalke S, Heuer H, Siemens J et al (2014) Fate and effects of veterinary antibiotics in soil. Trends Microbiol 22:536–545. <https://doi.org/10.1016/j.tim.2014.05.005>
- Jochimsen B, Lolle S, McSorley FR et al (2011) Five phosphonate operon gene products as components of a multi-subunit complex of the carbon-phosphorus lyase pathway. Proc Natl Acad Sci USA 108:11393–11398. <https://doi.org/10.1073/pnas.1104922108>
- Kepler RM, Epp Schmidt DJ, Yarwood SA et al (2020) Soil microbial communities in diverse agroecosystems exposed to the herbicide glyphosate. Appl Environ Microbiol 86:1–16. <https://doi.org/10.1128/AEM.01744-19>
- Khadra M, Planas D, Girard C, Amyot M (2018) Age matters: submersion period shapes community composition of lake biofilms under glyphosate stress. Facets 3:934–951. <https://doi.org/10.1139/facets-2018-0019>
- Klátyik S, Takács E, Mörtl M et al (2017) Dissipation of the herbicide active ingredient glyphosate in natural water samples in the presence of biofilms. Int J Environ Anal Chem 97:901–921. <https://doi.org/10.1080/03067319.2017.1373770>
- Kulikova NA, Zhelezova AD, Voropanov MG et al (2020) Monoammonium phosphate effects on glyphosate in soils: mobilization, phytotoxicity, and alteration of the microbial community. Eurasian Soil Sci 53:787–797. <https://doi.org/10.1134/S106422932006006X>
- la Cecilia D, Maggi F (2018) Analysis of glyphosate degradation in a soil microcosm. Environ Pollut 233:201–207. <https://doi.org/10.1016/j.envpol.2017.10.017>
- Lefrancq M, Jadas-Hécart A, La Jeunesse I et al (2017) High frequency monitoring of key pesticides in runoff water to improve understanding of their transport and environmental impacts. Sci Total Environ 587–588:75–86. <https://doi.org/10.1016/j.scitotenv.2017.02.022>



- Liao H, Li X, Yang Q et al (2021) Herbicide selection promotes antibiotic resistance in soil microbiomes. *Mol Biol Evol* 38:2337–2350. <https://doi.org/10.1093/molbev/msab029>
- Lipok J, Owsiak T, Młynarz P et al (2007) Phosphorus NMR as a tool to study mineralization of organophosphonates-The ability of *Spirulina* spp. to degrade glyphosate. *Enzyme Microb Technol* 41:286–291. <https://doi.org/10.1016/j.enzmictec.2007.02.004>
- Lorch M, Agaras B, García-Parisi P et al (2021) Repeated annual application of glyphosate reduces the abundance and alters the community structure of soil culturable pseudomonads in a temperate grassland. *Agric Ecosyst Environ* 319:107503. <https://doi.org/10.1016/j.agee.2021.107503>
- Lozano VL, Vinocur A, Sabio y García CA et al (2018) Effects of glyphosate and 2,4-D mixture on freshwater phytoplankton and periphyton communities: a microcosms approach. *Ecotoxicol Environ Saf* 148:1010–1019. <https://doi.org/10.1016/j.ecoenv.2017.12.006>
- Lupwayi NZ, Fernandez MR, Kanashiro DA, Petri RM (2021) Profiles of wheat rhizobacterial communities in response to repeated glyphosate applications, crop rotation, and tillage. *Can J Soil Sci* 101:157–167. <https://doi.org/10.1139/cjss-2020-0008>
- Mac Loughlin TM, Peluso ML, Marino DJG (2022) Multiple pesticides occurrence, fate, and environmental risk assessment in a small horticultural stream of Argentina. *Sci Total Environ* 802:149893. <https://doi.org/10.1016/j.scitotenv.2021.149893>
- Mamy L, Barriuso E, Gabrielle B (2016) Glyphosate fate in soils when arriving in plant residues. *Chemosphere* 154:425–433. <https://doi.org/10.1016/j.chemosphere.2016.03.104>
