

Soil Carbon Dynamics Under Changing Climate—A Research Transition from Absolute to Relative Roles of Inorganic Nitrogen Pools and Associated Microbial Processes: A Review



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ABSTRACT

It is globally accepted that soil carbon (C) dynamics are at the core of interlinked environmental problems, deteriorating soil quality and changing climate. Its management remains a complex enigma for the scientific community due to its intricate relationship with soil nitrogen (N) availability and moisture-temperature interactions. This article reviews the management aspects of soil C dynamics in light of recent advances, particularly in relation to the availability of inorganic N pools and associated microbial processes under changing climate. Globally, drastic alterations in soil C dynamics under changing land use and management practices have been primarily attributed to the variation in soil N availability, resulting in a higher decomposition rate and a considerable decline in soil organic C (SOC) levels due to increased soil CO₂ emissions, degraded soil quality, and increased atmospheric CO₂ concentrations, leading to climate warming. Predicted climate warming is proposed to enhance SOC decomposition, which may further increase soil N availability, leading to higher soil CO₂ efflux. However, a literature survey revealed that soil may also act as a potential C sink, if we could manage soil inorganic N pools and link microbial processes properly. Studies also indicated that the relative, rather than the absolute, availability of inorganic N pools might be of key importance under changing climate, as these N pools are variably affected by moisture-temperature interactions, and they have variable impacts on SOC turnover. Therefore, multi-factorial studies are required to understand how the relative availability of inorganic N pools and associated microbial processes may determine SOC dynamics for improved soil C management.

Key Words: agro-management, immobilization, NH₄⁺-N to NO₃⁻-N ratio, nitrification, relative availability, soil CO₂ efflux

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INTRODUCTION

Changing climate and declining soil quality have drawn global attention towards soil and its carbon (C) dynamics, which have been found at the core of these interlinked problems (FAO, 2001). Soil is a structurally and functionally complex ecosystem, which stores significant amounts of C (*e.g.*, twice that of vegetation and thrice that of atmosphere) (Lal, 2008; Srivastava *et al.*, 2016c). It plays a regulatory role in biogeochemical cycling and biosphere functioning. Soil C transfer

among various soil C pools (*i.e.*, C turnover) and the regulatory variables constitute soil C dynamics, including the kinetics as well as the factors governing the temporal variations in soil organic C (SOC) across various soil compartments. Soil C dynamics chiefly depend on soil vegetation, texture, moisture, temperature, and management (Ladd *et al.*, 1996; Lal, 2004; Alston *et al.*, 2009; van Wesemael *et al.*, 2010; De Gryze *et al.*, 2011; Srivastava *et al.*, 2016c, d). The multi-functionality and living nature of soil is primarily a function of SOC and its dynamics, which closely de-

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termine soil physicochemical and biological properties (Smith *et al.*, 2000). For example, SOC determines retention and supply of plant nutrients, soil aggregation, water-holding capacity, and erosion (Tisdall and Oades, 1982; Brady and Weil, 2002). Soil organic C is, therefore, considered as an important indicator of soil fertility and quality. Currently, researches are being done to explore how we can manage/regulate soil C dynamics in agro-ecosystems under the changing climate *via* appropriate management. In this regard, multi-factorial experimentations are now required to identify some integrative indicators of SOC dynamics, which can be used for improving soil C management.

Agro-ecosystem soils may act as both a source and sink of atmospheric CO₂, depending upon the C saturation, management, and climate (Srivastava *et al.*, 2015). Although cultivation depletes SOC, improvement in SOC has also been observed under reduced tillage, rotation, and manuring (Bronick and Lal, 2005; Srivastava *et al.*, 2016c, d). This C accumulation in soil as SOC has been widely considered as a promising option for the mitigation of global climate change and soil infertility (Lal, 2004). Therefore, understanding the factors and biological processes which govern the soil's behavior as a source or sink of atmospheric CO₂ would be of vital importance, particularly under changing climatic conditions. Additionally, how such factors and processes are affected and how they could be managed to achieve beneficial SOC dynamics for improving soil fertility as well as climate stability require

investigation in light of recent advances in researches. In the present review, some novel factors and processes, which might potentially govern SOC dynamics under climate change scenarios, are discussed.

