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Impacts of soil storage on microbial parameters

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Abstract. This review aims to determine the impact of soil storage on microbial parameters (e.g. abundance, biomass, activity, and various diversity metrics). The literature dealing with the impact of storage practices (cold storage, freezing, drying, freeze-drying, and ambient storage) on soil microbial parameters was analysed and covered 76 articles representing 289 basic data (the impact of a given storage practice on a microbial parameter). Globally, more than 75 % of these data showed a significant impact of storage on the measured microbial parameters, compared with those measured on fresh, non-stored soil samples. The storage practices showed various effects on the soil microbial parameters, with sometimes opposite effects across different soil types. For instance, the effects of a given storage practice on different enzyme activities in the same soil were not constant; moreover, the effects of a given storage practice on a given enzyme activity varied across different soils. Several factors may explain the variability in the storage impact (e.g. storage duration, soil type and/or land use, and climate condition), but the available data are too scattered to elucidate their respective roles. However, a few storage recommendations can be made, depending on the microbial parameters studied. Storage practices for soil samples, when unavoidable, should be carefully selected according to (1) the conditions that prevail in the native soil environment and (2) the microbial parameters that are analysed (even though there is rarely consensus on a best practice), and different storage practices should be utilised for different microbial parameters if necessary.

1 Introduction

Knowledge about soil microbial parameters (e.g. abundance, biomass, activity, and diversity), their spatial distribution, and their response to various stresses and disturbances is essential for understanding matter and energy fluxes as well as predicting ecosystem services associated with soils (Delgado-Baquerizo et al., 2020; Wagg et al., 2019). However, the links between microbial diversity and ecosystem functions remain incompletely elucidated (Graham et al., 2016; Nannipieri et al., 2003). Moreover, the analysis of fresh soil samples can be problematic, especially for (1) soils originating from sites that are located several hours (or even days) from laboratory facilities or (2) soils from sampling sites located at large distances from each other, as samples cannot be processed rapidly due to transport or shipping constraints (e.g. Creamer et al., 2016; Gillespie et al., 2021). Furthermore, archived soils provide an interesting resource for soil scientists to examine time series (e.g. Benucci et al., 2020); study long-term impacts, such as those of climate or land use changes (Clark and Hirsch, 2008; Hu et al., 2023; Manter et al., 2017); or inventory soil properties (Karimi et al., 2018). Thus, as soil storage is inevitable, a question arises regarding the best storage option.

The objective of storage is to suppress soil enzyme activities that could alter biochemical (nutrient or carbon contents) and/or microbial parameters, which inevitably occurs if the soil samples are stored under ambient temperature and field moisture conditions. The suppression of enzyme activity can be achieved by sharply decreasing water availability (drying samples), temperature (storage typically at 4, −20, or −80 °C), or both (freeze-drying samples). However, lowering the water availability or temperature can have other adverse effects, as both influence the physicochemical properties of soils (Blake et al., 2000; Kühnel et al., 2019; Sun et al., 2015; Villada et al., 2016), with potential site-specific effects (e.g. Kaiser et al., 2015). Drying, by inhibiting solute diffusion, prevents soil microbial activ-

ity; however, drying also directly impacts microbial physiology. To face extreme dry conditions, micro-organisms can either reduce their internal solute potential by accumulating osmolytes or go dormant, with various micro-organisms implementing diverse physiological responses when facing dry conditions (Schimel, 2018). Bacteria and fungi occupy different water-related niches, with soil fungi being generally more resistant but less resilient than bacteria (e.g. Barnard et al., 2013; de Vries et al., 2018). Both the speed at which the soils are dried and the duration of storage (Meisner et al., 2013) could matter. Freezing generates osmotic stress for microbial cells due to the increased salt concentration in the liquid phase during ice formation; moreover, ice crystal formation can damage cells, leading to cell lysis (Mazur, 1984; Stenberg et al., 1998). Contrary to freezing, cold storage (generally at 4 °C) does not imply osmotic stress or cell lysis due to ice crystal formation. At low temperatures, proteins are less flexible and the cell membrane loses its fluidity, affecting nutrient transport (Chattopadhyay, 2006) and inhibiting replication and transcription (D'Amico et al., 2006); however, after an acclimation phase, the synthesis of proteins and, subsequently, microbial activity can restart to some extent (Barria et al., 2013). Micro-organisms implement various physiological responses to cold conditions (Barria et al., 2013). Some micro-organisms can enter a dormant state or, for cold-adapted organisms, accumulate molecules that help maintain an active metabolism. Furthermore, microbial activity (especially the mineralisation of easily available organic carbon) may even continue under subzero conditions, especially for soils from cold environments (Jansson and Tas, 2014), leading to reduced C and nutrient availability.

For some analyses, especially those implying incubation, dry samples have to be rewetted and frozen samples have to be thawed in order to reactivate the soil microbial community. These steps can induce further effects on soil micro-organisms. Thus, freezing–thawing may result in enhanced N mineralisation following the release of substrates by lysed microbial cells (e.g. Stenberg et al., 1998). Remoistening of soils that were previously dried (either in the field or in the lab) strongly impacts the microbial community (Bartlett and James, 1980) and causes the germination of fungal spores or the reactivation of bacteria that had resisted drying in various forms (Wingfield, 1980). Moreover, in dried soils, the rapid increase in the soil water potential may cause osmotic shock, leading to cell lysis or the release of intra-cellular osmoregulatory solutes (Fierer and Schimel, 2002). The resulting increase in the dissolved organic carbon and nitrogen contents (e.g. Makarov et al., 2013) may stimulate the growth and activity of micro-organisms (Birch, 1958). For instance, a recent study by Schroeder et al. (2021) showed that a 14 d pre-incubation (at 45 % water-holding capacity and 15 °C) had the most pronounced effect on the soil microbial respiration rate and microbial biomass, compared with the effects of dry, ambient, or freezing storage.

Drying–rewetting or freezing–thawing procedures can also induce a physical disruption to soil aggregates (Stenberg et al., 1998), releasing previously protected cells or biomolecules and further providing a better yield for the biomolecule extraction procedure. Thus, the physicochemical properties of the soil, including the clay content, microaggregation, and soil porosity, can explain the occurrence of microsites where micro-organisms can be protected under unfavourable conditions. For instance, Jones et al. (2019) suggested that the soil clay content (with clay providing potential protective microsites) may enhance the preservation of microbial functions under long-term storage or even following drying. Furthermore, freeze–thawing or drying–rewetting procedures could create an expanded niche for some micro-organisms, with both aggregate disruption and microbial cell lysis providing nutrients and carbon to storage-resistant micro-organisms (Fierer and Schimel 2002; Stenberg et al., 1998). Alternatively, Goberna et al. (2005) suggested that slow-growing organisms (*K* strategists) would be favoured under a disturbed (e.g. freezing–thawing) regime.

The various microbial biomolecules and functional parameters that are used for the characterisation of the soil microbial community have different levels of stability; for instance, rRNA degrades very rapidly (Wang et al., 2012), phospholipid-derived fatty acids (PLFAs) are rapidly metabolised following cell death (Hill et al., 2000), and DNA is deemed less recalcitrant than other biomolecules. Consequently, the effects of storage on the soil microbial parameters, resulting from the interactions between several parameters (such as temperature adaptation, water availability, and nutritional status of the soil micro-organisms), are complex and difficult to foresee.

There is currently no comprehensive synthesis of the knowledge acquired about the effects of storage practices on the various microbial parameters that are used in soil microbial ecology (although Schroeder et al., 2021, recently proposed a nice synthesis in their introduction). Here, I analysed the studies assessing the effects of soil storage practices on various soil microbial parameters. The usual storage options include the following: cold storage (generally at 4 °C – hereafter referred to as COLD); freezing (conservation at generally −20 °C – hereafter referred to as FREEZE); air-drying (hereafter referred to as DRY); freeze-drying, which is rarely used because the option is seldom available far from laboratory facilities (hereafter referred to as FREEZE-DRYING); and storage at ambient temperature (hereafter referred to as AMBIENT). The corpus of literature dealing with this topic frequently failed to provide adequate data (in particular the effect size of storage practices) and gathered very dissimilar results from several storage practices and microbial parameters, resulting in highly fragmented information. As a result, I could not carry out a meta-analysis; rather, I intended to provide a "state of the art" of the knowledge on this topic. Hence, the aim of this study was to assess the consistency of the storage impacts (i.e. whether a given storage practice

always had the same impact on a given microbial parameter across different soil and climate conditions) and to provide the authors of future studies with contextualised elements.

2 Methodology

2.1 Data source and collection

A systematic literature review was done. In October 2024, relevant peer-reviewed publications were selected using Web of Science with the following keywords: "soil AND storage AND (microb* OR bacteria* OR fung*) AND (dry OR freez* OR cold OR ambient)" in the field TOPIC. The 1438 articles were screened by relevance, and only papers that explicitly assessed the effects of various storage conditions and that compared microbial parameters analysed on stored soils with those obtained on fresh soils were retained. Additional references were retrieved when citing or being cited by the previous ones. I excluded articles that assessed uncommon microbial properties and specific microbial groups (e.g. rhizobia and pathogens) as well as papers dealing with substrates other than soils (e.g. compost and litter).