- Mandl K, Cantelmo C, Gruber E, Faber, Friedrich, B, Zaller, JG (2018) Effects of glyphosate-, glufosinate-and flazasulfuron-based herbicides on soil microorganisms in a vineyard *Bull Environ Contam Toxicol* 101:562–569. <https://doi.org/10.1007/s00128-018-2438-x>
- Manogaran M, Shukor MY, Yasid NA et al (2017) Isolation and characterisation of glyphosate-degrading bacteria isolated from local soils in Malaysia. *Rend Lincei* 28:471–479. <https://doi.org/10.1007/s12210-017-0620-4>
- Manogaran M, Shukor MY, Yasid NA et al (2018) Optimisation of culture composition for glyphosate degradation by *Burkholderia vietnamiensis* strain AQ5–12. *3 Biotech* 8:108. <https://doi.org/10.1007/s13205-018-1123-4>
- Maqueda C, Undabeytia T, Villaverde J, Morillo E (2017) Behaviour of glyphosate in a reservoir and the surrounding agricultural soils. *Sci Total Environ* 593–594:787–795. <https://doi.org/10.1016/j.scitotenv.2017.03.202>
- Martinez DA, Loening UE, Graham MC (2018) Impacts of glyphosate-based herbicides on disease resistance and health of crops: a review. *Environ Sci Eur* 30:2. <https://doi.org/10.1186/s12302-018-0131-7>
- Masotti F, Garavaglia BS, Piazza A et al (2021) Bacterial isolates from Argentine Pampas and their ability to degrade glyphosate. *Sci Total Environ* 774:145761. <https://doi.org/10.1016/j.scitotenv.2021.145761>
- Medalie L, Baker NT, Shoda ME et al (2020) Influence of land use and region on glyphosate and aminomethylphosphonic acid in streams in the USA. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2019.136008>
- Mendez MJ, Aimar SB, Aparicio VC et al (2017) Glyphosate and aminomethylphosphonic acid (AMPA) contents in the respirable dust emitted by an agricultural soil of the central semiarid region of Argentina. *Aeolian Res* 29:23–29. <https://doi.org/10.1016/j.aeolia.2017.09.004>
- Mercado CA, Mactal AG (2021) Degradation dynamics of glyphosate in two types of soil from corn fields of the Philippines. *Int J Agric Technol* 17:185–192
- Mesnager R, Benbrook C, Antoniou MN (2019) Insight into the confusion over surfactant co-formulants in glyphosate-based herbicides. *Food Chem Toxicol* 128:137–145. <https://doi.org/10.1016/j.fct.2019.03.053>
- Morrás H (2015) Porosidad y microestructura de suelos. In: Loaiza J, Stoops G, Poch R, Casmitjana M (eds) *Manual de micromorfología de suelos y técnicas complementarias*. Fondo Editorial Pascual Bravo, Medellín, pp 205–260
- Morriën E, Hannula SE, Snoek LB et al (2017) Soil networks become more connected and take up more carbon as nature restoration progresses. *Nat Commun* 8:14349. <https://doi.org/10.1038/ncomms14349>
- Muola A, Fuchs B, Laihonon M et al (2021) Risk in the circular food economy: glyphosate-based herbicide residues in manure fertilizers decrease crop yield. *Sci Total Environ* 750:141422. <https://doi.org/10.1016/j.scitotenv.2020.141422>
- Muskus AM, Krauss M, Miltner A et al (2019) Effect of temperature, pH and total organic carbon variations on microbial turnover of <sup>13</sup>C<sup>15</sup>N-glyphosate in agricultural soil. *Sci Total Environ* 658:697–707. <https://doi.org/10.1016/j.scitotenv.2018.12.195>
- Muskus AM, Krauss M, Miltner A et al (2020) Degradation of glyphosate in a Colombian soil is influenced by temperature, total organic carbon content and pH. *Environ Pollut* 259:113767. <https://doi.org/10.1016/j.envpol.2019.113767>
- Newman MM, Lorenz N, Hoilett N et al (2016) Changes in rhizosphere bacterial gene expression following glyphosate treatment. *Sci Total Environ* 553:32–41. <https://doi.org/10.1016/j.scitotenv.2016.02.078>
