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Author

Amarasinghe, Apsara, Chen, Chengrong, Van Zwieten, Lukas, Rashti, Mehran Rezaei

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Review

The role of edaphic variables and management practices in regulating soil microbial resilience to drought - A meta-analysis

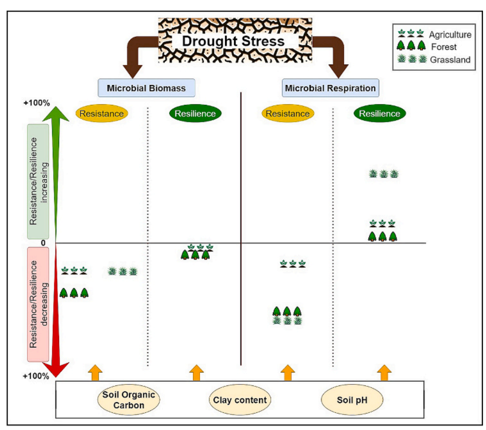
Apsara Amarasinghe [a], Chengrong Chen [a], Lukas Van Zwieten [a,b], Mehran Rezaei Rashti [a,*]

[a] Australian Rivers Institute, School of Environment and Science, Griffith University, 170 Kessels Road, Nathan, QLD 4111, Australia
[b] NSW Department of Primary Industries, Wollongbar, New South Wales, Australia

HIGHLIGHTS

- Drought stress decreased microbial biomass (−31.6 %) and respiration (−43.5 %)
- In recovery of drought, respiration rose (+30 %) but not microbial biomass (−0.3 %)
- Respiration resistance and resilience in agricultural soils regulated by soil pH
- Resistance and resilience of forest soils affected by pH, clay, and organic carbon
- Microbial biomass resilience regulated by soil organic carbon in grassland soils

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental disturbances such as drought can impact soil health and the resistance (ability to withstand environmental stress) and resilience (ability to recover functional and structural integrity after stress) of soil microbial functional activities. A paucity of information exists on the impact of drought on soil microbiome and how soil biological systems respond to and demonstrate resilience to drought stress. To address this, we conducted a systematic review and meta-analysis (using only laboratory studies) to assess the response of soil microbial biomass and respiration to drought stress across agriculture, forest, and grassland ecosystems. The meta-analysis revealed an overall negative response of microbial biomass in resistance (−31.6 %) and resilience (−0.3 %) to drought, suggesting a decrease in soil microbial biomass content. Soil microbial respiration also showed a negative response in resistance to drought stress indicating a decrease in soil microbial respiration in agriculture (−17.5 %), forest (−64.0 %), and grassland (−65.5 %) ecosystems. However, it showed a positive response in resilience to drought, suggesting an effective recovery in microbial respiration post-drought. Soil organic carbon (SOC), clay content, and pH were the main regulating factors of the responses of soil microbial biomass and respiration to drought. In agriculture ecosystem, soil pH was primarily correlated with soil microbial respiration resistance and resilience to drought, potentially influenced by frequent land preparation and fertilizer

* Corresponding author.
E-mail address: m.rezaeirashti@griffith.edu.au (M.R. Rashti).

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applications, while in forest ecosystem SOC, clay content, and pH significantly impacted microbial biomass and respiration resistance and resilience. In grassland ecosystem, SOC was strongly associated with biomass resilience to drought. The impact of drought stress on soil microbiome showed different patterns in natural and agriculture ecosystems, and the magnitude of microbial functional responses regulated by soil intrinsic properties. This study highlighted the importance of understanding the role of soil properties in shaping microbial responses to drought stress for better ecosystem management.

1. Introduction

Soil is a diverse mix of minerals, organic matter, and a network of water- and air-filled pore spaces which hosts a range of organisms from micro to macro scales (Joos and De Tender, 2022). Drought stress can significantly influence physicochemical and biological properties of soil and alter soil functions. The concepts of 'soil resistance' and 'soil resilience' assess the influence of environmental stresses on soil sustainability (Griffiths and Philippot, 2013; Silva et al., 2013). The term 'soil resistance', evaluates the capacity of a soil to sustain environmental and anthropogenic pressures, while maintaining its functions (de Vries et al., 2012; Isbell et al., 2015). Conversely, 'soil resilience' denotes the capacity of a soil to recover its functional (e.g., microbial activity, decomposition of organic matter, and nutrient cycling) and structural (e.g., soil aggregate stability, and porosity) integrity to original status (similar level of function) after experiencing a specific disturbance (Griffiths et al., 2008; Li et al., 2019; Quinlan et al., 2016; Schwalm et al., 2017). The resistance and resilience of soil functional properties to environmental stresses can be assessed by comparing the response variables of the target function relative to that of undisturbed soil (Orwin and Wardle, 2004). Fig. 1 summarizes the soil properties and mechanisms that are responsible for regulating the resistance and resilience of soil ecosystem to drought stress.

Microbial biomass and respiration represent vital components in soil health, actively contributing to nutrient cycling, organic matter decomposition, and overall ecosystem productivity (Babur et al., 2022). Drought stress significantly impacts microbial biomass and respiration in soil ecosystems. Soil bacterial and fungal communities respond differently to long-term drought history, with certain fungi being more drought-tolerant due to unique features like chitinous cell walls and hyphal growth (Barnard et al., 2013; Preece et al., 2019; Wan et al., 2023). The chitinous cell wall present in the fungi will increase the resistance to environmental perturbations and the characteristic nature of hyphal growth enabling fungi to penetrate small areas of dry soil and survive the stress (Ene et al., 2015; Sun et al., 2020). Long-term drought can cause acclimatization of soil microbial communities and create a drought-tolerant fungal-dominated microbial community (Dacal et al., 2022; Leizeaga et al., 2021). However, regions with consistent soil moisture history (i.e., no history of drought) may develop a microbiome sensitive to moisture due to changes in soil microbial biomass and composition (Wang and Allison, 2021). Additionally, reduced soil moisture restricts the diffusion of oxygen, crucial for microbial respiration processes. As a result, microbial respiration, tends to decrease during drought periods (Barnard et al., 2013; Liu et al., 2023). These alterations in microbial biomass and reduced respiration rates can profoundly influence the overall nutrient cycling and carbon sequestration processes within the soil profile, potentially impacting the long-term fertility and health of the soil ecosystem.

Human interventions in soil management play a pivotal role in shaping not only soil properties but also microbial biomass and respiration, influencing the overall resilience of soil microbial communities to drought stress. In recent decades, intensive agricultural practices (e.g., use of heavy machinery, large-scale farming with monocropping, excessive usage of chemical fertilizers) have contributed to many negative environmental impacts, including widespread degradation of fertile soils (Akamani, 2021; Kibblewhite et al., 2008). Changes in agricultural practices and land-use alterations have been shown to have profound effects on the quantity and diversity of soil microbial

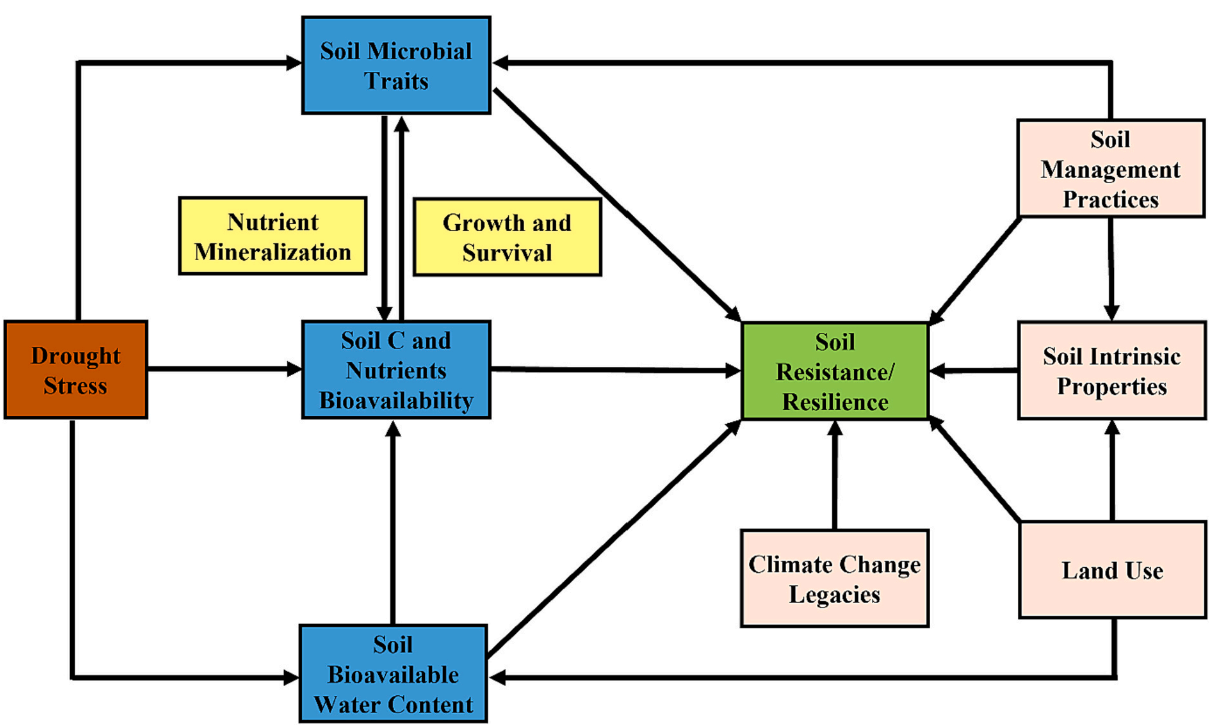

Fig. 1. The properties and mechanisms that are responsible for regulating the resistance and resilience of soil ecosystem to drought stress.

populations (McKinley, 2019). Currently, many farming systems are interested in using ecosystem-based management practices (sustainable management practices) to enhance soil health and resilience. Ecosystem-based management is considered as an integrated management of resources (i.e., land, water, and living beings) that enhances conservation and sustainable use. These practices are designed to foster soil health and productivity while balancing nutrient requirements for crop growth (Abdourahamane Illiassou and Oeba, 2020; Delacámara et al., 2020). Soil biological resilience is a collective output of past and present soil management, as well as the prospect of possible soil responses to future disturbances (Ludwig et al., 2018). Therefore, human interventions and management practices, ranging from agricultural techniques to land management strategies, significantly influence soil properties and microbial diversity. The way these practices alter soil conditions can either support or undermine microbial resilience to drought stress.