2.2 Data screening

The data (in addition to bibliographic information) retrieved for each paper are outlined in Sect. 2.2.1–2.2.5.

2.2.1 Background information

The following background information was collected: the soil type (e.g. forest, arable, mountain, or urban), climate conditions (e.g. temperate, tropical, or Mediterranean), and storage duration. For the latter, as authors sometimes assessed the impact of different storage durations, we based our conclusion, when necessary, on the results from the longer storage term.

2.2.2 Storage methods

The following storage methods were considered: cold storage (+2 to +4 °C – COLD); freezing (generally at −20 °C – FREEZE); storage after air-drying at ambient temperature (DRY); storage at ambient temperature and field moisture (AMBIENT); and freeze-drying (FREEZE-DRY). I did not consider freezing at −80 °C in addition to freezing at −20 °C, as the devices required for deep freezing are generally lacking at sites far from laboratory facilities. For microbial analyses, especially those based on incubation for activity measurements that require the rewetting of DRY soils or the thawing of FREEZE soils, the effect of rewetting or thawing was considered to be a part of the storage method, and the studies generally considered the microbial parameter as having been analysed on rewetted (for DRY), thawed (for FREEZE), or warmed soil samples (for COLD). The same was true for methods requiring a pre-incubation period prior to or as part of the measurement, to stabilise the biomass (fumigation–incubation technique) or to allow the microbial enzymes to reactivate (e.g. for substrate-induced respiration – SIR); although pre-incubation can impact soil microbial parameters (e.g. Petersen and Klug, 1994), I considered this step to be part of the storage procedure.

I should have distinguished between the storage procedure and duration, as both may impact soil properties (e.g. Rubin et al., 2013; Turner and Romero, 2010; Yoshikura et al., 1980). However, because of the low number of studies that use various storage durations and as storage practices often have contrasting effects on different microbial properties, I only considered the storage practice (with, when relevant, additional comments about the effect of storage duration), with the hope of drawing recommendations for suitable storage.

2.2.3 Methodological approach

Because a given microbial parameter can be estimated using different approaches (for instance, microbial biomass can be estimated by PLFA extraction, fumigation–extraction, or DNA recovery), I first characterised the methodological approach used:

- CFE – chloroform-fumigation extraction (for determination of microbial C, N, or P);
- COUNTS – for direct microbial cell counts (microscopy or cytometry);
- CULTURE – culture-based microbial parameters (colony-forming unit, cfu, counts or morphotypes);
- DNA – DNA-based (or, rarely, RNA-based) microbial parameters after extraction;
- INCUBATION – for parameters estimated following incubation (e.g. enzyme activities or the community-level physiological profile);
- PLFA-based analyses (hereafter PLFA).

2.2.4 Microbial parameters characterised

The microbial parameters that were characterised in the study are as follows:

- *abundance*, which can be based on direct COUNTS, CULTURE (cfus), or DNA (qPCR);
- *activity*, generally following INCUBATION (basal respiration, SIR, denitrification enzyme activity (DEA), community-level physiological profile (CLPP), specific soil enzyme activities, etc.);
- *biomass*, which can be based on DNA/PLFA extraction or on CFE (microbial biomass C, N, or P);

- *composition*, comprising a list of species, taxa, or operational taxonomic units (OTUs) detected in the samples, mainly for sequencing (after DNA extraction);

- *structure*, comprising species/taxa/OTU (for sequencing) or group-specific PLFAs and their relative abundance, band position and intensity for molecular fingerprinting, or metabolised substrates and their rate of utilisation (for CLPP);

- *diversity*, expressed using OTU richness or the Shannon index, number of cfu morphotypes, etc.

2.2.5 Scoring of storage effects

Because the impact of several storage methods can be analysed on several microbial parameters in a paper, I used the impact of each storage method on each microbial parameter as an elemental piece of information (e.g. the impact of COLD storage on soil basal respiration). For each microbial parameter, the effect of the storage practice was scored as follows (when several soils were tested, I scored a single effect that was consistent (null, positive, negative, or effective; see below) or inconsistent (variable) across the tested soils.

- A null score was attributed when the storage did not significantly increase, decrease, or change the microbial parameter, compared with values determined in fresh, field-moist, non-stored soil.

- For quantitative parameters (abundance, activity, biomass, and diversity), a null score was attributed when the storage did not significantly increase or decrease the value, compared to that of fresh, non-stored soil, whereas a positive or negative score was attributed when the storage significantly increased or decreased the microbial parameter, respectively.

- For qualitative parameters (structure and composition), the impact of storage practice was recorded as null when the difference was statistically non-significant or as effective when the microbial parameter was significantly different.

- A score of "variable" was attributed when the storage had inconsistent effects across different soils, sampling dates, or soil enzyme activities.

  When relevant, I distinguished between bacterial, fungal, and archaeal parameters (DNA- and CULTURE-based parameters). When several storage practices were compared, I also noted their relative effects (and if they were consistent across soil types) as well as whether the ranking between samples was conserved (compared to the ranking between fresh, non-stored soil samples), when this information was given by the authors. The relative effects of different practices were rated on the basis of the conclusions drawn by the authors.

3 Results

3.1 Global assessment of storage impacts

A total of 76 articles (see the captions of Tables 1 and 2) were used for this synthesis. The number of published articles dealing with this issue has increased globally (10 articles between 1961 and 1980, 16 articles between 1981 and 2000, and 50 articles between 2001 and 2024), with some shifts in the methodological approaches used for the characterisation of storage impacts: an increasing proportion of studies are employing DNA-based approaches, although a high proportion of studies are still using INCUBATION-based approaches, the latter of which were used in more than 50 % of articles (Table 1).

The impact of storage on microbial abundance was assessed using CULTURE- (cfu counts, 8 papers) or DNA-based (2 papers, using qPCR) approaches. Storage impacts on microbial biomass used CFE (16 papers), DNA yield (4 papers), or PLFA (7 papers). Microbial diversity and composition were investigated using DNA (5 and 3 papers, respectively). The structure of the soil microbial community was characterised using PLFA (11 papers), DNA (molecular fingerprinting, 8 papers; DNA sequencing, 5 papers), or CLPP (6 papers). Finally, the impact of storage on microbial activity was investigated using various INCUBATION-based approaches, with a total of 51 papers (see below).

Many papers investigated the impact of several storage practices, and sometimes these investigations involved several microbial parameters; thus, the synthesis allowed for the recovery of a total of 289 data (effect of a given storage practice on a given microbial parameter in one or several soil samples). COLD (90 data), DRY (82 data), and FREEZE (74 data) were the most frequently studied practices, whereas the AMBIENT and FREEZE-DRY practices were rarely addressed (34 and 9 data, respectively). Overall, 219 data (75.7 % of the data) showed significant impacts of storage on the studied soil microbial parameter for at least one of the soils tested, while 70 data (24.2 %) showed no significant impact, compared to microbial parameters measured immediately following sampling on non-stored field-moist soil samples. All of the practices showed overwhelmingly significant impacts on soil microbial parameters compared with those measured on non-stored soil samples (74 % for COLD, 68 % for FREEZE, 80 % for DRY, 88 % for AMBIENT, and 30 % for FREEZE-DRY, although only nine data were available for the latter). Because storage practices are expected to have different impacts on different microbial parameters, these impacts were analysed by methodological approach and microbial parameter. Significant impacts of storage were recorded for 24 out of 29 data for CFE-based parameters (83 %), 15 out of 17 data for CULTURE-based parameters (88 %), 38 out of 75 data across all DNA-based parameters (51 %), 113 out of 133 data for INCUBATION-based parameters (85 %), and 29 out of 35 data for PLFA-

Table 1. Evolution of the number of articles and of the methodological approaches used for the characterisation of storage impacts on soil microbial parameters (1961–2024). The number of articles (n) listed in this table is 104 (rather than 76) because some articles use several methodological approaches.

Period (n)	CFE	CULTURE	DNA	INCUBATION	PLFA
1961–1970 ($n = 3$)		(55)		(22), (56)	
1971–1980 ($n = 7$)	(44)	(37), (52), (69)		(37), (38), (44), (69), (72), (73)	
1981–1990 ($n = 3$)		(58)		(4), (53)	
1991-2000 ($n = 13$)	(45), (50), (54)	(28), (49)	(21)	(5), (28), (30), (45), (49), (50), (51), (54), (62), (68)	(41), (48)
2001–2010 ($n = 22$)	(6), (12), (15), (20), (27), (60), (75), (76)	(8), (40)	(8), (26), (27), (40), (61), (65)	(6), (10), (12), (13), (17), (18), (27), (40), (43), (59), (60), (65), (74), (75), (76)	(20), (27), (29), (59), (71)
2011-2024 ($n = 28$)	(2), (31), (33)	(42)	(3), (9), (14), (19), (24), (25), (32), (46), (57), (66), (67)	(1), (7), (9), (11), (16), (23), (25), (31), (32), (34), (35), (36), (39), (64), (66), (70)	(36), (47), (63), (66)