- Nguyen DB, Rose MT, Rose TJ et al (2016) Impact of glyphosate on soil microbial biomass and respiration: a meta-analysis. *Soil Biol Biochem* 92:50–57. <https://doi.org/10.1016/j.soilbio.2015.09.014>
- Nguyen DB, Rose MT, Rose TJ, van Zwieten L (2018) Effect of glyphosate and a commercial formulation on soil functionality assessed by substrate induced respiration and enzyme activity. *Eur J Soil Biol* 85:64–72. <https://doi.org/10.1016/j.ejsobi.2018.01.004>
- Nivelle E, Verzeaux J, Chabot A et al (2018) Effects of glyphosate application and nitrogen fertilization on the soil and the consequences on aboveground and belowground interactions. *Geoderma* 311:45–57. <https://doi.org/10.1016/j.geoderma.2017.10.002>
- Norgaard T, De Jonge LW, Moldrup P et al (2015) Can simple soil parameters explain field-scale variations in glyphosate-, bromoxyniloctanoate-, diflufenican-, and bentazone mineralization? *Water Air Soil Pollut* 226:262. <https://doi.org/10.1007/s11270-015-2518-z>
- Nunan N, Wu K, Young IM et al (2003) Spatial distribution of bacterial communities and their relationships with the micro-architecture of soil. *FEMS Microbiol Ecol* 44:203–215. [https://doi.org/10.1016/S0168-6496\(03\)00027-8](https://doi.org/10.1016/S0168-6496(03)00027-8)
- Nunan N, Ritz K, Rivers M et al (2006) Investigating microbial microhabitat structure using X-ray computed tomography. *Geoderma* 133:398–407. <https://doi.org/10.1016/j.geoderma.2005.08.004>
- Okada E, Pérez D, De Gerónimo E et al (2018) Non-point source pollution of glyphosate and AMPA in a rural basin from the south-east Pampas, Argentina. *Environ Sci Pollut Res* 25:15120–15132. <https://doi.org/10.1007/s11356-018-1734-7>
- Okada E, Costa JL, Bedmar F (2019) Glyphosate dissipation in different soils under no-till and conventional tillage. *Pedosphere* 29:773–783. [https://doi.org/10.1016/S1002-0160\(17\)60430-2](https://doi.org/10.1016/S1002-0160(17)60430-2)
- Okada E, Allinson M, Barral MP et al (2020) Glyphosate and aminomethylphosphonic acid (AMPA) are commonly found in urban streams and wetlands of Melbourne, Australia. *Water Res* 168:115139. <https://doi.org/10.1016/j.watres.2019.115139>
- Ololade IA, Oladoja NA, Oloye FF et al (2014) Sorption of glyphosate on soil components: the roles of metal oxides and organic

- materials. *Soil Sediment Contam* 23:571–585. <https://doi.org/10.1080/15320383.2014.846900>
- Padilla JT, Selim HM (2019) Time-dependent sorption and desorption of glyphosate in soils: multi-reaction modeling. *Vadose Zone J* 18:180214. <https://doi.org/10.2136/vzj2018.12.0214>
- Padilla JT, Selim HM (2020) Environmental behavior of glyphosate in soils. *Adv Agron* 159:1–34
- Pimentel D (1996) Green revolution agriculture and chemical hazards. *Sci Total Environ* 188:S86–S98. [https://doi.org/10.1016/0048-9697\(96\)05280-1](https://doi.org/10.1016/0048-9697(96)05280-1)
- Pires NL, Passos CJS, Morgado MGA et al (2020) Determination of glyphosate, AMPA and glufosinate by high performance liquid chromatography with fluorescence detection in waters of the Santarém Plateau, Brazilian Amazon. *J Environ Sci Health B* 55:794–802. <https://doi.org/10.1080/03601234.2020.1784668>
- Ramirez Haberkon NB, Aparicio VC, Buschiazzi DE et al (2020) Glyphosate and AMPA concentrations in the respirable dust emitted experimentally by soil aggregates, shortly after herbicide application. *Geoderma* 369:114334. <https://doi.org/10.1016/j.geoderma.2020.114334>
- Ramirez-Villacis DX, Finkel OM, Salas-González I et al (2020) Root microbiome modulates plant growth promotion induced by low doses of glyphosate. *mSphere*. <https://doi.org/10.1128/msphere.00484-20>