The changes in soil microbial biomass and respiration are inevitable with historical climatic events (i.e., frequent and prolonged periods of drought worldwide) which ultimately influence the bioavailability of soil carbon and nutrients. Thus, employing a systematic review and meta-analysis, this study aimed to evaluate the influence of drought stress on soil microbial functional characteristics (microbial biomass, and microbial respiration) and performance (resistance, and resilience to disturbance). Further, we explored the role of edaphic variables and management practices in regulating soil microbial resilience to drought stress. This may enable future land management practices to consider factors that promote soil resistance and resilience under drought conditions to maximize productivity during and post-drought periods.

2. Methods

2.1. Study selection

The research for this meta-analysis was retrieved from Web of Science databases for the period between 2000 and 2023 using the search terms “drought” AND “microbial” AND “resilience” AND “resistance” AND “soil”. We first screened the titles, abstracts and methods sections of peer-reviewed publications returned from searches for appropriateness considering drought's effects on microbial biomass and respiration. Our search initially yielded in 167 papers spanning from 2000 to 2023. Following title and abstract screening, 56 papers were selected, and ultimately, 17 articles (only laboratory studies) were chosen for the meta-analysis through full-text screening. The eligibility criteria for inclusion of the studies in the meta-analysis were considered during full text screening. The criteria included: (i) The studies must contain information on microbial respiration and microbial biomass data, (ii) The studies should have clearly defined treatment (drought stress) and control (no stress) groups, (iii) The studies should report standard error or are able to convert the data to standard error, (iv) The study must be a primary study (Grados et al., 2022; Zhang et al., 2021). Based on the minimum requirement of a reliable comparison of drought stress effect on microbial biomass and respiration during resistance and resilience phases, 17 studies were then selected. The data reported in field experiments were not included in the analysis, as this study focused on the nature of microbial change only affected by drought stress. Field data could be affected by many other factors other than the drought stress, as control conditions cannot be implemented under field conditions (Table S1).

2.2. Data acquisition

Relevant data on soil texture, pH (H_2O/KCl), and soil organic carbon content (SOC) were extracted from the figures and tables of the selected studies (Table S2). “PlotDigitizer” was used to extract relevant data points when data was provided in graphical format. The measurements were standardized to common units. Microbial biomass was reported in g kg^{-1} soil, and microbial respiration was reported in μg CO_2-C g^{-1} soil h^{-1}. When soil organic matter content was provided, the following formula was used to calculate the SOC content:

Soil organic carbon (SOC, %) = Soil organic matter (SOM, %) / 1.724 (Rashti et al., 2015).

The resistance (RS) and resilience (RL) indexes were calculated where necessary (i.e., to calculate the indexes using the mean values provided in the manuscript) using the following formulas (Orwin and Wardle, 2004):

$$\text{Resistance (RS)} = 1 - [(2 \times |D_{rs}|)/(C_{rs} + |D_{rs}|)]$$

$$\text{Resilience (RL)} = [(2 \times |D_{rs}|)/(|D_{rs}| + |D_{rl}|)] - 1$$

where D_{rs} is the difference between soil response (i.e., microbial biomass or respiration) value in the control condition (C_{rs}) and the stressed condition at the end of the RS phase. D_{rl} is the difference between soil response (i.e., microbial biomass or respiration) value in the control condition and the stressed condition at the end of the RL phase. The values of RS and RL indices range between −1 and +1. The value of +1 indicates the maximum RS (no impact of stress) or RL (complete recovery from the stress), and lower values indicate less RS or RL of soil microbial biomass and respiration to drought stress. Negative values of the RS index indicate a change >100 % in the response variable compared with that in the control condition. If the absolute value of D_{rl} becomes higher than the absolute value of D_{rs}, then the RL index will have a negative value. Mathematically, the RL index of control condition will be infinitely close to +1, while it has been considered as +1 in the RL equation.

2.3. Statistical analysis

The meta-analysis was conducted using the OrchaRd 2.0 function in R to synthesize data from multiple studies (i.e., sample size, means, standard deviation). First, standardized mean difference (SMD) of the parameters (i.e., microbial biomass and respiration) between the control (without stress) and the treatment (drought stress) was used to calculate the effect size (Nakagawa et al., 2021). Subsequently, the meta-analysis was conducted using the ‘mod_results’ function, which facilitated the combination of effect sizes across studies using random-effects model. Heterogeneity among studies was assessed using statistical measures such as the Q statistic and I^2. I^2 values of 25 %, 50 %, and 75 % considered as low, moderate, and high heterogeneity, respectively (Dougherty, 2023). If the 95 % confidence interval (CI) did not contain zero, the mean difference within the group was considered significant (null hypothesis). In addition to the overall analysis, the effect of potential moderator, soil intrinsic properties (i.e., SOC%, Clay% and pH), and type of land use (i.e., Agriculture, Forest and Grassland) on microbial biomass and respiration was analysed during drought stress and upon releasing the drought stress. To analyse the impact of different moderators, a meta-regression model was conducted including one moderator at a time as a fixed effect, considering it as either categorical or continuous. Each moderator was examined in a separate model and did not assess interactions between the moderators (Nakagawa et al., 2021). The Q_M statistics was used to assess significance of each moderator on the response of microbial attributes to drought stress. The Orchard plot summarised the meta-analysis by indicating whether the overall or subgroup effect was based on many or few studies, and whether studies differed significantly. Publication bias was assessed using the funnel plot asymmetry (Fig. S1). A one-way ANOVA was performed to compare the mean resistance and resilience indexes for microbial biomass and respiration among different land uses (i.e., Agriculture, Forest, and Grassland) followed by Tukey's HSD. Regression analysis followed by a Principal Component Analysis of the soil intrinsic properties affecting the resistance and resilience index was conducted using the SPSS statistical package.

3. Results and discussion

3.1. Resistance and resilience of soil microbial biomass to drought stress

Soil microbial biomass carbon as an indicator of heterotrophic respiration (decomposition of soil organic matter by microorganisms) is a crucial component of soil ecosystem and is responsible for many important functions such as nutrient cycling and soil structure formation. The meta-analysis of the effect of drought stress on soil microbial biomass indicated that the observed standardized mean differences between control and drought treatments on the resistance of soil microbial biomass was negative (−1.58, 95%CI [−2.19, −0.97]) and statistically significant ($p < 0.0001$, Fig. 2a). According to the Q-test, the true outcomes were heterogeneous (Q = 87.14, p < 0.0001, $I^2 = 59$ %), and the linear regression test indicated no funnel plot asymmetry ($p = 0.04$; Fig. S1a). The test of the moderator variable (land use) was not significant ($p = 0.51$, Fig. 2b) and the estimated mean effects were negative for all three land use types, suggesting that mean biomass value in control was higher than the drought treatment. The mean effect sized was lower in forest ecosystem (−2.28) compared to agriculture (−1.42) and grassland (−1.42) ecosystems.

The analysis for resilience of microbial biomass to drought stress showed that the overall standard mean difference between control and drought treatments was not significantly different from zero ($p = 0.93$, Fig. 2c). However, we observed both positive and negative effects of drought stress on microbial biomass resilience. According to the Q-test, the true outcomes were heterogeneous (Q = 66.95, p < 0.0001, $I^2 = 70$ %), and there was no funnel plot asymmetry according to the linear regression test ($p = 0.48$, Fig. S1b). Additionally, the type of land use had no effect on microbial biomass resistance to drought stress ($p = 0.96$, Fig. 2d). The overall effect size for agriculture and forest ecosystems were −0.06, 95 % CI [−1.02, 0.91] and −0.11, 95 % CI [−1.79, 1.57], respectively.