The importance of nitrogen (N) availability in SOC dynamics under climate change scenarios has been emphasized in many studies (Davidson *et al.*, 2007; Srivastava *et al.*, 2016c, d; Yue *et al.*, 2016). Nitrogen cycle may potentially regulate climate change through its influence on C sequestration in soils (Liang *et al.*, 2016). Recent studies suggest a crucial and interestingly differential role of inorganic N pools in SOC dynamics under changing moisture-temperature interactions (Srivastava *et al.*, 2015, 2016a, c, d). Such variable effects of NH₄⁺-N and NO₃⁻-N availabilities on soil CO₂ emissions have been a subject of considerable debate in the literature (Min *et al.*, 2011; Moseman-Valtierra *et al.*, 2011; Cheng *et al.*, 2017; Fang *et al.*, 2017) (Table I). In a wide literature survey, we identified that the relative, rather than the absolute, availability of inorganic N pools might have an unexplored role in determining soil C dynamics. Therefore, we critically assessed the literature available on SOC dynamics and climate change in relation to the absolute and relative availabilities of inorganic N pools along with associated soil microbial processes using the Scopus database. We attempted to discuss this issue in a hierarchical manner. This review will help to clarify: i) how climate change may affect soil C dynamics, ii) how inorganic N dynamics may be crucial in soil C dy-

TABLE I
Relationships of soil NO₃⁻-N and NH₄⁺-N with CO₂ efflux

Region	Ecosystem	Relationship ^{a)} with soil CO ₂ efflux		Reference
		NO ₃ ⁻ -N	NH ₄ ⁺ -N	
Subtropical China	Paddy soil	-	+	Lou <i>et al.</i> , 2007
Subtropical China	Pine plantation	+	++	Liu <i>et al.</i> , 2008
UK	Ombrotrophic peatland	-	+	Currey <i>et al.</i> , 2010
Eastern China	Tropical ecosystem	+	+	Fang <i>et al.</i> , 2010
	Subtropical ecosystem	+	+	
	Boreal ecosystem	NS	NS	
	Temperate ecosystem	NS	NS	
UK	Ombrotrophic peatland	--	--	Johnson <i>et al.</i> , 2010
South Korea	Wetland	+	NS	Min <i>et al.</i> , 2011
Northeast China	Secondary forest	-	--	Yang <i>et al.</i> , 2014
	Larch plantation	-	--	
Southwestern China	Experimental field	+	NS	Wang <i>et al.</i> , 2015
Southern China	Subtropical slash pine plantation	++	+	Li <i>et al.</i> , 2015
Southeastern China	Min River estuary marsh	+	++	Hu <i>et al.</i> , 2017
Northern China	Temperate grassland	+	-	Luo <i>et al.</i> , 2016
China	Alpine meadows	NS	NS	Liang <i>et al.</i> , 2017
North China	Boreal forest	+	-	Cheng <i>et al.</i> , 2017

^{a)}NS = not significant; - and + = negative and positive relationships, respectively, with variable numbers representing the strength of relationships.

namics, iii) how microbial functional community might respond to changing moisture-temperature interactions and thus affect soil C dynamics, and iv) how we can manage these microbial functional guilds *via* appropriate management to nullify positive climate change feedback on C cycle. Moreover, it would help researchers and agro-management experts with the identification of novel and integrative indicators of SOC dynamics. These indicators can be regulated *via* site-specific management plans to achieve beneficial soil C dynamics for sustainable agriculture and stable climate.