- Rampazzo N, Todorovic GR, Mentler A, Blum WEH (2013) Adsorption of glyphosate and aminomethylphosphonic acid in soils. *Int Agrophys* 27:203–209. <https://doi.org/10.2478/v10247-012-0086-7>
- Ramula S, Mathew SA, Kalske A et al (2021) Glyphosate residues alter the microbiota of a perennial weed with a minimal indirect impact on plant performance. *Plant Soil*. <https://doi.org/10.1007/s11104-021-05196-1>
- Rodrigues JJV, Worsham AD, Corbin FT (1982) Exudation of glyphosate from wheat (*Triticum aestivum*) plants and its effects on interplanted corn (*Zea mays*) and soybeans (*Glycine max*). *Weed Sci* 30:316–320. <https://doi.org/10.1017/s0043174500040601>
- Ronco AE, Marino DJG, Abelando M et al (2016) Water quality of the main tributaries of the Paraná Basin: glyphosate and AMPA in surface water and bottom sediments. *Environ Monit Assess* 188:458. <https://doi.org/10.1007/s10661-016-5467-0>
- Rosa SM, Behrends Kraemer F, Soria MA et al (2014) The influence of soil properties on denitrifying bacterial communities and denitrification potential in no-till production farms under contrasting management in the Argentinean Pampas. *Appl Soil Ecol* 75:172–180. <https://doi.org/10.1016/j.apsoil.2013.11.012>
- Rossi F, Carles L, Donnadiou F et al (2021) Glyphosate-degrading behavior of five bacterial strains isolated from stream biofilms. *J Hazard Mater* 420:126651. <https://doi.org/10.1016/j.jhazmat.2021.126651>
- Sasal MC, Boizard H, Andriulo AE et al (2017) Platy structure development under no-tillage in the northern humid Pampas of Argentina and its impact on runoff. *Soil Tillage Res* 173:33–41. <https://doi.org/10.1016/j.still.2016.08.014>
- Schlatter DC, Yin C, Hulbert S et al (2017) Impacts of repeated glyphosate use on wheat-associated bacteria are small and depend on glyphosate use history. *Appl Environ Microbiol* 83:e01354–e1417. <https://doi.org/10.1128/AEM.01354-17>
- Schlatter DC, Yin C, Burke I et al (2018) Location, root proximity, and glyphosate-use history modulate the effects of glyphosate on fungal community networks of wheat. *Microb Ecol* 76:240–257. <https://doi.org/10.1007/s00248-017-1113-9>
- Sheng M, Hamel C, Fernandez MR (2012) Cropping practices modulate the impact of glyphosate on arbuscular mycorrhizal fungi and rhizosphere bacteria in agroecosystems of the semiarid prairie. *Can J Microbiol* 58:990–1001. <https://doi.org/10.1139/W2012-080>
- Sidoli P, Baran N, Angulo-Jaramillo R (2016) Glyphosate and AMPA adsorption in soils: laboratory experiments and pedotransfer rules. *Environ Sci Pollut Res* 23:5733–5742. <https://doi.org/10.1007/s11356-015-5796-5>
- Silva V, Montanarella L, Jones A et al (2018) Distribution of glyphosate and aminomethylphosphonic acid (AMPA) in agricultural topsoils of the European Union. *Sci Total Environ* 621:1352–1359. <https://doi.org/10.1016/j.scitotenv.2017.10.093>
- Singh BK, Walker A (2006) Microbial degradation of organophosphorus compounds. *FEMS Microbiol Rev* 30:428–471. <https://doi.org/10.1111/j.1574-6976.2006.00018.x>
- Singh S, Kumar V, Singh J (2019) Kinetic study of the biodegradation of glyphosate by indigenous soil bacterial isolates in presence of humic acid, Fe (III) and Cu (II) ions. *J Environ Chem Eng* 7:103098. <https://doi.org/10.1016/j.jece.2019.103098>
- Singh S, Kumar V, Gill JPK et al (2020) Herbicide glyphosate: toxicity and microbial degradation. *Int J Environ Res Public Health* 17:1–18. <https://doi.org/10.3390/ijerph17207519>