Resistance index of soil microbial biomass to drought stress for all

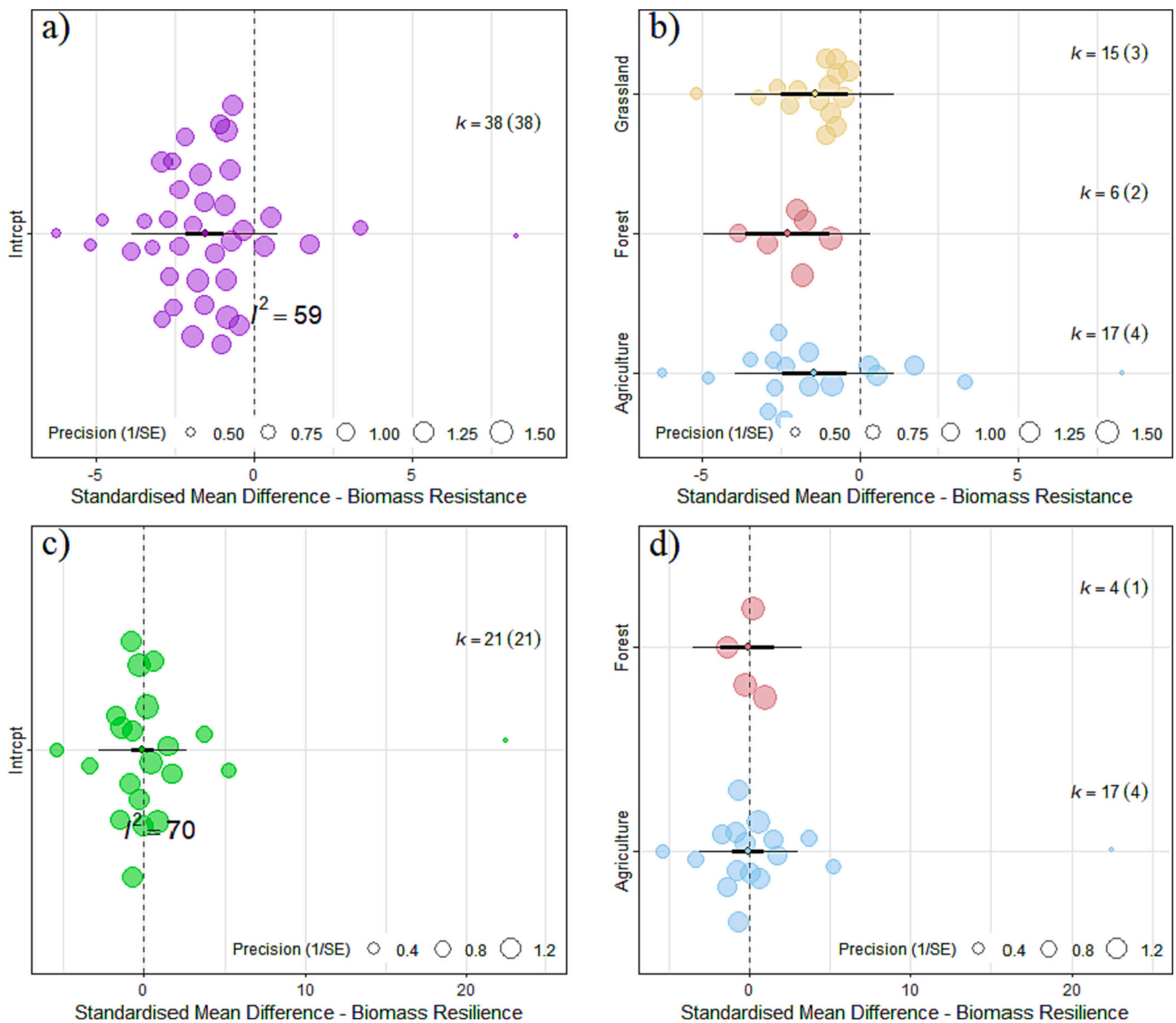

Fig. 2. Orchard plots of the meta-analytic model showing the overall response of microbial biomass to drought between the control and treatment during resistance (a) and resilience (c) phases and meta-regression model showing the effect of land use type on resistance (b) and resilience (d) of microbial biomass to drought. Mean effect sizes with 95 % confidence intervals (bold lines) are shown in the middle of the dot charts, where individual dots are individual (i.e., different data points in the studies) effect sizes. The size of dots shows the precision (inverse of standard error) of the effect size estimate. Negative effect sizes larger values in control, while positive values mark larger values in treatment in the respective parameter.

three assessed ecosystems (agriculture, forest, and grassland) ranged from −0.32 to 1 with 65 % showed values higher than 0.5 (Fig. S3a). Resilience index of soil microbial biomass ranged from −1 to 0.96 with 42 % showed values higher than 0.5 (Fig. S3b). Overall, the resistance indices of soil microbial biomass to drought stress showed the order of agriculture (0.63) > forest (0.56) > grassland (0.53) while resilience was forest (0.44) > grassland (0.25) > agriculture (0.22). (Table 1). We further observed that grassland ecosystem separated from the agriculture and forest ecosystems for the resistance and resilience index of the microbial biomass (Fig. 4a and b).

Drought stress can have a significant effect on soil microbial communities (e.g., cell desiccation and lysis, or denaturation of microbial enzymes), which in turn can affect soil processes and ecosystem functioning (Berard et al., 2011; Göransson et al., 2013). Previous studies revealed both positive (due to release of labile C, N, and P via soil aggregate breakdown) and negative (due to stress-sensitive microorganisms) responses of microbial biomass to drying/wetting cycles (Guillot et al., 2019; Huang et al., 2020). Nevertheless, Homyak et al. (2017) reported possible mechanisms for increasing microbial biomass under drought conditions, such as changes in the composition of soil microbial communities; their transition into dormant states; or dominance of fungal communities capable of withstanding drought. Drought-tolerant microorganisms may therefore demonstrate metabolic changes, osmotic regulatory mechanisms, or alternative nutrient acquisition strategies that allow them to use bioavailable resources more efficiently and maintain growth and biomass production under drought condition. Therefore, drought stress triggers diverse microbial responses, encompassing both positive (increased biomass production) and negative (reduced biomass) outcomes.

Intensive land management practices - such as agricultural use - can shift the distribution of soil microbial biomass to bacterial, rather than fungal, dominated species (De Vries et al., 2013). Soil fungi are generally more resistant to drought stress, than soil bacteria, due to their thicker cell walls, sporulation activity and higher capacity to access water and nutrients under stress through fungal hyphae (Barnard et al., 2013; Schimel, 2018). In contrast, soil bacteria are more resilient to drought stress due to their rapid growth and reproduction capacity (de Vries et al., 2012). Therefore, the variation of the resistance and resilience indexes under different land uses can be attributed to the fungi: bacteria ratios under different land uses.

The observations of this study indicated a generally low resistance of soil microbial biomass to drought stress (significantly negative mean difference values) and its low resilience (non-significant mean difference values) to recover from drought stress compared with the pre-disturbance condition. Maestre et al. (2015) reported that microbial communities maintain their structure and functioning even under severe drought conditions and develop more resistance and resilience communities after the drought period is over. They suggested that the response of soil microbial communities were dependent on the severity of drought stress, with more severe droughts leading to a slower recovery of microbial biomass. Barnard et al. (2013) indicated that the resistance and resilience of soil microbial biomass to drought stress would vary depending on soil type and land use. We did not observe any

Table 1
Resistance and resilience indexes for the microbial biomass and microbial respiration in different land use types.

Land use	Microbial biomass		Microbial respiration	
	RS	RL	RS	RL
Agriculture	0.63 ± 0.05	0.23 ± 0.14	0.14 ± 0.12	0.44 ± 0.12
Forest	0.56 ± 0.10	0.44 ± 0.14	0.43 ± 0.10	0.54 ± 0.10
Grassland	0.53 ± 0.08	0.21 ± 0.18	0.20 ± 0.04	0.61 ± 0.04
P value	(0.56)	(0.76)	(0.15)	(0.55)

The table displays the individual column *p*-values calculated to assess the statistical significance of each variable. RS = Resistance, RL = Resilience.

significant differences in resistance and resilience of microbial biomass to drought stress within three land use types. However, more negative effect size in forest ecosystem for resistance in microbial biomass indicated that forest ecosystem tends to be less resistant to drought compared to agriculture and grassland ecosystems. The overall observations suggest a generally low resistance of soil microbial biomass to drought stress, with limited resilience, and the forest ecosystem exhibited less resistance compared to agriculture and grassland ecosystems.

3.2. Resistance and resilience of soil microbial respiration to drought stress

The results of the meta-analysis revealed that there was an overall negative effect size across the included studies for the microbial respiration during drought. Specifically, the standardized mean difference (SMD) between control and drought treatments was −0.87 (95 % CI [−1.68, −0.07]) which was statistically significant ($p = 0.03$, Fig. 3a). This negative effect size suggests that drought is associated with a decrease in microbial respiration. According to the Q-test, the true outcomes were heterogeneous (Q = 53.73, $p = 0.005$, $I^2 = 60$ %), and the linear regression test indicated potential funnel plot asymmetry ($p = 0.0002$; Fig. S1c). The multivariate meta-analysis model revealed that the type of land use had no effect on response of microbial respiration to drought stress. Overall, the mean effect of the land uses were negative in an order of grassland ecosystem (−1.31, 95 % CI [−2.90, 0.29]), forest ecosystem (−1.28, 95 % CI [−2.61, 0.06]), and agriculture ecosystem (−0.35, 95 % CI [−1.50, 0.81]) (Fig. 3b).