SCOPE OF THE REVIEW AND BIBLIOMETRIC ANALYSIS OF THE RELATED LITERATURE

A bibliometric analysis was performed to collect the relevant literature for the critical assessment of SOC dynamics in relation to the availability of inorganic N pools. Additionally, we emphasized the microbial processes associated with change in the relative availability of inorganic N pools and their prospective behavior under climate change scenarios. We observed that there were plenty of studies on soil C dynamics in the last few decades, with a central focus on N availability, deposition, and addition in soil. However, this topic still remains complex and of potential interest because of its key role in improved soil C management. The understanding of soil C dynamics is still a critical challenge because of its complicated relationships with soil N availability and biophysical processes. Therefore, a bibliometric analysis of the available literature (mainly published between 1990 and 2016) on soil C dynamics in relation to N availability, soil CO₂ efflux, and climate change was carried out on December 25, 2016 using Scopus database. The analysis was done with a major focus on yearly publications, country-wide publications, and publication types, based on different keywords for a comprehensive understanding. Three major search keywords, soil C or soil C dynamics, soil C or CO₂ efflux, and climate change, were selected and searched along with N availability using Scopus database. The list of publications was limited by selecting two major research areas, *viz.*, agricultural and biological sciences as well as environmental science. The initial publications obtained using these keywords were further sorted using a second-level keyword, *viz.*, ammonium or nitrate. After analyzing these results, we sorted the publications further using a third-level keyword, *viz.*, N mineralization or ammonification or nitrification for obtaining the list of publications focusing directly on i) the roles

of inorganic N pools and associated microbial processes in SOC dynamics and ii) their relative roles in the present climate change feedback mechanisms.

In our first-level literature searches, we observed an exponential increase in the number of publications on the selected topics during the recent past. We obtained 773 publications for the search terms soil C or soil C dynamics and N availability, which were reduced to 178 publications when sorted further by the second-level search terms and to 18 publications when sorted by the third-level search terms. Similarly, 75 publications were obtained using the first-level search terms (soil C or CO₂ efflux and N availability). Moreover, 1279 publications were obtained using the first-level search terms climate change and N availability, which were reduced to 242 publications when sorted by the second-level search terms and to 13 publications when sorted by the third-level search terms. Overall, these results signify that a major section of the research community is increasingly focusing on research pertaining to SOC dynamics in relation to inorganic N pools and processes. Interestingly, the relative roles of inorganic N pool availability and associated processes have been found to gradually evolve as an emergent research area, as indicated by the results of the third-level search terms. We observed that reviews that directly focus on the role of inorganic N pools, especially their relative availability in determining SOC dynamics under climate change scenarios, are currently unavailable. However, the latter has recently been found to be associated with soil C dynamics in some of the recent studies and affect soil C mineralization and CO₂ efflux (Srivastava *et al.*, 2015, 2016a, b; Luo *et al.*, 2016).

CARBON MINERALIZATION AND CO₂ EFFLUX: A CENTRAL ASPECT IN SOIL C DYNAMICS

Soil C mineralization and CO₂ efflux are functions of soil C dynamics happening inside the soil. Carbon mineralization (also known as soil respiration) is a process in which SOC is decomposed and released in the form of CO₂ (*i.e.*, soil CO₂ efflux) into atmosphere. Soil CO₂ efflux represents a significant C efflux (about 75 Pg C year⁻¹), which is identified as the second largest flux (contributing 20%–38%) of C between soil and atmosphere (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000). A relatively small shift in soil C dynamics may dramatically affect the atmospheric CO₂ concentration and C sequestration rate of soil. Therefore, understanding the belowground processes which affect soil CO₂ efflux is important for the mana-

gement of future global climate and soil fertility.

Soil C sequestration and/or its release as soil CO₂ efflux primarily depends on soil organic matter (SOM) decomposition, which is a major biological process in the biogeochemical transformation on the Earth. Decomposition of SOM is predominantly a microbial process, which is highly sensitive to land use changes and management. Its different behaviors under various management practices (as shown by SOC accumulation and soil CO₂ efflux) reflect the variable nature of abiotic-biotic interactions (*i.e.*, the biophysical interactions) happening in the soil. Its nature, therefore, determines the characteristics, storage, turnover, and transfer of C among various physical and biological compartments in soil. Recently, it has been found that soil microbial respiration and C utilization during decomposition are interactively regulated by soil moisture and temperature conditions and N availability (Xu *et al.*, 2016). This suggests that the impact of climate change on soil moisture and temperature conditions and associated N pool availability may have drastic consequences for soil respiration and CO₂ efflux.