The articles listed in the table are as follows: (1) Abellan et al. (2011), (2) Achat et al. (2012), (3) Brandt et al. (2014), (4) Breitenbeck and Bremmer (1987), (5) Brohon et al. (1999), (6) Černohlávková et al. (2009), (7) Chirinda et al. (2011), (8) Clark and Hirsch (2008), (9) Cui et al. (2014), (10) Dadenko et al. (2009), (11) De Castro Lopes et al. (2015), (12) De Nobili et al. (2006), (13) DeForest (2009), (14) Delavaux et al. (2020), (15) Fardoux et al. (2000), (16) Ginn et al. (2014), (17) Goberna et al. (2005), (18) Gonzalez-Quiñones et al. (2009), (19) Guerrieri et al. (2020), (20) Hamer et al. (2007), (21) Harry et al. (2000), (22) Ivarson and Sowden (1970), (23) Jones et al. (2019), (24) Kushwaha et al. (2024), (25) Lane et al. (2022), (26) Lauber et al. (2010), (27) Lee et al. (2000), (28) Lee et al. (2007), (29) Liu et al. (2009), (30) Luo et al. (1996), (31) Makarov et al. (2013), (32) Martí et al. (2012), (33) Maslov et al. (2019), (34) Meyer et al. (2019), (35) Moreira et al. (2017), (36) Moy and Nkongolo (2023), (37) Nicholson (1972), (38) Patten et al. (1980), (39) Peoples and Koide (2012), (40) Pesaro et al. (2003), (41) Petersen and Klug (1994), (42) Ramirez et al. (2017), (43) Riepert and Felgentreu (2002), (44) Ross et al. (1980), (45) Ross (1991), (46) Rubin et al. (2013), (47) Schnecker et al. (2012) (48) Schutter and Dick (2000), (49) Shishido and Chanway (1998), (50) Simek and Santruckova (1999), (51) Simek (2000), (52) Sparling and Cheshire (1979), (53) Speir and Ross (1981), (54) Stenberg et al. (1998), (55) Stotzky et al. (1962), (56) Tabatabai and Bremner (1970), (57) Tatangelo et al. (2014), (58) Tate and Jenkinson (2008), (59) Trabue et al. (2006), (60) Turner and Romero (2010), (61) Tzeneva et al. (2009), (62) Verchot (1999), (63) Veum et al. (2019), (64) Wakelin et al. (2013), (65) Wallenius et al. (2010), (66) Wang et al. (2015), (67) Weißbecker et al. (2017), (68) West et al. (1992), (69) Wingfield (1980), (70) Włodarczyk et al. (2014), (71) Wu et al. (2009), (72) Yoshikura et al. (1980), (73) Zantua and Bremner (1977), (74) Zorzona et al. (2006), (75) Zorzona et al. (2007), and (76) Zorzona et al. (2009).

based parameters (83 %). The results are shown in Table 2 and discussed below.

3.2 CFE-based parameters

The effect of storage on microbial biomass estimated following chloroform fumigation extraction (CFE) was assessed in 16 articles (13 on microbial biomass carbon, MBC; 2 on microbial biomass phosphorus, MBP; 1 on microbial biomass nitrogen, MBN; and 1 on MBC and MBN). The soil microbial biomass generally decreased following storage (in 20 out of 29 data), but the conclusions of the studies were very heterogeneous. Eight studies evaluated the impact of COLD storage on these parameters. Of these, six found lower MBC (Černohlávková et al., 2009; Lee et al., 2007; Maslov et al., 2019; Simek and Santruckova, 1999; Stenberg et al., 1998), MBN (Maslov et al., 2019), or MBP (Turner and Romero, 2010); one study found no impact on MBC (Ross, 1991); and one study found a variable impact according to soil types (Ross et al., 1980) compared with non-stored soils. Among the six articles addressing the effect of FREEZE storage, Lee et al. (2007), Stenberg et al. (1998), and Turner and Romero (2010) concluded that it resulted in negative effects; Černohlávková et al. (2009) and Maslov et al. (2019) reported null effect; and Ross et al. (1980) found variable effects on microbial biomass. A total of 12 papers assessed the impact of DRY storage on soil microbial biomass, with 12 data showing lower MBC, MBP, and/or MBN (Achat et al., 2012; Černohlávková et al., 2009; De Nobili et al., 2006; Fardoux et al., 2000; Hamer et al., 2007; Lee et al., 2007; Makarov et al., 2013; Maslov et al., 2019; Simek and Santruckova, 1999; Turner and Romero, 2010) and 2 data showing no effect on

Table 2. Synthesis of the impacts of storage practices (COLD, FREEZE, DRY, AMBIENT, and FREEZE-DRY) on the soil microbial parameters, compared with parameters estimated on fresh, non-stored soils. The changes are scored as no impact Ø (no significant change), increase ⇉ or decrease ⇇ (for quantitative parameters, i.e. higher and lower parameter values, respectively), change ⇋ (for significant change on non-quantitative parameters), or variable ⤮ (when storage showed inconsistent changes across soil samples or soil enzyme activities). References for studies that have shown significant impacts of storage are given in bold. For DNA-based analyses, the distinction was made between analyses targeting bacteria, archaea, and fungi (including arbuscular mycorrhizal fungi, AMF).

Methodological approach	Microbial parameter	COLD	FREEZE	DRY	AMBIENT	FREEZE -DRY
CFE	biomass (C, N, P)	Ø: (45); ⇉: **(6), (28), (33), (50), (54), (60);** ⤮: **(44)**	Ø: (6), (33); ⇉: (28), (54), (60); ⤮: (44)	Ø: (75), (76); ⇉: **(2), (6), (12), (15), (20), (28), (31), (33), (50), (60)**	⇉: **(60);** ⇉: **(58);** ⤮: **(44)**	
CULTURE	abundance (bacteria)	⇉: **(27), (49), (55)**	Ø: (37); ⤮: **(42);** ⇇: **(49)**	⇉: **(8), (37), (52)**		
CULTURE	abundance (fungi)	Ø: (69); ⇉: **(55);** ⇉: **(27), (49)**	⇉: **(37);** ⇉: **(49)**	⇉: **(37)**, **(52)**		
DNA	biomass	Ø: (21); ⇉: **(28)**	⇉: **(28), (40)**	⇉: **(21), (28)**	⇉: **(21)**	⇉: **(67)**
DNA	abundance (bacteria)	Ø: (3)	Ø: (3)	⇉: **(8)**		
DNA	abundance (archaea)	Ø: (3)	Ø: (3)			
DNA sequencing	diversity (bacteria)	Ø: (26); ⇉: **(24);** ⤮: **(19), (25)**	Ø: (14), (26); ⤮: **(25)**	Ø: (19); ⤮: **(25)**	Ø: (14); ⤮: **(25)**	⇉: **(67)**
DNA sequencing	diversity (fungi)	⇉: **(24);** ⤮: **(19)**	Ø: (14)	⤮: **(19)**	⤮: **(14)**	Ø: (67) AMF
DNA sequencing	diversity (archaea)	⇉: **(24)**				
DNA sequencing	composition (bacteria)		Ø: (14); ⇋: **(46)**		⇋: **(14), (46)**	Ø: (67)
DNA sequencing	composition (fungi)		Ø: (14)		⤮: **(14)**	Ø: (67) AMF
DNA fingerprinting	structure (bacteria)	Ø: (3), (32), (57)	Ø: (3), (32), (57), (65)	Ø: (32); ⇋: **(8), (57), (61), (65)**	Ø: (57)	
DNA fingerprinting	structure (fungi)		⇋: **(9)**	⇋: **(9)**		
DNA	structure (archaea)	Ø: (3)	Ø: (3); ⇋: **(40)**			
DNA sequencing	structure (bacteria)	Ø: (24), (26), (66); ⇋: **(19), (25)**	Ø: (26), (66); ⇋: **(25)**	Ø: (19), (66) ⇋: **(19), (25)**	⇋: **(25)**	
DNA sequencing	structure (fungi)	Ø: (19); ⇋: **(24)**		Ø: (19)		
DNA sequencing	structure (archaea)	Ø: (24)				

MBC after DRY storage (Zorzona et al., 2007; Zorzona et al., 2009) compared to non-stored soils. Finally, among the three studies dealing with the impact of storage at AMBIENT temperature, one showed lower MBC (Turner and Romero, 2010), one showed higher MBC (Tate and Jenkinson, 2008), and one showed VARIABLE impact (Ross et al., 1980) compared with non-stored soil samples. Among the seven studies exploring the impact of several storage methods on microbial biomass following CFE, the decrease in biomass following DRY storage was similar (Maslov et al., 2019; Simek and Santruckova, 1999) or stronger (Černohlávková et al., 2009; Lee et al., 2007; Turner and Romero, 2010) than following COLD storage, whereas it was comparable to (Turner and Romero, 2010) or stronger (Černohlávková et al., 2009; Lee et al., 2007; Maslov et al., 2019) than following FREEZE storage. The conclusions of the studies were highly hetero-

Table 2. Continued.