Soil microbial respiration during the recovery phase (i.e., following the breaking of drought; the resilience phase) showed an overall positive effect (0.30, 95 % CI [0.02, 0.57]) which was statistically significant ($p = 0.04$, Fig. 3c). The Q-test indicated that the results were not heterogeneous (Q = 27.37, $p = 0.50$, $I^2 = 2$ %). The linear regression test also indicated potential funnel plot asymmetry ($p < 0.0001$; Fig. S1d). The multivariate meta-analysis model indicated that the impact of land use on microbial respiration response to drought was not significant ($p = 0.26$). When considering all types of land use, including grassland, forest and agriculture ecosystems, the overall mean effect was positive. Specifically, the effect sizes for the forest, agriculture, and grassland ecosystems were estimated at 0.05 (95 % CI [−0.58, 0.67]), 0.24 (95 % CI [−0.07, 0.56]), and 0.74 (95 % CI [0.12, 1.37]), respectively (Fig. 3d).

Resistance index of soil microbial respiration for all three ecosystems ranged from −0.65 to 0.97 with 82 % of results showed values lower than 0.5 (Fig. S5a). Resilience index of soil microbial biomass also ranged from −0.71 to 0.99 with 52 % of results showed values lower than 0.5 (Fig. S5b). The resistance and resilience indices of soil microbial respiration to drought stress showed the order of forest (0.43) > grassland (0.20) > agriculture (0.12), and grassland (0.61) > forest (0.54) > agriculture (0.44), respectively (Table 1).

Soil microbial respiration is regulated by abundant microbial species with high functional redundancy (Shen et al., 2022). In response to drought stress, microbial communities would exhibit both resistance and resilience, which can have varying impacts on their respiration, as soil microbial biomass and SOC are considered the main contributors of soil respiration resilience (Yu et al., 2021). Microbial response to drought also varies depending on factors such as soil type and land use history, microbial community composition and duration and severity of drought stress. Generally, drought stress decreases soil microbial respiration when soil moisture content falls below the optimum level, while rewetting increases soil microbial respiration due to an increase in dissolved organic carbon and microbial biomass (Yu et al., 2021; Zhang et al., 2015). When soil microorganisms are under stress, they allocate more carbon and nutrients to survival pathways (e.g., synthesizing protective substances to stabilize proteins and osmolytes to maintain hydration) than to growth pathways. This would result in higher synthesis of molecules such as polyols or amino acids, which are

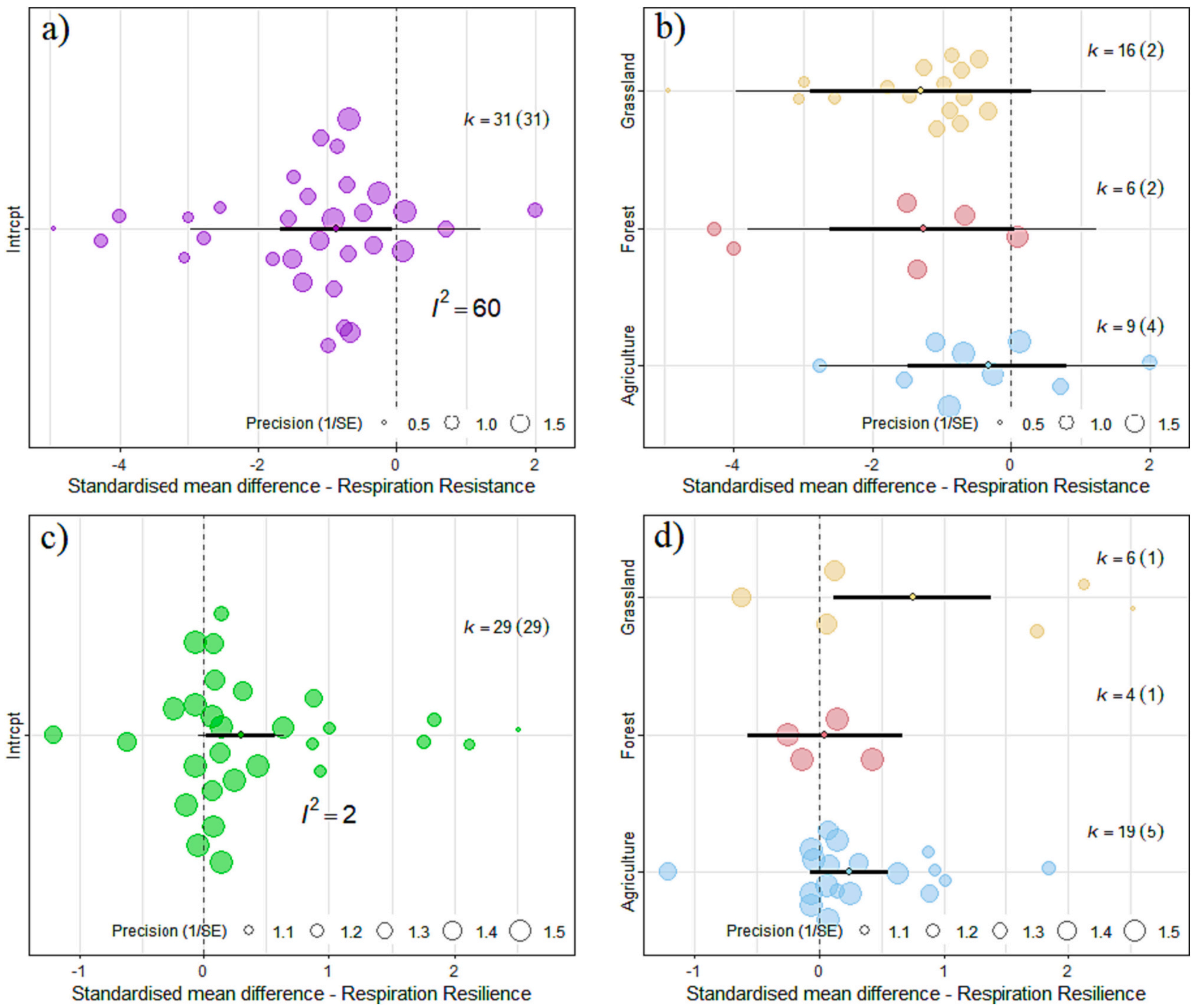

Fig. 3. Orchard plots of the meta-analytic model showing the overall response of microbial respiration to drought between the control and treatment during resistance (a) and resilience (c) phases and meta-regression model showing the effect of land use type on resistance (b) and resilience (d) of microbial respiration to drought. Mean effect sizes with 95 % confidence intervals (bold lines) are shown in the middle of the dot charts, where individual dots are individual (i.e., different data points in the studies) effect sizes. The size of dots shows the precision (inverse of standard error) of the effect size estimate. Negative effect sizes larger values in control, while positive values mark larger values in treatment in the respective parameter.

energetically expensive and consequently decrease soil microbial respiration (Guillot et al., 2019). Previous studies have shown that some microbial taxa (gram-positives such as Actinobacteria and Firmicutes) exhibit increased respiration activity during drought, while others (Gram-negatives such as Proteobacteria and Bacteroidetes) would show decreased activity (Graham et al., 2016; Lipson et al., 2015). The impact of drought on microbial respiration can vary depending on the specific microbial communities and environmental conditions involved (Barnard et al., 2013). Therefore, improved understanding of the mechanisms underlying microbial responses to drought, such as the capacity to survive drought induced osmotic shock, or to assimilate dissolved SOC during rewetting of soil aggregates, is crucial for predicting the long-term effects of ecosystem-based managements on ecosystem functioning (Homyak et al., 2018; Slessarev and Schimel, 2020; Sun et al., 2017). For example, it has been suggested that microbial communities can adapt to drought stress by altering their carbon utilization patterns (i.e., higher carbon use efficiency) or shifting to more drought-tolerant taxa (Drigo et al., 2017; Evans and Wallenstein, 2014). These adaptive responses may increase resistance and resilience, thereby enabling microbial communities to maintain their respiration activity and prevent significant disruptions to ecosystem functioning (de Nijs et al., 2019; Evans and Wallenstein, 2014).

3.3. Role of soil intrinsic properties and management practices in shaping resistance and resilience of soil microbiome to drought stress

Soil intrinsic properties shown mix effects on microbial (i.e., biomass and respiration) resistance and resilience to drought stress. For example, soil organic carbon (SOC) found to have significant impact on the response of microbial biomass to drought in the resistance phase ($p = 0.01$). The overall effect sizes were negative under both levels of SOC with −2.16 (95 % CI [−2.89, −1.42]) at >2 % SOC, and −0.91 (95 % CI [−1.67, −0.15]) at 1–2 % SOC contents (Fig. S2a). The overall effect sizes for different levels of clay content (Fig. S2b) and pH (Fig. S2c) were also negative, however they were not statistically significant. Soil texture is one of the major factors with significant influence on resistance and resilience of soil physical and biological properties to stressors (Corstanje et al., 2015; Seybold et al., 1999). It has been reported that microbial communities in sandy soils are more resilient to drought stress than clay soils, due to the higher frequency of drying/wetting events in sandy soils (Arthur et al., 2012; Perez-Guzman et al., 2020). The textural differences would affect soil resilience by processes such as the leaching of carbon and nutrients, and translocation of fine soil particles within the soil profile (Blanco-Canqui and Lal, 2010).