- Soracco CG, Villarreal R, Lozano LA et al (2018) Glyphosate dynamics in a soil under conventional and no-till systems during a soybean growing season. *Geoderma* 323:13–21. <https://doi.org/10.1016/j.geoderma.2018.02.041>
- Stenrød M, Charnay MP, Benoit P, Eklo OM (2006) Spatial variability of glyphosate mineralization and soil microbial characteristics in two Norwegian sandy loam soils as affected by surface topographical features. *Soil Biol Biochem* 38:962–971. <https://doi.org/10.1016/j.soilbio.2005.08.014>
- Stoops G (2021) Guidelines for analysis and description of soil and regolith thin sections, 2nd edn. Wiley Blackwell, Hoboken
- Sun M, Li H, Jaisi DP (2019) Degradation of glyphosate and bioavailability of phosphorus derived from glyphosate in a soil-water system. *Water Res* 163:114840. <https://doi.org/10.1016/j.watres.2019.07.007>
- Sviridov AV, Shushkova TV, Ermakova IT et al (2015) Microbial degradation of glyphosate herbicides. *Appl Biochem Microbiol* 51:188–195. <https://doi.org/10.1134/S0003683815020209>
- Tang FHM, Jeffries TC, Vervoort RW et al (2019) Microcosm experiments and kinetic modeling of glyphosate biodegradation in soils and sediments. *Sci Total Environ* 658:105–115. <https://doi.org/10.1016/j.scitotenv.2018.12.179>
- Todorovic GR, Rampazzo N, Mentler A et al (2014) Influence of soil tillage and erosion on the dispersion of glyphosate and aminomethylphosphonic acid in agricultural soils. *Int Agrophys* 28:93–100. <https://doi.org/10.2478/intag-2013-0031>
- Tomlin C (2006) A world compendium: the pesticide manual (14th ed.). British Crop Protection Council, Alton, Hampshire, UK
- Vandecraen J, Chandler M, Aertsen A, Van Houdt R (2017) The impact of insertion sequences on bacterial genome plasticity and adaptability. *Crit Rev Microbiol* 43:709–730. <https://doi.org/10.1080/1040841X.2017.1303661>
- Vera MS, Trinelli MA (2021) First evaluation of the periphyton recovery after glyphosate exposure. *Environ Pollut* 290:117998. <https://doi.org/10.1016/j.envpol.2021.117998>
- Vieublé Gonod L, Chadoeuf J, Chenu C (2006) Spatial distribution of microbial 2,4-dichlorophenoxy acetic acid mineralization from field to microhabitat scales. *Soil Sci Soc Am J* 70:64–71. <https://doi.org/10.2136/sssaj2004.0034>
- Villarreal R, Lozano LA, Polich NG et al (2020) Influence of soil water holding and transport capacity on glyphosate dynamics in two agricultural soils from Pampas Region. *Geoderma* 376:114566. <https://doi.org/10.1016/j.geoderma.2020.114566>
- Von Wiren-Lehr S, Komossa D, Glassgen WE et al (1997) Mineralization of [<sup>14</sup>C]glyphosate and its plant-associated residues in arable soils originating from different farming systems. *Pestic Sci* 51:436–442. [https://doi.org/10.1002/\(SICI\)1096-9063\(199712\)51:4%3c436::AID-PS630%3e3.0.CO;2-7](https://doi.org/10.1002/(SICI)1096-9063(199712)51:4%3c436::AID-PS630%3e3.0.CO;2-7)

- Vos M, Wolf AB, Jennings SJ, Kowalchuk GA (2013) Micro-scale determinants of bacterial diversity in soil. *FEMS Microbiol Rev* 37:936–954. <https://doi.org/10.1111/1574-6976.12023>
- Wang S, Seiwert B, Kästner M et al (2016) (Bio)degradation of glyphosate in water-sediment microcosms—a stable isotope co-labeling approach. *Water Res* 99:91–100. <https://doi.org/10.1016/j.watres.2016.04.041>
- Wilkes TI, Warner DJ, Davies KG, Edmonds-Brown V (2020) Tillage, glyphosate and beneficial arbuscular mycorrhizal fungi: optimising crop management for plant–fungal symbiosis. *Agric* 10:520. <https://doi.org/10.3390/agriculture10110520>