SOIL C DYNAMICS AND CLIMATE CHANGE

The possible consequences of climate change for SOC dynamics are still a matter of debate among scientists across the world (Davidson and Janssens, 2006). Terrestrial ecosystems would give a positive and amplifying feedback (*i.e.*, increased SOC decomposition and soil CO₂ efflux) of an uncertain proportion with an increase in the Earth's temperature (Heimann and Reichstein, 2008). The increased N availability with increased temperature is stated to be the primary reason behind this assumption (Mack *et al.*, 2004). However, such a massive release of CO₂ due to increased SOC decomposition in response to climate warming is highly debated (Melillo *et al.*, 2002; Knorr *et al.*, 2005; Srivastava *et al.*, 2015). Moreover, the detrimental changes in soil C dynamics under changing climate have been attributed to the considerable impacts of altered moisture and temperature regimes on soil microbial community. On the contrary, it has also been proposed that soils would acclimatize to these warming conditions *via* adaptive changes in soil microbial community (Srivastava *et al.*, 2015). Thus, a global consensus on the temperature sensitivity of SOC decomposition has yet to be reached (Davidson and Janssens, 2006). This dilemma is primarily attributed to the intricate interrelationship between soil N availability and SOC dynamics, which is further complicated under varying moisture-temperature interactions (Neff

et al., 2002).

Climate change is proposed to impact soil C dynamics by causing changes in soil moisture and temperature as well as their interactions. These two factors have been proposed as key determinants of biosphere functioning under changing climatic conditions (Davidson *et al.*, 2007). Appropriate soil moisture and temperature promote high rates of SOC decomposition, and these factors lower the SOC level (Reichstein *et al.*, 2002). However, the impact of moisture on SOM decomposition varies remarkably depending on the temperature range and ecosystem (Melling *et al.*, 2005). It defines the spatial variations in SOC levels across the world's soils (Paustian *et al.*, 1998; Freibauer *et al.*, 2004). The impacts of global warming on soil CO₂ emissions have been found to primarily depend upon soil moisture conditions (Wood *et al.*, 2013). Therefore, compared to drier soils, wetter soils emit more CO₂ into the environment under equal temperature rise *via* heterotrophic respiration (Zhou *et al.*, 2014). It is, therefore, reported that though high temperatures increase soil respiration, the consequent low soil moisture limits the response of microbial respiration to such high temperatures (Bao *et al.*, 2016). Thus, it was observed that soil moisture predominantly influences the seasonal variation of soil CO₂ efflux, whereas temperature plays a key role in controlling diurnal variation (Wangluk *et al.*, 2013). As warming decreases the soil water content, it is suggested that the effects of soil moisture variation on soil respiration should be examined regarding interactions with temperature in future studies (Zhang *et al.*, 2015). Moreover, factors that integrate the effects of moisture-temperature interactions in soil and those that are related to soil C dynamics or soil CO₂ efflux are currently being explored in light of changing climate for the improved management of SOC (Srivastava *et al.*, 2015, 2016a, b; Singh *et al.*, 2017a, b).

Soil moisture and temperature, both individually and interactively, affect soil CO₂ efflux by affecting soil physicochemical and microbial properties (Olayinka, 2003; Pregitzer and King, 2005). Soil moisture-temperature interactions considerably affect N mineralization processes, which determine the availability of NO₃⁻-N and NH₄⁺-N in soil. It was observed that moisture, temperature, and their interactions have differential effects on ammonification and nitrification processes. Recently, soil microbial respiration and C utilization during the decomposition process were found to be interactively regulated by N availability as well as soil moisture and temperature conditions (Xu *et al.*, 2016). Moreover, it was suggested that the roles

of available N and C dynamics should be considered along with soil moisture and temperature while studying the effect of N availability on soil CO₂ efflux (Wendu *et al.*, 2012). Regulating soil inorganic N pool availability and associated processes *via* appropriate agro-management might be a possible mechanism of nutrient conservation under changing climate conditions (Srivastava *et al.*, 2015).