Microorganisms are known for their ability to adapt to various environmental conditions. For instance, certain microbial taxa may possess traits that enable them to tolerate challenging conditions (i.e., low organic carbon, low clay content, and high pH soils), and thrive under drought stress. We also observed few positive effects of microbial biomass to drought in the agriculture ecosystem, compared to forest and grassland ecosystems, which indicates more resistance to drought and its association with alkaline pH (pH > 7.5), low soil organic carbon (SOC < 2 %) and low clay content (Clay <5 %) (Fig. S2a, b and c). Further, we observed positive effect sizes for the microbial biomass resilience to drought under conditions such as 1–2 % SOC (Fig. S2d), clay contents of <5 % and >15 % (Fig. S2e), and pH of 7–8 (Fig. S2f). However, they were not statistically significant.

The overall effect sizes for different levels of SOC% (Fig. S4a), clay% (Fig. S4b) and pH (Fig. S4c) were negative for microbial respiration resistance (not statistically significant). However, the negative values decreased with increases in SOC%, clay% and neutral and acidic pH values. This indicated that higher SOC, clay content, and neutral and acidic soils would favour microbial respiration during the drought and potentially increase the resistance to drought stress. Contradictory, the overall effect sizes of microbial respiration, under different levels of SOC, clay, and pH, were positive (not statistically significant) during the resilience phase and the positive values increased with higher SOC contents (Fig. S4d, e, and f respectively). Further, we observed that soil pH was a vital factor for determination of the resistance and resilience of soil microbial respiration to drought in agricultural soils (Fig. 4c and d, Table 2). It has also been reported that soil microbial composition and functions can be regulated by soil pH in different soils (Yang et al., 2020), and the bacterial growth would be stimulated by an increase in soil pH values (Silva-Sánchez et al., 2019), resulting in a lower respiration resilience to drying/wetting cycles (Hu et al., 2021). Therefore, soil acidity/alkalinity management is one of the main factors to be considered in soil management practices. Since topsoil is usually disturbed in agricultural fields, surface application of organic amendments may not be able to effectively improve soil microbial resistance and resilience to drought stress.

Resistance and resilience indexes for microbial biomass and respiration indicated that, there was no clear separation of the three land use types (agriculture, forest, and grassland) for respiration under drought stress as observed for microbial biomass (Fig. 4c and d). In both grassland and forest ecosystems, microbial biomass resistance and resilience were strongly associated with SOC content, while forest ecosystem additionally exhibited a strong association with clay content and pH (Table 2). The positive association of soil microbial biomass resistance to drought, with soil pH could be due to higher bioavailability of Al and its toxicity, as well as lower bioavailability of plant-derived C in acidic soils (Rousk et al., 2009). Further, the resistance and resilience of microbial respiration in agriculture ecosystem was primarily regulated by soil pH, whereas in forest ecosystem it was strongly associated with SOC, clay content, and soil pH (Table 2). While pH is an important factor in both agriculture and forest ecosystems, the specific context of agricultural management practices (i.e., more intensive management practices,

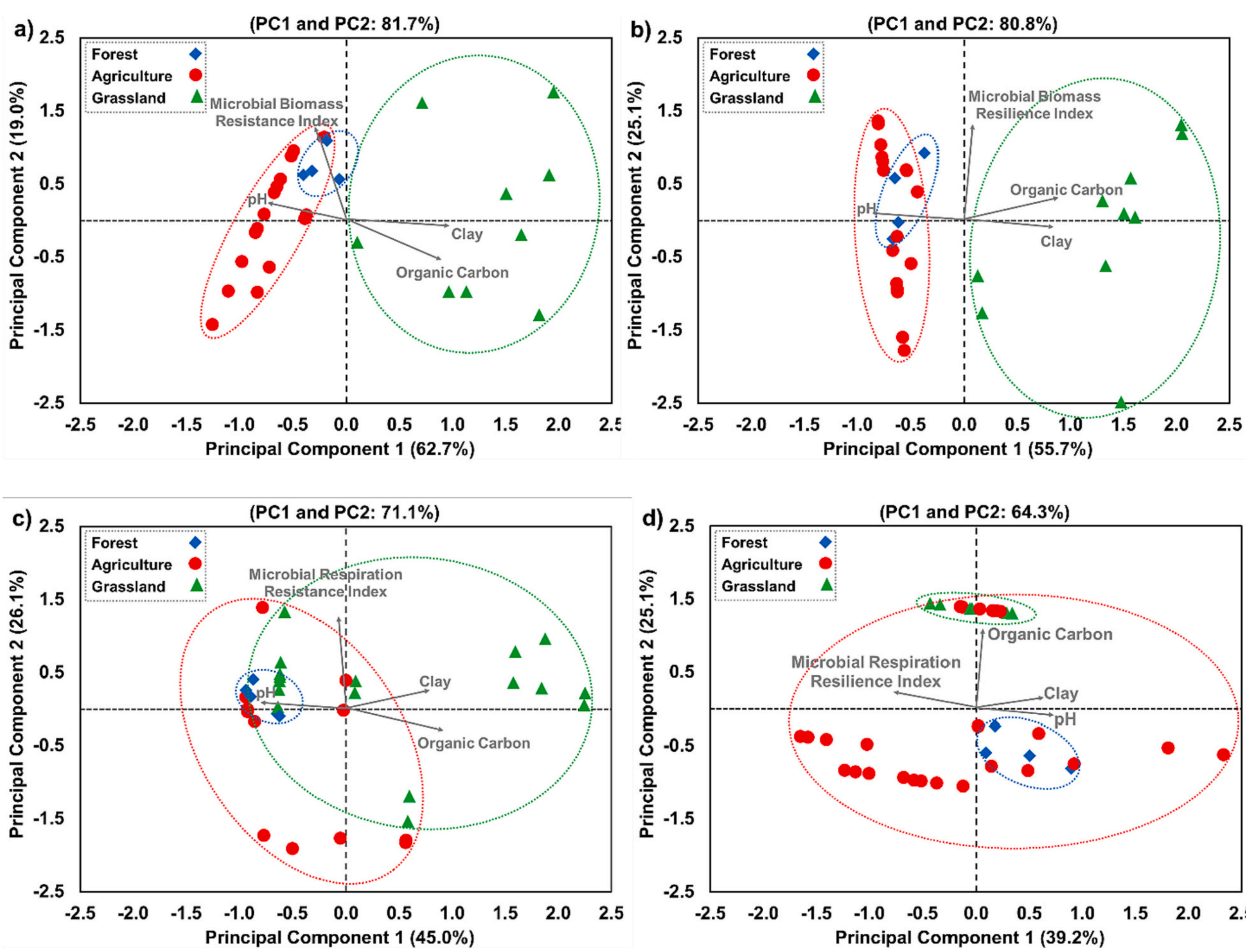

Fig. 4. Principle component analysis (PCA) showing the separation of land use for resistance and resilience indexes of microbial biomass (a and b) and microbial respiration (c and d) under drought stress.

Table 2
Association between resistance and resilience index with soil intrinsic properties.

Soil properties	Microbial biomass					
	Resistance			Resilience		
	Agriculture	Forest	Grassland	Agriculture	Forest	Grassland
SOC	−0.41 ($p = 0.10$)	−0.97** ($p = 0.001$)	−0.70** ($p = 0.002$)	0.48 ($p = 0.05$)	0.85 ($p = 0.15$)	0.75** (p = 0.01)
Clay	−0.09 ($p = 0.72$)	−0.87 ($p = 0.13$)	−0.18 ($p = 0.52$)	0.05 ($p = 0.86$)	−0.79 ($p = 0.21$)	0.09 ($p = 0.79$)
pH	0.42 ($p = 0.09$)	0.97** (p = 0.001)	0.06 (p = 0.86)	−0.31 ($p = 0.22$)	−0.96** (p = 0.04)	−0.22 ($p = 0.54$)

Soil properties	Microbial respiration					
	Resistance			Resilience		
	Agriculture	Forest	Grassland	Agriculture	Forest	Grassland*
SOC	−0.19 (p = 0.48)	0.94** ($p = 0.006$)	−0.62** ($p < 0.001$)	−0.04 ($p = 0.83$)	0.47 ($p = 0.53$)	– –
Clay	−0.13 ($p = 0.61$)	0.58 ($p = 0.42$)	−0.09 (p = 0.72)	−0.3 (p = 0.09)	−0.68 ($p = 0.32$)	– –
pH	0.52** ($p = 0.03$)	−0.94** (p = 0.006)	0.27 ($p = 0.19$)	−0.47** ($p = 0.02$)	−0.58 (p = 0.42)	– –

[*] Could not compute due to limited data availability.
[**] Correlation is significant at 0.01 level (the table displays the individual cell p-values calculated to assess the statistical significance of the correlation between resistance and resilience index with soil intrinsic properties).

including the use of fertilizers, pesticides, and soil amendments), often amplifies the influence of pH on microbial respiration resistance and resilience to drought in agricultural settings. Factors such as clay content and SOM are also important in both agriculture and forest ecosystems, while they may have more stable and established roles in undisturbed forest environments.