Methodological approach	Microbial parameter	COLD	FREEZE	DRY	AMBIENT	FREEZE -DRY
INCUBATION	activity (CLPP)	Ø: (64)	⇉: **(9)**	⇉: **(9)**		
INCUBATION	structure (CLPP)	⇌: **(17), (18), (49)**; ⤭: **(66)**	⇌: **(9), (17), (49), (66)**	⇌: **(9), (23)**; ⤭: **(66)**	⇌: **(17)**	
INCUBATION	activity (basal respiration)	Ø: (34), (45); ⇉: **(5), (27), (32), (66)**; ⇉: **(6), (51), (54)**	Ø: (34); ⇉: **(6), (22), (27), (32), (66)**; ⇉: **(54)**	Ø: (23), (66), (75), (76); ⇉: **(12), (32), (34), (50), (68)**; ⇉: **(27), (37)**; ⤭: **(6), (70)**	⇉: **(5)**	
INCUBATION	activity (SIR)	Ø: (54); ⇉: **(5), (32)**; ⇉: **(6), (45), (51)**	Ø: (40), (54); ⇉: **(32)**; ⤭: **(6)**	⇉: **(32)**; ⇉: **(50)**; ⤭: **(6), (70)**	⇉: **(50)**; ⇉: **(5)**	
INCUBATION	activity (DEA)	Ø: (4); ⇉: **(7)**; ⇉: **(51), (54)**	⇉: **(4)**; ⇉: **(54)**	⇉: **(30), (38), (70)**;	⇉: **(4), (30)**	
INCUBATION	activity (various)	⇉: **(16), (59), (62)**; ⤭: **(27), (44), (50), (69)**	Ø: (40); ⇉: **(31)**; ⇉: **(43)**; ⤭: **(44), (50)**	Ø: (16); ⇉: **(12)**	⇉: **(43), (59)**; ⇉: **(50)**; ⤭: **(44)**	
INCUBATION	activity (enzyme activities)	⇉: **(1), (5), (10), (28), (56), (60)**; ⤭: **(13), (25), (36)**	Ø: (56), (73); ⇉: **(22), (39)**; ⇉: **(1), (10), (28), (43), (60)**; ⤭: **(13), (25), (65)**	Ø: (73), (74), (76); ⇉: **(23), (39)**; ⇉: **(1), (10), (28), (60), (72)**; ⤭: **(11), (25), (35), (53), (65)**	Ø: (73); ⇉: **(5), (43), (56), (60)**; ⤭: **(25)**	⇉: **(72)**
PLFA	biomass	Ø: (41), (47); ⇉: **(59)**; ⇉: **(28), (36), (66)**	Ø: (47); ⇉: **(28) (66)**	Ø: (66); ⇉: **(28)**	Ø: (66); ⇉: **(59)**; ⇉: **(41)**	⇉: **(71)**
PLFA	structure	Ø: (41); ⇌: **(29), (47), (48), (59)**; ⤭: **(28)**	⇌: **(29), (47), (48)**; ⤭: **(28)**	⇌: **(20), (28), (29), (48), (63)**	⇌: **(41), (59), (63)**	⇌: **(29), (71)**

The articles listed in the table are as follows: (1) Abellan et al. (2011), (2) Achat et al. (2012), (3) Brandt et al. (2014), (4) Breitenbeck and Bremmer (1987), (5) Brohon et al. (1999), (6) Černohlávková et al. (2009), (7) Chirinda et al. (2011), (8) Clark and Hirsch (2008), (9) Cui et al. (2014), (10) Dadenko et al. (2009), (11) De Castro Lopes et al. (2015), (12) De Nobili et al. (2006), (13) DeForest (2009), (14) Delavaux et al. (2020), (15) Fardoux et al. (2000), (16) Ginn et al. (2014), (17) Goberna et al. (2005), (18) Gonzalez-Quiñones et al. (2009), (19) Guerrieri et al. (2020), (20) Hamer et al. (2007), (21) Harry et al. (2000), (22) Ivarson and Sowden (1970), (23) Jones et al. (2019), (24) Kushwaha et al. (2024), (25) Lane et al. (2022), (26) Lauber et al. (2010), (27) Lee et al. (2000), (28) Lee et al. (2007), (29) Liu et al. (2009), (30) Luo et al. (1996), (31) Makarov et al. (2013), (32) Martí et al. (2012), (33) Maslov et al. (2019), (34) Meyer et al. (2019), (35) Moreira et al. (2017), (36) Moy and Nkongolo (2023), (37) Nicholson (1972), (38) Patten et al. (1980), (39) Peoples and Koide (2012), (40) Pesaro et al. (2003), (41) Petersen and Klug (1994), (42) Ramirez et al. (2017), (43) Riepert and Felgentreu (2002), (44) Ross et al. (1980), (45) Ross (1991), (46) Rubin et al. (2013), (47) Schnecker et al. (2012) (48) Schutter and Dick (2000), (49) Shishido and Chanway (1998), (50) Simek and Santruckova (1999), (51) Simek (2000), (52) Sparling and Cheshire (1979), (53) Speir and Ross (1981), (54) Stenberg et al. (1998), (55) Stotzky et al. (1962), (56) Tabatabai and Bremner (1970), (57) Tatangelo et al. (2014), (58) Tate and Jenkinson (2008), (59) Trabue et al. (2006), (60) Turner and Romero (2010), (61) Tzeneva et al. (2009), (62) Verchot (1999), (63) Veum et al. (2019), (64) Wakelin et al. (2013), (65) Wallenius et al. (2010), (66) Wang et al. (2015), (67) Weißbecker et al. (2017), (68) West et al. (1992), (69) Wingfield (1980), (70) Włodarczyk et al. (2014), (71) Wu et al. (2009), (72) Yoshikura et al. (1980), (73) Zantua and Bremner (1977), (74) Zorzona et al. (2006), (75) Zorzona et al. (2007), and (76) Zorzona et al. (2009).

geneous, with some of them recommending FREEZE (e.g. Lee et al., 2007; Stenberg et al., 1998) or AMBIENT storage (Turner and Romero, 2010) for the determination of CFE-based soil microbial biomass and with DRY storage having the strongest effects compared with COLD or FREEZE storage.

3.3 CULTURE-based microbial abundance

In the eight papers evaluating the impact of storage on culturable microbial counts in soil samples, COLD had negative impact on bacterial abundance (Lee et al., 2007; Shishido and Chanway, 1998; Stotzky et al., 1962), while it had null (Stotzky et al., 1962), positive (Stotzky et al., 1962), or negative (Lee et al., 2007; Shishido and Chanway, 1998) impact on fungal abundance. FREEZE had no (Nicholson, 1972), variable (Ramirez et al., 2017), or negative impact (Shishido and Chanway, 1998) on bacterial abundance, while it had a positive (Nicholson, 1972) or negative (Shishido and Chanway, 1998) impact on fungal abundance. A negative impact of DRY storage was shown on bacterial counts in Clark and Hirsch (2008), Nicholson (1972), and Sparling and Cheshire (1979) and on fungal counts in Nicholson (1972) and Sparling and Cheshire (1979).

3.4 DNA-based parameters

The impact of soil storage on DNA-based parameters was investigated in 18 papers, with several parameters addressed in most of the papers (Table 2). DNA extract can be used to address soil microbial group-specific abundance (using qPCR), biomass (DNA yield), microbial diversity, composition, or structure.

Brandt et al. (2014) showed no impact of either COLD or FREEZE storage for 10 d on bacterial or archaeal abundance using qPCR, while Clark and Hirsch (2008) showed a decreased abundance of *Pseudomonas* spp. 16S rDNA following long-term DRY storage. The four studies assessing the storage effect on soil DNA yield (as a proxy for biomass) found a negative impact of COLD (Lee et al., 2007, but not Harry et al., 2000), FREEZE (Lee et al., 2007, and Pesaro et al., 2003, with freeze–thaw), DRY (Harry et al., 2000; Lee et al., 2007), AMBIENT (Harry et al., 2000), and FREEZE-DRY (Weißbecker et al., 2017) storage compared with freshly sampled soil. Harry et al. (2000) reported the absence of a 1-year COLD-storage impact on DNA yield and expressed a preference for this storage method. The few studies available for DNA-based diversity reported that COLD storage had null (Lauber et al., 2010, for bacteria), negative (Kushwaha et al., 2024, for archaea), or variable (Guerrieri et al., 2020; Kushwaha et al., 2024; and Lane et al., 2022, for bacteria and fungi) effects. FREEZE storage showed no (Delavaux et al., 2020; Lauber et al., 2010) or variable impact on bacterial (according to the diversity index considered; Lane et al., 2022) or fungal (Delavaux et al., 2020) diversities, while DRY storage displayed null (Guerrieri et al., 2020) or variable (Lane et al., 2022) effects on bacterial diversity but variable effects on fungal diversity (Guerrieri et al., 2020). AMBIENT storage had null (Delavaux et al., 2020) or variable (Lane et al., 2022) effects on bacterial diversity but a variable effect on fungal diversity (Delavaux et al., 2020), and FREEZE-DRY decreased (for bacteria; Weißbecker et al., 2017) or did not impact (arbuscular mycorrhizal fungi; Weißbecker et al., 2017) molecular diversity. Guerrieri et al. (2020) only found a storage impact on both fungal and bacterial molecular diversity when rare taxa were considered. Finally, no study provided a conclusion regarding a better storage method. Lane et al. (2022) showed that different storage practices sometimes overestimated and sometimes underestimated bacterial richness, although with minimal impact on the Shannon bacterial diversity, with some significant interactions between storage practices, land use type, and storage duration.