SOIL C DYNAMICS AND N AVAILABILITY

In studies on SOC dynamics, the effects of soil N availability (*via* fertilization and atmospheric deposition) have been widely assessed (Neff *et al.*, 2002; Reay *et al.*, 2008; Du *et al.*, 2014). Moreover, agricultural management has been reported to define SOC dynamics by affecting soil processes, associated with N availability (Ogle *et al.*, 2005). It is well known that inappropriate management in agro-ecosystems affects SOC dynamics *via* affecting microbe-mediated nutrient cycling processes, particularly those associated with soil N availability (Gruber and Galloway, 2008; Vitousek *et al.*, 2009; Janssens *et al.*, 2010; Taylor and Townsend, 2010). This has resulted in significant changes in nutrient balance in soil (*i.e.*, changes in the relative availability of nutrients). Recently, the stoichiometry between inorganic and organic N availabilities has also been reported in studies controlling soil C cycle (Du *et al.*, 2014). Soil N availability has also been proposed to increase under warming conditions due to increased microbe-mediated mineralization of SOM. However, variations in soil NH₄⁺-N and NO₃⁻-N availabilities could be observed due to the variable influence of soil moisture-temperature interactions on nitrification and ammonification processes. Although temperature has a positive effect on nitrification, increase in soil moisture availability reduces nitrification (Lodhi *et al.*, 2009). Similarly, ammonification (as determined by NH₄⁺-N availability in soil) increases with time as moisture and temperature increase, with the increase being more pronounced at higher moisture levels (Lodhi *et al.*, 2009). Inappropriate changes in both of these N pools may potentially worsen the future course of climate change by detrimentally affecting SOC dynamics. However, as mentioned earlier, it is still highly debated and controversial.

The impact of climate change on N cycle has been reported as particularly relevant in arid ecosystems, where biological activity is primarily limited by water availability (Delgado-Baquerizo *et al.*, 2013; Hu *et al.*, 2014). These ecosystems are strictly and inherently limited by the climate and nutrients (Singh *et al.*, 1989; Singh *et al.*, 2017c). Hart (2006) repor-

ted that a small increase in the mean annual temperature along with climate change may have large impacts on soil N cycling, soil-atmosphere trace gas exchanges, and soil microbial community even under water-limited conditions. Literature findings suggest that the predicted increase in aridity with changing climate/warming conditions would reduce soil C and N in these ecosystems (Delgado-Baquerizo *et al.*, 2013). Additionally, it may considerably affect the ecosystem services *via* decoupling the soil biogeochemical cycles of C and N (Delgado-Baquerizo *et al.*, 2013). Despite such a grim projection, these dry ecosystems have also shown the potential to counter the detrimental effects of higher temperatures *via* some microbe-mediated adaptive changes, depending on the management practices (Srivastava *et al.*, 2015, 2016d). It is suggested that long-term warming studies in such nutrient-limited ecosystems may provide some crucial insights into the complex interactions between soil N availability and SOC dynamics, particularly under variable moisture-temperature interactions. For example, high moisture content has been reported to conserve N in soil due to its negative impact on SOM mineralization, whereas high temperatures have shown a positive influence (Lodhi *et al.*, 2009). This suggests that these nutrient-limited ecosystems would be an important area/region of research on soil C dynamics in changing climate in the future, where moisture-temperature interactions are proposed to change drastically.

To our knowledge, information on the climate warming effects on the possible behavior and dynamics of soil inorganic N pools (Bai *et al.*, 2013) and SOC dynamics is unavailable. Therefore, understanding possible behavior of soil inorganic N pools in relation to changing climate is required for its implications for future SOC dynamics and its prospective use in the management of our agro-ecosystems. Moreover, addition of this understanding to climate models of terrestrial C cycling may bring realistic predictions of the future climate. Therefore, a thorough exploration of the aforesaid global relationships under varied soil moisture-temperature interactions is critically required for the accurate prediction of future global climate and improved SOC management. Because SOM mineralization and N availability are closely linked with soil microbial community and processes, the latter also needs to be considered in such studies.

SOIL C DYNAMICS AND MICROBIAL COMMUNITY DYNAMICS IN SOIL FUNCTIONING

The drastic changes in soil C dynamics under changing climate have been attributed to the considerable

impacts of altered moisture and temperature regimes on the structure and function of soil microbial community. It is reported that a change in soil microbial community affects soil ecological functioning (Delgado-Baquerizo *et al.*, 2016). The differential temporal variability and patterns of soil microbial community structure under various land uses, even under the same climatic conditions, are suggested to be of greater ecological significance than anticipated previously (Lauber *et al.*, 2013). This indicates that even a small variation in the microbial community structure in soil under changing climate may considerably affect ecosystem functioning. Despite such importance, how belowground microbial communities acclimate and adapt to rapid environmental changes or how they can be prompted to do so is still unexplored (Bardgett and van der Putten, 2014). In this context, the importance of compositional differences in soil microbial community is also scarcely studied.