The strong negative association between SOC and resistance of microbial biomass to drought stress could be related to the fact that higher SOC levels would result in a soil microbial community which is more sensitive to disturbances (Bastida et al., 2017; Orwin and Wardle, 2005). Therefore, the ecosystem might become more fragile or prone to disruptions due to the dependence of microorganisms to a specific organic carbon substrate. Any disturbances can have a more significant impact on these specialized microbial populations, leading to a lower resistance. However, SOC exhibited a positive association with resilience of microbial biomass, which could be due to a balanced availability of organic substrates with the cessation of drought. The negative association between clay content and resistance and resilience of microbial biomass during drought stress could be attributed to factors such as limited water drainage and oxygen availability due to the dense structure of clay particles (Perez-Guzman et al., 2020). Further, the physical barrier created by fine-textured clay can impede microbial movement and access to nutrients, contributing to the decreased ability of the microbial community to withstand and recover from drought-induced stress.

Adoption of ecosystem-based management practices enables the development of a self-recovering soil ecosystem against disturbances (Orwin and Wardle, 2004). These include management practices such as organic farming systems (minimal use of external resources), conservation agriculture (minimum soil disturbance, diversified crop rotations, and maintenance of organic soil cover) (Chabert and Sarthou, 2020; Nyanga et al., 2020), no-till and low-till farming, mix cropping, crop rotation, cover crops (i.e., crops grown to protect soil surface and improve soil quality), minimum use of off-farm inputs, reliance on biological processes for pest management, and application of organic amendments (Akamani, 2021; Horrigan et al., 2002; Jian et al., 2020) (Table 3). The stability of a soil ecosystem is a vital factor for its sustainable productivity that is governed by various soil and environmental processes. It has been reported that the structural stability of soil can be increased by utilising a no-till cropping system, due to the potential for development of uniform aggregate strength with more resistant to breakdown after rewetting (Skaalsveen et al., 2019), as well as increasing the number and continuity of soil macropores (Dang et al., 2020). Other than the reduction in soil disturbance, no-till systems can also increase soil organic carbon (SOC) content due to higher retention of crop residues in the soil surface (de Moraes Sa et al., 2014). Additionally, it has been found that the addition of biochar can lead to an increase in the resistance of both bacterial and fungal networks to drought, and biochar-amended soils usually characterized by a faster recovery of soil microbial properties to basal values (Liang et al., 2014).

The ecosystem-based management practices should ensure an increase in soil organic matter, which is one of the main factors regulating soil resilience to disturbance. Organic amendments and cover crops coupled with no−/reduced-tillage practices can enhance soil physical, chemical, and biological properties and increase soil resilience to different environmental stresses. However, the rate and magnitude of recovery attributed to the management practices can be varied with the type of cover crop/organic amendment / intensity of the tillage (no/reduced), microbial resource availability and intrinsic properties of soil, and climatic conditions (de Vries and Shade, 2013; Kaisermann et al., 2013; Shen et al., 2022; Wallenstein and Hall, 2012). It has been reported that soils with high organic matter content have higher resistance and resilience of soil functions (e.g., soil respiration, and N cycling) to disturbances than soils with low organic matter content (Dacal et al., 2022). Organic matter content in soil determines the aggregate stability, porosity and compaction, available water capacity, hydrology and macropore connectivity, and erodibility (Blanco-Canqui and Lal, 2010). Therefore, the magnitude of improvement in soil resilience, due to adoption of ecosystem-based management practices, is a cumulative outcome of land management practices, soil intrinsic properties, and climatic factors.

4. Conclusions

Soil microbial communities are essential components of soil ecosystem that play vital roles in maintaining soil fertility, nutrient cycling, and plant productivity. Environmental stresses such as drought can severely affect soil microbial biomass and respiration, with negative

Table 3
The effects of ecosystem-based management practices on soil properties.

Management strategy	Region	Management outcome	Reference
No-tillage/ reduced tillage	USA	No-tillage enhanced soil structural stability and soil carbon than conventional tillage.	(Nouri et al., 2021)
	Guadeloupe	Reduced tillage (replacing mouldboard ploughing with disc harrowing) resulted in diminishing SOC losses by 4-fold.	(Chopin and Sierra, 2019)
	Spain	Long-term (20 years) no-tillage management stimulated soil biological activity and formation of water-stable macroaggregates.	(Pareja-Sánchez et al., 2017)
	USA	No-till promote soil resilience in terms of moisture retention, effectiveness of drought mitigation, and crop yields.	(Eeswaran et al., 2021)
Organic amendments	Germany	High organic carbon soil amendment (i.e., wheat straw) effectively buffered an excess of nitrogen at a field scale.	(Reichel et al., 2018)
	Australia	Biochar and biochar-compost soil managements improved soil organic carbon, nutrient contents, and water holding capacity.	(Agegnehu et al., 2016; Lan et al., 2019)
	Canada	Beef feedlot manure applied to the plots where topsoil has been removed had a legacy effect on enhancing soil carbon fraction values and soil aggregation.	(Larney et al., 2016)
	Guadeloupe	The use of organic amendments (i.e., manure, sugar scum, sewage sludge, vinasse, and compost) reduced SOC losses by 1.5-fold.	(Chopin and Sierra, 2019)
	Spain	In an incubation experiment, organic amendment increased soil water holding capacity, Organic C and total N contents, and soil enzyme activities (i.e., β-glucosidase and phosphomonoesterase).	(Hueso et al., 2011)
	China	Long-term organic matter inputs (corn straw and farmyard manure) increased SOC, decreased soil bulk density and increased soil porosity.	(Song et al., 2015)
Cover cropping	France	Cover cropping enhanced soil resilience to nitrogen fertilization by increasing functional redundancy and complementarity within soil bacterial communities and across soil horizons.	(Alahmad et al., 2019)
	Hesston, Kansas	Cover cropping (i.e., sunn hemp and late-maturing soybean) reduced the near-surface soil's susceptibility to compaction and improved the physical properties of soil and SOC contents.	(Blanco-Canqui et al., 2011)
	Italy	The introduction of different cover crops (non-legume cover crop, low nitrogen supply legume cover crop, and high nitrogen supply legume cover crop) increased SOC content at various rates (0.08, 0.32 and 0.34 Mg ha^{-1} $year^{-1}$ respectively) as compared with the control. All cover crops significantly increased soil total N content compared to the control.	(Mazzoncini et al., 2011)
	Brazil	Cropping systems with summer legume cover crops had higher potential for improving SOM in no-till cropping systems by increasing either the stocks or lability of soil organic C.	(Bayer et al., 2009)

impacts on soil fertility and ecosystem functioning. Our investigation into the resistance and resilience of soil microbial biomass and respiration to drought stress revealed distinct patterns across different ecosystems (agriculture, forest, and grassland) and intrinsic soil properties (SOC, Clay content and Soil pH). Soil microbial biomass exhibited a generally low resistance to drought stress, with limited resilience, and the forest ecosystem displayed lower resistance compared to agriculture and grassland ecosystems. The resistance and resilience of microbial respiration also varied across land uses, with an overall decrease during drought and a positive recovery during the resilience phase. Soil intrinsic properties such as SOC, clay content, and pH, played a crucial role in shaping microbial responses, influencing both resistance and resilience. Additionally, our findings underscore the importance of ecosystem-based management practices in enhancing soil resilience, with practices such as organic farming, conservation agriculture, and the addition of biochar showing potential to mitigate the impacts of drought on soil microbial communities. Overall, the response of soil microbial communities to drought is a complex process that is influenced by many factors. Therefore, understanding the underlying mechanisms that drive these responses, such as intrinsic soil properties and microbial community dynamics, can help to identify the land management practices that promote soil health and resilience.

CRediT authorship contribution statement

Apsara Amarasinghe: Conceptualization, Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. **Chengrong Chen:** Conceptualization, Writing – original draft, Writing – review & editing. **Lukas Van Zwieten:** Conceptualization, Writing – original draft, Writing – review & editing. **Mehran Rezaei Rashti:** Conceptualization, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Mehran Rezaei Rashti reports financial support was provided by Cooperative Research Centre for High Performance Soils.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