Only three studies in the synthesis reported the impact of soil storage on the bacterial (Delavaux et al., 2020; Rubin et al., 2013; Weißbecker et al., 2017), fungal (Delavaux et al., 2020), or AM fungal (Weißbecker et al., 2017) molecular composition following DNA sequencing. Two of them (Delavaux et al., 2020, and Weißbecker et al., 2017) concluded no impact of FREEZE and FREEZE-DRY, respectively, whereas Rubin et al. (2013) found a significant impact of FREEZE on the bacterial composition. AMBIENT storage impacted both the fungal (Delavaux et al., 2020, with variable effects) and bacterial (Delavaux et al., 2020; Rubin et al., 2013) composition. Delavaux et al. (2020) and Rubin et al. (2013) both recommended FREEZE rather than AMBIENT storage.

Molecular fingerprinting was used for the characterisation of community structure in eight articles. No impact of COLD storage on community structure was reported for bacteria (Brandt et al., 2014; Martí et al., 2012; Tatangelo et al., 2014) or archaea (Brandt et al., 2014). FREEZE storage generally had no impact on bacterial fingerprinting (Brandt et al., 2014; Martí et al., 2012; Tatangelo et al., 2014; Wallenius et al., 2010), while significant impacts were reported for archaeal (Pesaro and al., 2003, but not Brandt et al., 2014) and fungal (Cui et al., 2014) molecular fingerprints. DRY storage generally had a significant impact on bacterial (Clark and Hirsch, 2008; Tatangelo et al., 2014; Tzeneva et al., 2009; Wallenius et al., 2010; but not Martí et al., 2012) or fungal (Cui et al., 2014) structure. Finally, Tatangelo et al. (2014) reported no impact of AMBIENT storage on bacterial terminal restriction fragment length polymorphism (T-RFLP) patterns. Overall, more frequent and stronger impacts were reported following DRY storage compared with COLD and FREEZE, especially for bacteria, while archaea and fungi could be more sensitive to FREEZE storage. For the characterisation of the community structure based on sequence data, the six available studies (Guerrieri et al., 2020; Kushwaha et al., 2024; Lane et al., 2022; Lauber et al., 2010; and Wang et al., 2015, for bacteria; Guerrieri et al., 2020, for fungi; and Kushwaha et al., 2024, for archaea) found no significant impact of COLD, FREEZE, or DRY storage on community structure except for significant storage effects on the bacterial (Guerrieri et al., 2020; Kushwaha et al., 2024) and fungal (Guerrieri et al., 2020) community structure following COLD storage. Lane et al. (2022) found that all storage practices impacted the structure of the soil bacterial community, depending on soil types, with the strongest compositional shift under DRY and AMBIENT storage conditions.

3.5 INCUBATION-based microbial parameters

Six studies evaluated the impact of storage on the outcomes of CLPP (Biolog or MicroResp™ analyses). Cui et al. (2014) found that both DRY and FREEZE storage impacted the soil microbial metabolic activity, although with a stronger impact of DRY over FREEZE storage. Wakelin et al. (2013) found no effect of COLD storage on activity using MicroResp™, compared with fresh soil samples. All studies characterising the soil microbial functional structure using CLPP showed a significant impact of the various storage practices (Cui et al., 2014; Goberna et al., 2005; Gonzalez-Quiñones et al., 2009; Jones et al., 2019; Shishido and Chanway, 1998; Wang et al., 2015), although with a stronger impact of COLD (Gob-

erna et al., 2005; Shishido and Chanway, 1998) and AMBIENT (Goberna et al., 2005) storage compared with that of FREEZE storage. Wang et al. (2015) also reported various impacts of COLD and DRY storage across different soil types, while FREEZE had more consistent effects in this study.

The impact of storage on basal and substrate-induced respiration (SIR) rates was evaluated in 18 and 8 papers, respectively. COLD storage resulted in similar (Meyer et al., 2019; Ross, 1991), enhanced (Brohon et al., 1999; Lee et al., 2000; Martí et al., 2012; Wang et al., 2015), or reduced (Černohlávková et al., 2009; Stenberg et al., 1998) basal respiration rates. COLD storage sometimes showed comparable effects on the SIR, with enhanced (Brohon et al., 1999; Martí et al., 2012) or reduced (Černohlávková et al., 2009; Simek, 2000) values, although a decreased SIR was reported in Ross (1991) (compared with a null effect on basal respiration), while an unchanged SIR after 13 months of storage was reported in Stenberg et al. (1998) (compared with a negative effect on basal respiration measured in the same soils). FREEZE storage generally enhanced basal respiration (Černohlávková et al., 2009; Ivarson and Sowden, 1970; Lee et al., 2000; Martí et al., 2012; Wang et al., 2015), except in Meyer et al. (2019) (no impact) and Stenberg et al. (1998) (reduced respiration rates), compared with that of fresh soils. FREEZE storage showed null (Pesaro and al., 2003; Stenberg et al., 1998), variable (Černohlávková et al., 2009), or enhanced (Martí et al., 2012, similar to basal respiration) effects on SIR rates. A total of 13 studies investigating the effect of DRY storage on soil microbial basal respiration reported null (Jones et al., 2019; Wang et al., 2015; Zorzona et al., 2007; Zorzona et al., 2009), positive (De Nobili et al., 2006; Martí et al., 2012; Meyer et al., 2019; Simek and Santruckova, 1999; West et al., 1992), negative (Lee et al., 2000; Nicholson, 1972), or variable (Černohlávková et al., 2009; Włodarczyk et al., 2014) effects, while 3 studies characterising SIR showed either enhanced (Martí et al., 2012, as for basal respiration) or variable (Černohlávková et al., 2009; Włodarczyk et al., 2014, similar to basal respiration) SIR rates following DRY storage, compared with those in non-stored soils. Finally, the only study addressing the impact of AMBIENT storage showed decreased basal respiration and SIR rates (Brohon et al., 1999). Studies that compared several storage methods came to various conclusions, with recommendations that often diverge. It is worth noting that storage practices impacted basal respiration and SIR measured on same soil types differently (Černohlávková et al., 2009; Martí et al., 2012; Simek and Santruckova, 1999; Stenberg et al., 1998).

Seven studies assessed the impact of soil storage on potential denitrification activity (DEA). COLD storage had null (Breitenbeck and Bremmer, 1987), positive (Chirinda et al., 2011), or negative (Simek, 2000; Stenberg et al., 1998) effects on DEA rates; FREEZE storage resulted in enhanced (Breitenbeck and Bremmer, 1987) or decreased (Stenberg et al., 1998) DEA rates; DRY storage consistently enhanced (Luo et al., 1996; Patten et al., 1980; Włodarczyk et al., 2014) DEA rates; and AMBIENT storage decreased (Breitenbeck and Bremmer, 1987; Luo et al., 1996) DEA rates. When comparing COLD and FREEZE, Dadenko et al. (2009) and Stenberg et al. (1998) found a stronger impact of COLD over FREEZE on DEA, while Breitenbeck and Bremmer (1987) reported a lower impact of COLD over FREEZE. These authors emphasised that responses to storage practices were dependent on land use and time.

Various other soil activities were assessed by a few studies (De Nobili et al., 2006; Ginn et al., 2014; Lee et al., 2000; Makarov et al., 2013; Pesaro and al., 2003; Riepert and Felgentreu, 2002; Ross et al., 1980; Trabue et al., 2006; Verchot, 1999; Wingfield, 1980), and these publications often reported variable impacts of a given storage practice on activities (e.g. Lee et al., 2000; Ross et al., 1980; Simek and Santruckova, 1999; Wingfield, 1980).

A total of 21 studies addressed the impact of soil storage on various soil enzyme activities in one or several soils, gathering a total of 43 data about the effect of a storage practice on one or several enzyme activities (9 data for COLD, 12 for FREEZE, 15 for DRY, 6 for AMBIENT, and 1 for FREEZE-DRY). When considering the authors' conclusions across all enzyme activities, the following points were found: COLD mainly decreased enzyme activities (Abellan et al., 2011; Brohon et al., 1999; Dadenko et al., 2009; Lee et al., 2007; Tabatabai and Bremner, 1970; Turner and Romero, 2010), although DeForest (2009), Lane et al. (2022), and Moy and Nkongolo (2023) reported variable effects across different soils and/or enzymes. FREEZE storage resulted in decreased (Abellan et al., 2011; Dadenko et al., 2009; Lee et al., 2007; Riepert and Felgentreu, 2002; Turner and Romero, 2010), less frequently enhanced (Ivarson and Sowden, 1970; Peoples and Koide, 2012), or similar enzyme activities (Tabatabai and Bremner, 1970; Zantua and Bremner, 1977) and was found to have variable effects (DeForest, 2009; Lane et al., 2022; Wallenius et al., 2010) on various enzyme activities and/or soil types. DRY storage showed negative (Abellan et al., 2011; Dadenko et al., 2009; Lee et al., 2007; Turner and Romero, 2010; Yoshikura et al., 1980), null (Zantua and Bremner, 1977; Zorzona et al., 2006; Zorzona et al., 2009), positive (Jones et al., 2019; Peoples and Koide, 2012), or variable (De Castro Lopes et al., 2015; Lane et al., 2022; Moreira et al., 2017; Speir and Ross, 1981; Wallenius et al., 2010) effects. Preservation at AMBIENT temperature decreased enzyme activities (Brohon et al., 1999; Riepert and Felgentreu, 2002; Tabatabai and Bremner, 1970; Turner and Romero, 2010), although a null impact was reported in Zantua and Bremner (1977). Finally, soil enzyme activity decreased following FREEZE-DRY storage in Yoshikura et al. (1980). Comparison between storage practices yielded contrasting results. FREEZE was sometimes identified as more suitable for the measurement of soil microbial enzyme activities than DRY (Abellan et al., 2011; Lee et

al., 2007; Peoples and Koide, 2012; Wallenius et al., 2010) or than COLD (Abellan et al., 2011; Tabatabai and Bremner, 1970), but other studies identified COLD as the preferred practice (Dadenko et al., 2009; Lee et al., 2007). Turner and Romero (2010) recommended AMBIENT storage over other practices for long-term (more than 2 weeks) storage.