INTERACTION STUDIES FOR UNDERSTANDING SOIL C DYNAMICS

The interactions among C cycle, N cycle, and the climate need critical exploration under changing environments to improve management of ecosystem functioning (Gruber and Galloway, 2008). Moreover, recent studies advocate that microbe-mediated feedbacks might hold crucial importance in this regard (Bardgett *et al.*, 2008; Singh *et al.*, 2010). The microbial responses to climate warming are primarily linked to the moisture regime (Peltoniemi *et al.*, 2015), which primarily determines SOM decomposition. In this regard, the microbial processes playing key roles in greenhouse gaseous efflux are proposed to respond rapidly to such global changes (Singh *et al.*, 2010). Climate change mitigation by reduced SOC decomposition and soil CO₂ emissions *via* the management of these soil microbial processes may have important future prospects (Singh *et al.*, 2010). Therefore, the thorough understanding of mechanisms through which microorganisms might regulate terrestrial CO₂ efflux is critically required (Singh *et al.*, 2010). In this context, soil microbial community, having a crucial role in determining soil CO₂ emissions (*i.e.*, broad functioning) and nitrification (*i.e.*, specialized functioning), might hold crucial significance (Delgado-Baquerizo *et al.*, 2016). Soil CO₂ emissions have shown a closer relationship with specific compositional changes in soil bacterial community and associated soil processes (Moraes *et al.*, 1995). It is believed that compositional changes in soil microbial community resulting from variations

in soil temperature, moisture, and/or their interactions under changing climatic conditions may alter SOM decomposition patterns through some unknown mechanisms, which are not yet considered under current simulation models (Zogg *et al.*, 1997). It is surprising that despite the predominance of soil microbial community and processes in determining biosphere functioning, their potential and prospective roles in the management of future climate are still highly underestimated and unexplored.

In order to manage SOC dynamics, the consideration of complex interactions of soil microorganisms with other biotic and abiotic factors is warranted (Singh *et al.*, 2010). It was observed that biotic-abiotic interactions strongly affect the microbial community structure, which in turn governs soil ecological processes (Singh *et al.*, 2009). Soil microorganisms are reported to regulate SOC dynamics by following three feedback mechanisms: i) changed soil microbial community composition, which leads to reduced temperature sensitivity of heterotrophic respiration; ii) the differential induction of genes leading to the decomposition of labile rather than recalcitrant C, which maintains the long-term stability and storage of SOC, and iii) the effects on soil nutrient cycling processes (Reay *et al.*, 2008). We found that the microbial community changes affecting N cycling processes were central to the management of SOC dynamics under changing climatic conditions. Therefore, it is strongly advocated that we can appropriately manage soil C dynamics *via* the management of soil microbial community associated with inorganic N dynamics, as the latter plays a critical role in SOC mineralization based on recent researches (Srivastava *et al.*, 2015, 2016a, c, d; Luo *et al.*, 2016).

Literature studies indicate that researches on the microbial functional guilds related to N cycle, relative to agro-ecosystem functioning, are scarcely explored (Hallin *et al.*, 2009). It is proposed that long-term meticulous agro-management considering microbial functional guilds and linked processes in soil may ultimately restore the lost equilibrium in soil N dynamics and linked C dynamics (Canfield *et al.*, 2010). Similarly, the relative significance of functional microbial diversity in determining the terrestrial ecosystem response to upcoming environmental changes is also unexplored. Moreover, how extrinsic factors modulate this diversity-function relationship needs investigation (Bardgett and van der Putten, 2014). It has been observed that the sizes of microbial functional guilds and total bacterial community are greatly affected by fertilization regimes (Hallin *et al.*, 2009). Recently, it has been found that the soil microbial com-

munity composition is relatively more important than diversity (Rampelotto *et al.*, 2013). This is ascribed to the fact that microbial community composition, rather than richness, is important in specific microbial processes (Peter *et al.*, 2011). These compositional shifts in soil bacterial community correlate with soil chemical properties and microbial functions (Lopes *et al.*, 2015). It is plausible that an in-depth understanding of such interrelationships, which may have implications for soil ecological functioning, would help in the fine-tuned management of SOC dynamics. Therefore, multi-factorial studies to understand the interactions between soil microbial responses (structural and functional) associated with N cycling and SOC dynamics are urgently needed in the present warming scenario (Bardgett *et al.*, 2008; Björnsne *et al.*, 2014). This would help in the reliable prediction of future climate and the management of ecosystem responses to future climate change.