Abdourahamane Illiassou, S., Oeba, V.O., 2020. Ecosystem-based approach for sustainable agricultural development in addressing food security and nutrition. In: *In* "Zero Hunger". Springer, pp. 252–262.
Agegnehu, G., Bass, A.M., Nelson, P.N., Bird, M.I., 2016. Benefits of biochar, compost and biochar–compost for soil quality, maize yield and greenhouse gas emissions in a tropical agricultural soil. Sci. Total Environ. 543, 295–306.
Akamani, K., 2021. An ecosystem-based approach to climate-smart agriculture with some considerations for social equity. Agronomy 11, 1564.
Alahmad, A., Decocq, G., Spicher, F., Kheirbeik, L., Kobaissi, A., Tetu, T., Dubois, F., Duclercq, J., 2019. Cover crops in arable lands increase functional complementarity and redundancy of bacterial communities. J. Appl. Ecol. 56 (3), 651–664.
Arthur, E., Schjønning, P., Moldrup, P., de Jonge, L.W., 2012. Soil resistance and resilience to mechanical stresses for three differently managed sandy loam soils. Geoderma 173-174, 50–60.
Babur, E., Dindaroğlu, T., Riaz, M., Uslu, O.S., 2022. Seasonal variations in litter layers' characteristics control microbial respiration and microbial carbon utilization under mature pine, cedar, and beech forest stands in the Eastern Mediterranean Karstic Ecosystems. Microb. Ecol. 84, 153–167.
Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. ISME J. 7, 2229–2241.
Bastida, F., Torres, I.F., Hernandez, T., Garcia, C., 2017. The impacts of organic amendments: do they confer stability against drought on the soil microbial community? Soil Biol. Biochem. 113, 173–183.
Bayer, C., Dieckow, J., Amado, T.J.C., Eltz, F.L.F., Vieira, F.C.B., 2009. Cover crop effects increasing carbon storage in a subtropical no-till sandy Acrisol. Commun. Soil Sci. Plant Anal. 40 (9-10), 1499–1511.
Berard, A., Bouchet, T., Sevenier, G., Pablo, A.L., Gros, R., 2011. Resilience of soil microbial communities impacted by severe drought and high temperature in the context of Mediterranean heat waves. Eur. J. Soil Biol. 47 (6), 333–342.
Blanco-Canqui, H., Lal, R., 2010. Soil resilience and conservation. In: *In* "Principles of Soil Conservation and Management". Springer, pp. 425–447.
Blanco-Canqui, H., Mikha, M.M., Presley, D.R., Claassen, M.M., 2011. Addition of cover crops enhances no-till potential for improving soil physical properties. Soil Sci. Soc. Am. J. 75 (4), 1471–1482.
Chabert, A., Sarthou, J.-P., 2020. Conservation agriculture as a promising trade-off between conventional and organic agriculture in bundling ecosystem services. Agric. Ecosyst. Environ. 292, 106815.
Chopin, P., Sierra, J., 2019. Reduced tillage and organic amendments can offset the negative impact of climate change on soil carbon: a regional modelling study in the Caribbean. Soil Tillage Res. 192, 113–120.
Corstanje, R., Deeks, L., Whitmore, A., Gregory, A., Ritz, K., 2015. Probing the basis of soil resilience. Soil Use Manag. 31, 72–81.
Dacal, M., García-Palacios, P., Asensio, S., Wang, J., Singh, B.K., Maestre, F.T., 2022. Climate change legacies contrastingly affect the resistance and resilience of soil microbial communities and multifunctionality to extreme drought. Funct. Ecol. 36, 908–920.
Dang, Y.P., Page, K.L., Dalal, R.C., Menzies, N.W., 2020. No-till farming systems for sustainable agriculture: an overview. In: No-till Farming Systems for Sustainable Agriculture, pp. 3–20.
de Moraes Sa, J.C., Tivet, F., Lal, R., Briedis, C., Hartman, D.C., dos Santos, J.Z., dos Santos, J.B., 2014. Long-term tillage systems impacts on soil C dynamics, soil resilience and agronomic productivity of a Brazilian Oxisol. Soil Tillage Res. 136, 38–50.
de Nijs, E.A., Hicks, L.C., Leizeaga, A., Tietema, A., Rousk, J., 2019. Soil microbial moisture dependences and responses to drying-rewetting: the legacy of 18 years drought. Glob. Chang. Biol. 25, 1005–1015.
de Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under climate change. Front. Microbiol. 4.
de Vries, F.T., Liiri, M.E., Bjornlund, L., Bowker, M.A., Christensen, S., Setala, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Chang. 2, 276–280.
De Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Bracht Jørgensen, H., Brady, M.V., Christensen, S., De Ruiter, P.C., 2013. Soil food web properties explain ecosystem services across European land use systems. Proc. Natl. Acad. Sci. 110, 14296–14301.
Delacámara, G., O'Higgins, T.G., Lago, M., Langhans, S., 2020. Ecosystem-based management: moving from concept to practice. In: Ecosystem-Based Management, Ecosystem Services and Aquatic Biodiversity. Springer, Cham, pp. 39–60.
Dougherty, L.R., 2023. The effect of individual state on the strength of mate choice in females and males. Behav. Ecol. 34, 197–209.
Drigo, B., Nielsen, U.N., Jeffries, T.C., Curlevski, N.J.A., Singh, B.K., Duursma, R.A., Anderson, I.C., 2017. Interactive effects of seasonal drought and elevated atmospheric carbon dioxide concentration on prokaryotic rhizosphere communities. Environ. Microbiol. 19, 3175–3185.
Eeswaran, R., Nejadhashemi, A.P., Alves, F.C., Saravi, B., 2021. Evaluating the applicability of soil moisture-based metrics for gauging the resiliency of rainfed agricultural systems in the midwestern United States. Soil Tillage Res. 205, 104818.
Ene, I.V., Walker, L.A., Schiavone, M., Lee, K.K., Martin-Yken, H., Dague, E., Gow, N.A., Munro, C.A., Brown, A.J., 2015. Cell wall remodeling enzymes modulate fungal cell wall elasticity and osmotic stress resistance. MBio 6, e00986-15.
Evans, S.E., Wallenstein, M.D., 2014. Climate change alters ecological strategies of soil bacteria. Ecol. Lett. 17, 155–164.
Göransson, H., Godbold, D.L., Jones, D.L., Rousk, J., 2013. Bacterial growth and respiration responses upon rewetting dry forest soils: impact of drought-legacy. Soil Biol. Biochem. 57, 477–486.
Grados, D., Butterbach-Bahl, K., Chen, J., van Groenigen, K.J., Olesen, J.E., van Groenigen, J.W., Abalos, D., 2022. Synthesizing the evidence of nitrous oxide mitigation practices in agroecosystems. Environ. Res. Lett. 17, 114024.
Graham, E.B., Knelman, J.E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A., Beman, J., Abell, G., Philippot, L., Prosser, J., 2016. Microbes as engines of ecosystem function: when does community structure enhance predictions of ecosystem processes? Front. Microbiol. 7, 214.
Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. FEMS Microbiol. Rev. 37, 112–129.
Griffiths, B.S., Hallett, P.D., Kuan, H.L., Gregory, A.S., Watts, C.W., Whitmore, A.P., 2008. Functional resilience of soil microbial communities depends on both soil structure and microbial community composition. Biol. Fertil. Soils 44, 745–754.
Guillot, E., Hinsinger, P., Dufour, L., Roy, J., Bertrand, I., 2019. With or without trees: resistance and resilience of soil microbial communities to drought and heat stress in a Mediterranean agroforestry system. Soil Biol. Biochem. 129, 122–135.
Homyak, P.M., Allison, S.D., Huxman, T.E., Goulden, M.L., Treseder, K.K., 2017. Effects of drought manipulation on soil nitrogen cycling: a meta-analysis. J. Geophys. Res. Biogeosci. 122, 3260–3272.
Homyak, P.M., Blankinship, J.C., Slessarev, E.W., Schaeffer, S.M., Manzoni, S., Schimel, J.P., 2018. Effects of altered dry season length and plant inputs on soluble soil carbon. Ecology 99, 2348–2362.
Horrigan, L., Lawrence, R.S., Walker, P., 2002. How sustainable agriculture can address the environmental and human health harms of industrial agriculture. Environ. Health Perspect. 110, 445–456.
Hu, Z.K., Chen, C.Y., Chen, X.Y., Yao, J.N., Jiang, L., Liu, M.Q., 2021. Home-field advantage in soil respiration and its resilience to drying and rewetting cycles. Sci. Total Environ. 750.
Huang, L.B., Bai, J.H., Wen, X.J., Zhang, G.L., Zhang, C.D., Cui, B.S., Liu, X.H., 2020. Microbial resistance and resilience in response to environmental changes under the higher intensity of human activities than global average level. Glob. Chang. Biol. 26, 2377–2389.
Hueso, S., Hernández, T., García, C., 2011. Resistance and resilience of the soil microbial biomass to severe drought in semiarid soils: the importance of organic amendments. Appl. Soil Ecol. 50, 27–36.
Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., De Luca, E., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577.
Jian, J., Lester, B.J., Du, X., Reiter, M.S., Stewart, R.D., 2020. A calculator to quantify cover crop effects on soil health and productivity. Soil Tillage Res. 199, 104575.
Joos, L., De Tender, C., 2022. Soil under stress: The importance of soil life and how it is influenced by (micro) plastic pollution. Comput. Struct. Biotechnol. J. 20, 1554–1566.
Kaisermann, A., Roguet, A., Nunan, N., Maron, P.A., Ostle, N., Lata, J.C., 2013. Agricultural management affects the response of soil bacterial community structure and respiration to water-stress. Soil Biol. Biochem. 66, 69–77.
Kibblewhite, M., Ritz, K., Swift, M., 2008. Soil health in agricultural systems. Philos. Trans. R. Soc. B 363, 685–701.
Lan, Z.M., Chen, C.R., Rashti, M.R., Yang, H., Zhang, D.K., 2019. Linking feedstock and application rate of biochars to N2O emission in a sandy loam soil: Potential mechanisms. Geoderma 337, 880–892.
Larney, F.J., Li, L., Janzen, H.H., Angers, D.A., Olson, B.M., 2016. Soil quality attributes, soil resilience, and legacy effects following topsoil removal and one-time amendments. Can. J. Soil Sci. 96 (2), 177–190.
Leizeaga, A., Hicks, L.C., Manoharan, L., Hawkes, C.V., Rousk, J., 2021. Drought legacy affects microbial community trait distributions related to moisture along a savannah grassland precipitation gradient. J. Ecol. 109 (9), 3195–3210.
Li, X., Li, Y., Chen, A., Gao, M., Slette, I.J., Piao, S., 2019. The impact of the 2009/2010 drought on vegetation growth and terrestrial carbon balance in Southwest China. Agric. For. Meteorol. 269, 239–248.
Liang, C., Zhu, X., Fu, S., Méndez, A., Gascó, G., Paz-Ferreiro, J., 2014. Biochar alters the resistance and resilience to drought in a tropical soil. Environ. Res. Lett. 9, 064013.
Lipson, D.A., Raab, T.K., Parker, M., Kelley, S.T., Brislawn, C.J., Jansson, J., 2015. Changes in microbial communities along redox gradients in polygonized Arctic wet tundra soils. Environ. Microbiol. Rep. 7, 649–657.
Liu, X.Y., Rezaei Rashti, M., Van Zwieten, L., Esfandbod, M., Rose, M.T., Chen, C.R., 2023. Microbial carbon functional responses to compaction and moisture stresses in two contrasting Australian soils. Soil Tillage Res. 234, 105825.
Ludwig, M., Wilmes, P., Schrader, S., 2018. Measuring soil sustainability via soil resilience. Sci. Total Environ. 626, 1484–1493.
Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proc. Natl. Acad. Sci. 112, 15684–15689.
Mazzoncini, M., Sapkota, T.B., Barberi, P., Antichi, D., Risaliti, R., 2011. Long-term effect of tillage, nitrogen fertilization and cover crops on soil organic carbon and total nitrogen content. Soil Tillage Res. 114 (2), 165–174.
McKinley, V.L., 2019. Effects of land use and restoration on soil microbial communities. In: Understanding Terrestrial Microbial Communities, pp. 173–242.