In a given study, storage practices sometimes yielded contrasting impacts on different soil enzyme activities. For instance, in DeForest (2009), COLD and FREEZE storage showed no impact on β-glucosidase and peroxidase activities, whereas these storage methods presented variable impacts on *N*-acetyl-glucosaminidase, phenoloxidase, and phosphatase (see also Jones et al., 2019; Lee et al., 2007; Moreira et al., 2017; Wallenius et al., 2010). Storage practices also had inconsistent impacts on soil enzyme activities across different soil types (e.g. Lane et al., 2022; Moy and Nkongolo, 2023). Because studies often investigate several enzyme activities (1 to 10 activities, with a median of 3) that can respond differently, in a second step I analysed the impacts of storage practices on specific enzyme activities. Here, I report the conclusions for the main soil enzyme activities (for which at least five studies are available) in Table 3. Storage practices generally significantly impacted all soil enzyme activities, compared with those measures in fresh, non-stored samples. Regarding the six main enzyme activities, 21 papers gathering a total of 105 individual data (i.e. results on the impact of a storage practice on a given soil enzyme activity in one or several soils) were analysed. DRY was the practice most frequently addressed (39 data), whereas AMBIENT was the less frequently addressed (with only 9 data). Across all practices and enzymes, the impact of storage resulted in variable effects across soil types (53 data), reduced enzyme activities (35 data), or enhanced enzyme activities (a single study: Speir and Ross, 1981) compared with those measured in fresh, non-stored soil samples. Enzyme activity was found to be unaffected in 16 data points out of 105, i.e. in 15 % of analysed data (Table 3).

For dehydrogenase activity (five articles), studies reported no (Abellan et al., 2011) or variable (Brohon et al., 1999; Dadenko et al., 2009) effects of COLD storage, negative (Riepert and Felgentreu, 2002) or variable (Dadenko et al., 2009; Ivarson and Sowden, 1970) effects of FREEZE storage, negative (Abellan et al., 2011) or variable (Dadenko et al., 2009) effects of DRY storage, and negative (Riepert and Felgentreu, 2002) or variable (Brohon et al., 1999) effects of AMBIENT storage. For arylsulfatase activity (six articles), COLD storage resulted in negative (Tabatabai and Bremner, 1970) or variable (Lee et al., 2007; Moy and Nkongolo, 2023) effects; FREEZE storage resulted in variable (Lee et al., 2007; Wallenius et al., 2010) or null (Tabatabai and Bremner, 1970) effects; and DRY storage resulted in negative (De Castro Lopes et al., 2015; Lee et al., 2007), variable (Wallenius et al., 2010), or null (Moreira et al., 2017) effects. Tabatabai and Bremner (1970) recommended FREEZE over COLD storage for this enzyme. The six articles using glucosaminidase activity found variable (DeForest, 2009; Lane et al., 2022; Turner and Romero, 2010), negative (Moy and Nkongolo, 2023), or null (Lee et al., 2007) effects of COLD; a variable (DeForest, 2009; Lane et al., 2022; Lee et al., 2007; Turner and Romero, 2010) or negative (Peoples and Koide, 2012) effect of FREEZE; a negative (Jones et al., 2019; Lane et al., 2022; Peoples and Koide, 2012; Turner and Romero, 2010) or variable (Lee et al., 2007) effect of DRY storage; and a negative effect of AMBIENT storage (Lane et al., 2022; Turner and Romero, 2010), with no best storage practice identified. Glucosidase activity was assessed in 12 studies, showing variable (Lane et al., 2022; Lee et al., 2007; Turner and Romero, 2010) or null (Abellan et al., 2011; DeForest, 2009) effects of COLD; variable (Abellan et al., 2011; Lane et al., 2022; Lee et al., 2007; Turner and Romero, 2010; Wallenius et al., 2010) or null (DeForest, 2009) effects of FREEZE; negative (Abellan et al., 2011; De Castro Lopes et al., 2015; Lane et al., 2022; Turner and Romero, 2010; Wallenius et al., 2010; Yoshikura et al., 1980), variable (Lee et al., 2007; Zorzona et al., 2009), or null (Zorzona et al., 2006) effects of DRY storage; and variable effects of AMBIENT storage (Lane et al., 2022). The impact of storage practices was assessed on several types of phosphatases across 16 studies (see the footnote of Table 3). The impact of COLD storage was recorded as negative (Brohon et al., 1999, for phosphoesterase, and Moy and Nkongolo, 2023, and Turner and Romero, 2010, for phosphomonoesterase), variable (De Forest, 2009, and Lane et al., 2022, for acid phosphatase; Lee et al., 2007, for alkaline phosphatase; and Turner and Romero, 2010, for phosphodiesterase), or null (Abellan et al., 2011, for alkaline phosphatase, and Lee et al., 2007, for acid phosphatase). The impact of FREEZE was negative (Lee et al., 2007, for alkaline phosphatase; Peoples and Koide, 2012, and Wallenius et al., 2010, for phosphomonoesterase) or variable (Abellan et al., 2021, for alkaline phosphatase; DeForest, 2009, Lane et al., 2022, and Lee et al., 2007, for acid phosphatase; Turner and Romero, 2010, and Wallenius et al., 2010, for phosphomonoesterase and phosphodiesterase). Finally, AMBIENT storage decreased phosphatase activity or had variable effects in Stenberg et al. (1998) and Turner and Romero (2010). COLD was the most conservative practice in Abellan et al. (2011) and Lee et al. (2007), compared with FREEZE and DRY. However, overall, a given practice could have different impacts on different phosphatase activities measured in a same set of soil samples (e.g. acid vs. alkaline phosphatase in Lee et al., 2007; phosphomonoesterase vs. phosphodiesterase in Turner and Romero, 2010, and Wallenius et al., 2010). Finally, among the seven studies evaluating the impact of soil storage on urease activity, null (Jones et al., 2019) or variable (Lee et al., 2007) effects of COLD storage were reported; null (Zantua and Bremner, 1977), negative (Abellan et al., 2011), or variable (Lee et al., 2007) effects of FREEZE were noted; and variable (Jones et al., 2019; Lee et al., 2007; Zorzona et al., 2009), null (Zantua and Bremner, 1977; Zorzona et al., 2006), negative (Abel-

Table 3. Synthesis of the impacts of storage practices (COLD, FREEZE, DRY, and AMBIENT) on the main soil enzyme activities (compared with those estimated on fresh, non-stored soils). The changes are scored as no impact Ø (no significant change), increase ⇉, decrease ⇉, or variable ⤮ (when storage had inconsistent changes across soil samples). References for studies that have shown significant impacts of storage are given in bold.

Soil enzyme activity	COLD	FREEZE	DRY	AMBIENT
Dehydrogenase	Ø: (1); ⤮: **(5), (10)**	⇉: **(43)**; ⤮: **(10), (22)**	⇉: **(1)**; ⤮: **(10)**	⇉: **(43)**; ⤮: **(5)**
Arylsulfatase	⇉: **(56)**; ⤮: **(28), (36)**	Ø: (56); ⤮: **(28), (65)**	Ø: (35); ⇉: **(11), (28)**; ⤮: **(65)**	⇉: **(56)**
Glucosaminidase	Ø: (28); ⇉: **(36)**; ⤮: **(13), (25), (60)**	⇉: **(39)**; ⤮: **(13), (25), (28), (60)**	⇉: **(23), (25), (39), (60)**; ⤮: **(28)**	⤮: **(25), (60)**
Glucosidase	Ø: (1), (13); ⤮: **(25), (28), (36), (60)**	Ø: (13); ⤮: **(1), (25), (28), (60), (65)**	Ø: (74); ⇉: **(1), (11), (25), (60), (65), (72)**; ⤮: **(28), (76)**	⤮: **(25)**
Phosphatase	Ø: (1), (28)[a]; ⇉: **(5), (36), (60)**[a]; ⤮: **(13), (25), (28)**[b], **(60)**[b]	⇉: **(39)**, **(28)**[b], **(65)**[a]; ⤮: **(1), (13), (25), (28)**[a], **(60)**[a,b], **(65)**[b]	Ø: (74), (76); ⇉: **(1), (11), (28)**[b], **(39)**, **(60)**[a,b], (65)[a,b]; ⤮: **(25), (28)**[a], **(35), (53)**	⇉: **(5), (60)**[a]; ⤮: **(60)**[b]
Urease	Ø: (1); ⤮: **(28)**	Ø: (73); ⇉: **(1)**; ⤮: **(28)**	Ø: (73), (74); ⇉: **(1)**; ⇉: **(53)**; ⤮: **(23), (28), (76)**	