- Wilpizeski RL, Aufrecht JA, Retterer ST et al (2019) Soil aggregate microbial communities: towards understanding microbiome interactions at biologically relevant scales. *Appl Environ Microbiol* 85:e00324–e419. <https://doi.org/10.1128/AEM.00324-19>
- Woignier T, Morell M, Morell O et al (2011) Low water transport in fractal microstructure of tropical soils: application to chlordecone pesticide trapping. *Ecohydrol Hydrobiol* 11:121–127. <https://doi.org/10.2478/v10104-011-0035-2>
- Woignier T, Clostre F, Fernandes P et al (2018) The pesticide chlordecone is trapped in the tortuous mesoporosity of allophane clays. *Environ Sci Pollut Res* 25:21350–21361. <https://doi.org/10.1007/s11356-017-9370-1>
- Wolmarans K, Swart WJ (2014) Influence of glyphosate, other herbicides and genetically modified herbicideresistant crops on soil microbiota: a review. *S Afr J Plant Soil* 31:177–186. <https://hdl.handle.net/10520/EJC163053>
- Wu K, Zhang X (2011) Modelling soil structure and processes. In: Ritz K, Young I (eds) *The architecture and biology of soils: life in inner space*. CABI, Wallingford, Oxfordshire
- Xing Y, Wu S, Men Y (2020) Exposure to environmental levels of pesticides stimulates and diversifies evolution in *Escherichia coli* toward higher antibiotic resistance. *Environ Sci Technol* 54:8770–8778. <https://doi.org/10.1021/acs.est.0c01155>
- Yang X, Wang F, Bento CPM et al (2015) Decay characteristics and erosion-related transport of glyphosate in Chinese loess soil under field conditions. *Sci Total Environ* 530–531:87–95. <https://doi.org/10.1016/j.scitotenv.2015.05.082>
- Yang Y, Deng Q, Yan W et al (2018) Comparative study of glyphosate removal on goethite and magnetite: adsorption and photo-degradation. *Chem Eng J* 352:581–589. <https://doi.org/10.1016/j.cej.2018.07.058>
- Yi SY, Cui Y, Zhao Y et al (2016) A novel naturally occurring class I 5-enolpyruvylshikimate-3-phosphate synthase from *Janibacter* sp. confers high glyphosate tolerance to rice. *Sci Rep* 6:19104. <https://doi.org/10.1038/srep19104>
- Yu XM, Yu T, Yin GH et al (2015) Glyphosate biodegradation and potential soil bioremediation by *Bacillus subtilis* strain Bs-15. *Genet Mol Res* 14:14717–14730. <https://doi.org/10.4238/2015.November.18.37>
- Zabaloy MC, Allegrini M, Tebbe DA, Schuster K, Gomez, EDV (2017) Nitrifying bacteria and archaea withstanding glyphosate in fertilized soil microcosms *Appl Soil Ecol* 117:88–95. <https://doi.org/10.1016/j.apsoil.2017.04.012>
- Zeng H, Xu H, Liu G et al (2021) Physiological and metagenomic strategies uncover the rhizosphere bacterial microbiome succession underlying three common environmental stresses in cassava. *J Hazard Mater* 411:125143. <https://doi.org/10.1016/j.jhazmat.2021.125143>
- Zhan H, Feng Y, Fan X, Chen S (2018) Recent advances in glyphosate biodegradation. *Appl Microbiol Biotechnol* 102:5033–5043. <https://doi.org/10.1007/s00253-018-9035-0>
- Zhang H, Liu J, Wang L, Zhai Z (2021) Glyphosate escalates horizontal transfer of conjugative plasmid harboring antibiotic resistance genes. *Bioengineered* 12:63–69. <https://doi.org/10.1080/21655979.2020.1862995>
- Zhao H, Tao K, Zhu J et al (2015) Bioremediation potential of glyphosate-degrading *Pseudomonas* spp. strains isolated from contaminated soil. *J Gen Appl Microbiol* 61:165–170. <https://doi.org/10.2323/jgam.61.165>
- Zobiolo LHS, Kremer RJ, Oliveira RS, Constantin J (2011) Glyphosate affects micro-organisms in rhizospheres of glyphosate-resistant soybeans. *J Appl Microbiol* 110:118–127. <https://doi.org/10.1111/j.1365-2672.2010.04864.x>

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