Nakagawa, S., Lagisz, M., O'Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W., Senior, A. M., 2021. The orchard plot: cultivating a forest plot for use in ecology, evolution, and beyond. Res. Synth. Methods 12, 4–12.
Nouri, A., Yoder, D.C., Raji, M., Ceylan, S., Jagadamma, S., Lee, J., Walker, F.R., Yin, X., Fitzpatrick, J., Trexler, B., Arelli, P., 2021. Conservation agriculture increases the soil resilience and cotton yield stability in climate extremes of the southeast US. Commun. Earth Environ. 2 (1), 155.
Nyanga, P., Umar, B., Chibamba, D., Mubanga, K., Kunda-Wamuwi, C., Mushili, B., 2020. Reinforcing ecosystem services through conservation agriculture in sustainable food systems. In: *In* "The Role of Ecosystem Services in Sustainable Food Systems". Elsevier, pp. 119–133.
Orwin, K.H., Wardle, D.A., 2004. New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. Soil Biol. Biochem. 36, 1907–1912.
Orwin, K.H., Wardle, D.A., 2005. Plant species composition effects on belowground properties and the resistance and resilience of the soil microflora to a drying disturbance. Plant Soil 278, 205–221.
Pareja-Sánchez, E., Plaza-Bonilla, D., Ramos, M.C., Lampurlanés, J., Álvaro-Fuentes, J., Cantero-Martínez, C., 2017. Long-term no-till as a means to maintain soil surface structure in an agroecosystem transformed into irrigation. Soil Tillage Res. 174, 221–230.
Perez-Guzman, L., Acosta-Martinez, V., Phillips, L.A., Mauget, S.A., 2020. Resilience of the microbial communities of semiarid agricultural soils during natural climatic variability events. Appl. Soil Ecol. 149.
Preece, C., Verbruggen, E., Liu, L., Weedon, J.T., Peñuelas, J., 2019. Effects of past and current drought on the composition and diversity of soil microbial communities. Soil Biol. Biochem. 131, 28–39.
Quinlan, A.E., Berbés-Blázquez, M., Haider, L.J., Peterson, G.D., 2016. Measuring and assessing resilience: broadening understanding through multiple disciplinary perspectives. J. Appl. Ecol. 53, 677–687.
Rashti, M.R., Wang, W., Moody, P., Chen, C., Ghadiri, H., 2015. Fertiliser-induced nitrous oxide emissions from vegetable production in the world and the regulating factors: a review. Atmos. Environ. 112, 225–233.
Reichel, R., Wei, J., Islam, M.S., Schmid, C., Wissel, H., Schröder, P., Schloter, M., Brüggemann, N., 2018. Potential of wheat straw, spruce sawdust, and lignin as high organic carbon soil amendments to improve agricultural nitrogen retention capacity: an incubation study. Front. Plant Sci. 9, 900.
Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Appl. Environ. Microbiol. 75, 1589–1596.
Schimel, J.P., 2018. Life in dry soils: effects of drought on soil microbial communities and processes. Annu. Rev. Ecol. Evol. Syst. 49, 409–432.
Schwalm, C.R., Anderegg, W.R., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Wolf, A., 2017. Global patterns of drought recovery. Nature 548, 202–205.
Seybold, C.A., Herrick, J.E., Brejda, J.J., 1999. Soil resilience: a fundamental component of soil quality. Soil Sci. 164, 224–234.
Shen, H., Zhang, Q., Bi, R., Xu, X., Zhang, X., Fan, C., Xiong, Z., 2022. Linkages of nitrogen-cycling microbial resistance and resilience to soil nutrient stoichiometry under dry-rewetting cycles with different fertilizations and temperatures in a vegetable field. Sci. Total Environ. 820, 153294.
Silva, F. J., de Aguiar, M. I., Maia, L. d. S., Magalhães, R. B., Araújo, F. d., Campanha, M., and de Oliveira, T. (2013). Soil quality, resistance and resilience in traditional agricultural and agroforestry ecosystems in Brazil's semiarid region.
Silva-Sánchez, A., Soares, M., Rousk, J., 2019. Testing the dependence of microbial growth and carbon use efficiency on nitrogen availability, pH, and organic matter quality. Soil Biol. Biochem. 134, 25–35.
Skaalsveen, K., Ingram, J., Clarke, L.E., 2019. The effect of no-till farming on the soil functions of water purification and retention in north-western Europe: a literature review. Soil Tillage Res. 189, 98–109.
Slessarev, E.W., Schimel, J.P., 2020. Partitioning sources of CO2 emission after soil wetting using high-resolution observations and minimal models. Soil Biol. Biochem. 143, 107753.
Song, Z., Gao, H., Zhu, P., Peng, C., Deng, A., Zheng, C., Mannaf, M.A., Islam, M.N., Zhang, W., 2015. Organic amendments increase corn yield by enhancing soil resilience to climate change. Crop J. 3 (2), 110–117.
Sun, D.S., Li, K.J., Bi, Q.F., Zhu, J., Zhang, Q.C., Jin, C.W., Lu, L.L., Lin, X.Y., 2017. Effects of organic amendment on soil aggregation and microbial community composition during drying-rewetting alternation. Sci. Total Environ. 574, 735–743.
Sun, Y., Chen, H.Y.H., Jin, L., Wang, C., Zhang, R., Ruan, H., Yang, J., 2020. Drought stress induced increase of fungi:bacteria ratio in a poplar plantation. CATENA 193, 104607.
Wallenstein, M.D., Hall, E.K., 2012. A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning. Biogeochemistry 109, 35–47.
Wan, Q., Li, L., Liu, B., Zhang, Z., Liu, Y., Xie, M., 2023. Different and unified responses of soil bacterial and fungal community composition and predicted functional potential to 3 years' drought stress in a semiarid alpine grassland. Front. Microbiol. 14, 1104944.
Wang, B., Allison, S.D., 2021. Drought legacies mediated by trait trade-offs in soil microbiomes. Ecosphere 12, e03562.
Yang, C., Wang, X., Miao, F., Li, Z., Tang, W., Sun, J., 2020. Assessing the effect of soil salinization on soil microbial respiration and diversities under incubation conditions. Appl. Soil Ecol. 155, 103671.
Yu, H.Y., Liu, X.D., Ma, Q.H., Yin, Z.T., Wang, Y.H., Xu, Z.Z., Zhou, G.S., 2021. Climatic warming enhances soil respiration resilience in an arid ecosystem. Sci. Total Environ. 756.
Zhang, X., Zhang, Y., Sha, L., Wu, C., Tan, Z., Song, Q., Liu, Y., Dong, L., 2015. Effects of continuous drought stress on soil respiration in a tropical rainforest in southwest China. Plant Soil 394, 343–353.
Zhang, L., Jing, Y., Chen, C., Xiang, Y., Rezaei Rashti, M., Li, Y., Deng, Q., Zhang, R., 2021. Effects of biochar application on soil nitrogen transformation, microbial functional genes, enzyme activity, and plant nitrogen uptake: a meta-analysis of field studies. GCB Bioenergy 13, 1859–1873.