References (1) and (28)[b] refer to alkaline phosphatase. Reference (5) refers to phosphoesterase. References (11), (13), (25), (28)[a], (35), (74), and (76) refer to acid phosphatase. Reference (36) refers to both acid and alkaline phosphatases Reference (53) refers to phosphatase without further clarification. References (60)[a] and (65)[a] refer to phosphomonoesterase. References (60)[b] and (65)[b] refer to phosphodiesterase. The articles listed in the table are as follows: (1) Abellan et al. (2011), (5) Brohon et al. (1999), (10) Dadenko et al. (2009), (11) De Castro Lopes et al. (2015), (13) DeForest (2009), (22) Ivarson and Sowden (1970), (23) Jones et al. (2019), (25) Lane et al. (2022), (28) Lee et al. (2007), (35) Moreira et al. (2017), (36) Moy and Nkongolo (2023), (39) Peoples and Koide (2012), (43) Riepert and Felgentreu (2002), (53) Speir and Ross (1981), (56) Tabatabai and Bremner (1970), (60) Turner and Romero (2010), (65) Wallenius et al. (2010), (72) Yoshikura et al. (1980), (73) Zantua and Bremner (1977), (74) Zorzona et al. (2006), and (76) Zorzona et al. (2009).

lan et al., 2011), or positive (Speir and Ross, 1981) effects of DRY storage were found. As for phosphatase, COLD was found to be the most conservative practice for urease activity in Abellan et al. (2011).

3.6 PLFA-based parameters

A total of 11 studies evaluated the impact of soil storage on PLFA-based microbial parameters. Storage had various impacts on soil microbial PLFA biomass. COLD storage showed negative (Lee et al., 2007; Moy and Nkongolo, 2023; Wang et al., 2015), null (Petersen and Klug, 1994; Schnecker et al., 2012), or positive (Trabue et al., 2006) impacts. FREEZE storage had either non-significant (Schnecker et al., 2012) or negative impacts (Lee et al., 2007; Wang et al., 2015) on soil biomass, while DRY storage had either no (Wang et al., 2015) or negative (Lee et al., 2007) effects. Finally, storage at AMBIENT temperature showed no (Wang et al., 2015), negative (Petersen and Klug, 1994), or positive (Trabue et al., 2006) impacts, and the only study reporting the impact of FREEZE-DRYING reported a negative impact on soil biomass compared with non-stored soils (Wu et al., 2009). The conclusions of the three studies comparing several storage methods were not consistent, with Schnecker et al. (2012) showing no impact of COLD or FREEZE, Trabue et al. (2006) showing a similar enhancement of PLFA biomass following COLD and AMBIENT storage, Wang et al. (2015) showing a stronger impact of COLD compared with FREEZE and DRY storage, and Lee et al. (2007) showing a stronger decrease following DRY compared with COLD or FREEZE storage. Regarding the structure of the microbial community based on the relative abundance of PLFA-group-specific biomarkers, the six studies on COLD storage reported significant (Liu et al., 2009; Schnecker et al., 2012; Schutter and Dick, 2000; Trabue et al., 2006), variable (Lee et al., 2007, on FAME), or null (Petersen and Klug, 1994) effects. The impact of FREEZE storage was

reported as significant in three studies (Liu et al., 2009; Schnecker et al., 2012; Schutter and Dick, 2000) and as variable in one study (Liu et al., 2009, on FAME). The five studies using DRY storage reported significant impacts on the soil microbial community structure (Hamer et al., 2007; Lee et al., 2007; Liu et al., 2009; Schutter and Dick, 2000; Veum et al., 2019). AMBIENT (Petersen and Klug, 1994; Trabue et al., 2006; Veum et al., 2019) and FREEZE-DRYING storage impacted the PLFA-based structure of the soil community in all reported studies (Liu et al., 2009; Wu et al., 2009). Among the studies reporting several storage practices, Liu et al. (2009) and Schnecker et al. (2012) reported a lower impact of FREEZE storage compared with COLD or DRY storage, whereas Schutter and Dick (2000) concluded to comparable impact of these three storage methods on PLFA patterns.

4 Discussion

Overall, considering the wide range of microbial parameters used in soil ecology and the methodological approaches available to characterise these parameters, the literature addressing the impacts of soil storage on soil microbial parameters is rather sparse, even though storage is a common, widespread practice. The present review suggest that these impacts are widespread and frequent (almost 76 % of published data), across all microbial parameters and storage practices. It would have been interesting to evaluate and compare the effect sizes of storage impacts, but the required data were not always available, particularly for older articles. Several studies suggest that these impacts can be strong; for instance, Makarov et al. (2013) found that soil MBC and MBN decreased by 2–3 times in dried mountain meadow soils, compared with those measured in fresh soils. Clark and Hirsch (2008) reported that "archived [dried] soils [...] contained dramatically less pseudomonad DNA than fresh soil". Goberna et al. (2005) concluded that "substantial changes can occur to the soil microbial community functions, regardless of the kind of storage [... depending on] the profile and sampling depth", and they also reported "a great sensitivity of CLPPs to storage treatment". Except for FREEZE-DRY storage (with nine data only), FREEZE recorded the lowest impact frequency (with 68 % of significant effects), while AMBIENT and DRY storage more frequently impacted the microbial parameters (86 % and 80 % of data, respectively). This result should be treated with caution, as these different practices are used preferentially for certain parameters (e.g. FREEZE for DNA-based parameters). Therefore, data on the impact of all practices are not available in an equivalent way for all parameters. Moreover, some authors have published several studies on the impact of a practice on certain microbial parameters for a given soil type (e.g. Zorzona et al., 2006; Zorzona et al., 2007; and Zorzona et al., 2009, on Mediterranean soils), thus distorting the representativeness of the available data.

This review identified three main factors that explain the variability in the impacts of the different storage practices: duration of storage, soil type and/or land use, and climate conditions.

Although the effects of storage duration have not been assessed here, numerous studies show that this duration influenced the impact of storage. For instance, Dadenko et al. (2009) showed that the differences in enzyme activities between soil samples stored under different conditions became less pronounced in the long term (> 12 weeks). Delavaux et al. (2020) and Rubin et al. (2013) even showed that the DNA thaw time and storage duration can impact soil microbial molecular parameters, respectively. Furthermore, several authors have recommend incubation or conditioning of the soil samples following storage before microbial analyses (Martí et al., 2012; Stenberg et al., 1998), although new microbial groups (i.e. groups that were not detected in fresh samples) can appear following incubation (e.g. in Martí et al., 2012). Incubation (conditioning) under moist conditions has been found to allow (Wang et al., 2015) or not allow (Riepert and Felgentreu, 2002; West et al., 1986) the restoration of the soil microbial parameters. For instance, Jones et al. (2019) showed that the soil microbial respiration and C biomass values that were retrieved after a few days of pre-incubation under moist conditions were similar to those of fresh soils, even for 36-year-old soil samples. However, the issue of pre-incubation effects is largely underestimated and would require more consistent studies.

This review also illustrates the wide differences in storage impacts across different soil type and/or land use conditions. Storage impacts on various soil microbial parameters varied according to soil type (e.g. Černohlávková et al., 2009; Dadenko et al., 2009; Martí et al., 2012; Włodarczyk et al., 2014). A recent study by Lane et al. (2022) showed that various parameters of the soil bacterial community were significantly affected by interactions between storage, land use, and (sometimes) storage duration. Benucci et al. (2020) studied the microbial communities of soils archived for 20 years and showed that bacterial and fungal diversity decreased over time, although the magnitude of this storage effect varied depending on the type of soil and the taxa considered. Regarding the role of soil type, numerous studies have shown contrasting effects of storage on different soil types (Table 2). In line with these findings, Sirois and Buckley (2019) reported that the rate of DNA degradation differed between soil types according to moisture, temperature, and habitat characteristics. Some authors have proposed an effect of soil textural parameters (Lee et al., 2007; Wallenius et al., 2010), with a high clay content providing abundant microsites for soil micro-organisms that may improve the preservation of microbial parameters following storage-associated disturbance (De Nobili et al., 2006; Jones et al., 2019). De Nobili et al. (2006) and Sirois and Buckley (2019) also suggested that

soils with a high amount of organic matter could better resist storage impacts. Gonzalez-Quiñones et al. (2009) hypothesised that the microbial parameters in soils with low organic C contents would be more affected by storage, but they observed the opposite, concluding that micro-organisms associated with large recalcitrant organic C pools (grassland or woodland) would be more prone to death during storage than micro-organisms relying on more easily degradable C sources (Gonzalez-Quiñones et al., 2009). Indeed, younger and more active micro-organisms may be more sensitive to drying–rewetting or freezing stress than more stable microbial biomass. In line with this finding, Gram-positive bacteria (especially Actinomycetota or Firmicutes) have been considered to be more stress-tolerant (e.g. Martí et al., 2012) than Gram-negative bacteria.

The third factor identified to explain the variability in storage impacts in different studies was climate conditions. The effects of different storage practices (decreased water availability and/or temperature) mimic, to some extent, the natural stresses that soil micro-organisms experience in ecosystems (Meisner et al., 2021). Consequently, soils frequently exposed to drying–rewetting may be more adapted to drought stress, due to the selection of microbial groups that are more resistant to osmotic stress (Fierer and Schimel, 2002; Evans and Wallenstein, 2012), and therefore less impacted by DRY storage (e.g. Hamer et al., 2007). For similar reasons, soil samples taken during the summer season might be less affected by dry storage than those taken during the cold, humid fall and winter seasons, as shown by Zorzona et al. (2007) using Mediterranean forest soils. Thus, the sampling season could influence storage impacts (Abellan et al., 2011). Indeed, Evans and Wallenstein (2014) proposed that the precipitation/soil moisture regime alters the ecological strategies of the soil microbial community, both through changes in community composition and strategy shifts within taxa. They found that a decade of more frequent exposure to intensified rainfall patterns increased the proportion of taxa exhibiting a stress-tolerant strategy. On the contrary, flooded (e.g. paddy) soils would be more impacted following air-drying preservation (e.g. Wang et al., 2015). Similarly, soil microbial communities in soils that regularly undergo in situ freezing might be less impacted by storage at −20 °C, presumably due to the adaptation of the microbial community to regular annual freezing (Rubin et al., 2013; Stenberg et al., 1998); conversely, microbial communities that are not naturally exposed to cold temperature (e.g. tropical soils) would be more sensitive to FREEZE storage (Turner and Romero, 2010). These data suggest that storage practices for soil storage could be regionalised (Lane et al., 2022; these authors also suggest that their results would be valid for studies carried out in similar climates).

The effects of storage might be tolerable if the storage procedure has the same proportional effect on soil samples collected across various sites or subjected to different experimental treatments (i.e. if the ranking or similarity between sample's microbial parameters is conserved following storage). Indeed, some authors explicitly state that differences (in ranking) between microbial parameters from different soil types or ecosystems are preserved independently of the storage method (e.g. Dadenko et al., 2009; Gonzalez-Quiñones et al., 2009; Meyer et al., 2019; Moreira et al., 2017; Tzeneva et al., 2009) or the storage duration (Gonzalez-Quiñones et al., 2009; Wallenius et al., 2010). However, several studies suggest that the storage practices do not impact various soil microbial parameters in a similar way (e.g. Černohlávková et al., 2009, and Włodarczyk et al., 2014, for SIR; De Castro Lopes et al., 2015, and DeForest, 2009, for soil enzymes; Lee et al., 2007, for PLFAs; Wang et al., 2015, for MicroResp™ CLPP, etc.).

As anticipated, the impacts of storage practices differed between microbial parameters, with frequent inconsistent effects reported across different studies. In the light of the results, one may question whether it is possible to provide recommendations for the storage of samples in order to assess the various microbial parameters. The fragmentation of the available information and the variability in the storage effects observed make this a tricky exercise.

Surprisingly, studies based on DNA sequencing analysis and reporting the effects of soil storage on microbial community structure or composition are very rare, although this practice is very common. Most available studies use immediately frozen soil samples as a reference (e.g. Brock et al., 2024; Finn et al., 2023; Hu et al., 2023; Wang et al., 2021) without considering the impact of freezing. Compared with a non-storage option (fresh soil), different storage times and freezing temperatures did not drastically change the community structure or composition in Kushwaha et al. (2024) or Rubin et al. (2013). FREEZE appears to be the best storage practice; however, again, it is difficult to draw conclusions from the small number of studies available. Statistics are also impossible due to the small number of articles available, but a few data suggest that bacteria and fungi are equally impacted, although they sometime respond differently (Delavaux et al., 2020; Guerrieri et al., 2020; Weißbecker et al., 2017). Studies dealing with archaea (Brandt et al., 2014; Kushwaha et al., 2024; Pesaro and al., 2003) are too sparse to draw conclusions about this group. Some studies showed that FREEZE storage can even have some effects on molecular microbial parameters (Lane et al., 2022; Lee et al., 2007; Pesaro and al., 2003; Schutter and Dick, 2000), contrary to what is generally accepted (Lee et al., 2007), although these impacts were detected at higher taxonomic levels (Delavaux et al., 2020; Rubin et al., 2013) or when rare taxa were considered (Guerrieri et al., 2020). This last point suggests that technological advances, allowing for more resolved taxonomic characterisation, could also reveal hitherto unsuspected effects of storage practices on microbial communities. The few available data have shown that storage generally impacted some microbial clades that become extinct or fell below the detection limit after only a few days of storage and that these effects

occurred in an unpredictable way (Rubin et al., 2013). For instance, for bacteria, Finn et al. (2023) showed that the relative abundance of Acidobacteria, Actinobacteria, and Thermoproteota was more affected by the storage practice than Bacteroidota, Firmicutes, and Planctomycetota. In line with these findings, the recent study by Hu et al. (2023) suggested that long-term FREEZE storage of soil samples destabilises bacterial co-occurrence patterns. These authors proposed that the removal of relic DNA (extracellular and dead microbe DNA) with chemical treatment would improve the accuracy of bacterial diversity in long-term frozen soil samples. Finally, certain commercial preservatives could be useful with respect to limiting the impact of room-temperature storage on DNA-based microbial community analyses (Smenderovac et al., 2024).

Regarding PLFAs, biomass measured using PLFAs was generally underestimated following all storage practices. The data suggest that FREEZE or COLD should be preferred over DRY storage. The effect of storage on PLFAs could be explained by the mechanism of temperature adaptation or response to stress, including a decrease in the degree of unsaturation (Petersen and Klug, 1994; see also Kaneda, 1991). Using PLFA biomarkers, Hamer et al. (2007) found that DRY storage favoured Gram-positive (over Gram-negative) bacteria and increased the bacteria : fungi ratio, whereas Liu et al. (2009) concluded that DRY storage of flooded soils increased the Gram-negative bacteria.

Microbial parameters determined following INCUBATION of the soil samples were frequently impacted by storage (with about 86 % of 133 data points indicating a significant impact). Impacts of storage practices on basal respiration and potential microbial activities (e.g. SIR and DEA) were often inconsistent across different soil types, with no consensus regarding a best storage option. Moreover (and worryingly), basal respiration and SIR, when assessed in the same study, could present opposite responses to storage practices, suggesting that soil samples should be stored in different ways for these analyses (see below). Similarly, for CLPP analysis, the available literature reports inconsistent storage effects. For microbial activity measurements, the storage condition may affect activity rates as well as other kinetic parameters. For instance, Brohon et al. (1999) showed that the latent time observed during the first hours of respiration analysis increased with storage time for soils stored at 4 or 37 °C. Finally, regarding soil enzyme activities, some authors have recommend COLD or FREEZE storage as the most conservative, whereas they have stated that DRY storage is the least desirable practice (Abellan et al., 2011; Lee et al., 2007; Tabatabai and Bremner, 1970; Wallenius et al., 2010); however, DRY storage could be suitable in some cases (De Castro Lopes et al., 2015; Zorzona et al., 2006). Nevertheless, the present synthesis concludes that there is a global, strong, and unpredictable impact of storage practices on soil enzyme activities, with highly variable effects across enzyme activities and soil types. In almost half of the data on individual enzyme activities (41 data out of 83; Table 3), the storage of the soil samples had variable impacts on a given soil enzyme activity across different soils. This suggests that any storage should be strongly avoided in studies dealing with enzyme activities in different soil types and in soils with different origins.

5 Conclusions

In a large majority of studies, the various soil microbial parameters were significantly impacted by storage, and these impacts often varied across different storage practices, microbial parameters, and soil types. Of course, storage cannot always be avoided, and it would be unrealistic to recommend avoiding it, especially when different soil types or soils of various geographical origins are compared. Although some studies suggest that preservation at field moisture and room temperature might be the best option for short-term storage, this should be for a few days only. If soil samples cannot be processed rapidly, the storage options should be carefully considered. As the different microbial parameters do not respond similarly to the various storage options, multiple sample storage methods may be used. This review also highlights the need to couple the storage option with the abiotic conditions (mean annual temperature, precipitation regime, etc.) that prevail in the native soil environment (see also Sheppard and Addison, 2007, who suggest that storage practices cannot be universal). Rhymes et al. (2021) recently proposed a procedure to determine the best storage method for soil C and N determination; they recommend a maximum storage length and suggest (in keeping with Kushwaha et al., 2024) running a pilot study (as has been done, for example, by Lee et al., 2021) to determine the best storage practice for a given soil type and microbial parameter and including the results in the publications: one can only fully support this latter recommendation. If such a pilot study is not feasible, the authors should systematically mention possible storage-related biases.

The present analysis clearly shows that, based on data available in the literature, it is very risky to prescribe a maximum storage duration for the determination of microbial parameters for all soil types, given the heterogeneity of authors' conclusions and recommendations. The good news is that the storage effects generally do not impair our capacity to assess the treatment effects on soil microbial parameters, at least for a given soil type subjected to different treatments (plant composition, management practice, etc.). The challenge of soil storage is more critical for studies dealing with multiple locations and/or soil types, as the effects of storage on microbial properties vary with soil types.

Data availability. The data used for this synthesis are available from the corresponding author upon request.

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