RELATIVE IMPORTANCE OF FACTORS AND PROCESSES IN SOIL C DYNAMICS

Worldwide, it is increasingly being recognized that soil attributes may have relative significance in governing SOC dynamics and soil multi-functionality (Delgado-Baquerizo *et al.*, 2016). It is proposed that climate warming may considerably affect the relative importance of the frequency and composition of microbial functional groups, their trophic interactions, and the processes that control these interactions

(Chakraborty *et al.*, 2012). This may be attributed to the impact of climate warming on the physiology of individual microbial groups (Mosier *et al.*, 2015) as well as functional community, which are specifically associated with N cycling (Yergeau *et al.*, 2012). Warming may affect the turnover of inorganic N pools, particularly due to its impact on the wetting-drying cycle (Morillas *et al.*, 2013), and thus, may have implications for SOC dynamics. These changes in soil properties may directly as well as indirectly (*via* influencing microbial abundance) affect soil respiration (Delgado-Baquerizo *et al.*, 2016). Recently, Srivastava *et al.* (2015, 2016c, d) observed that a relative shift in NH_4^+ -N and NO_3^- -N availabilities in soil might determine soil respiration, which may be crucial to proposed positive climate change feedback of C cycle. Therefore, it is highly possible that a relative shift in the associated microbial processes in soil (*i.e.*, ammonification, nitrification, and/or differential immobilization), which govern NH_4^+ -N and NO_3^- -N availabilities, may also have functional significance in the changing climate (Srivastava *et al.*, 2016a, b). Therefore, a thorough investigation of the relative changes in NH_4^+ -N and NO_3^- -N availabilities and associated microbial processes in soil in relation to SOC dynamics is highly required across management, ecosystem, and climate (Figs. 1 and 2). It may play a significant role in the mitigation of global climate change by acting as an indicator of soil C dynamics.

The differential impacts of climate change on NH_4^+ -N and NO_3^- -N availabilities are proposed to potentially

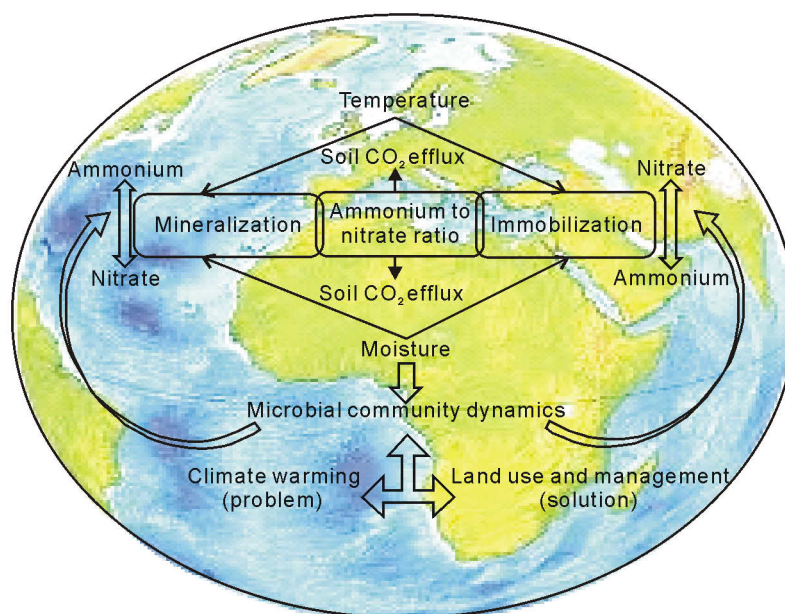


Fig. 1 A global perspective of the major and emergent determinants of soil carbon dynamics.

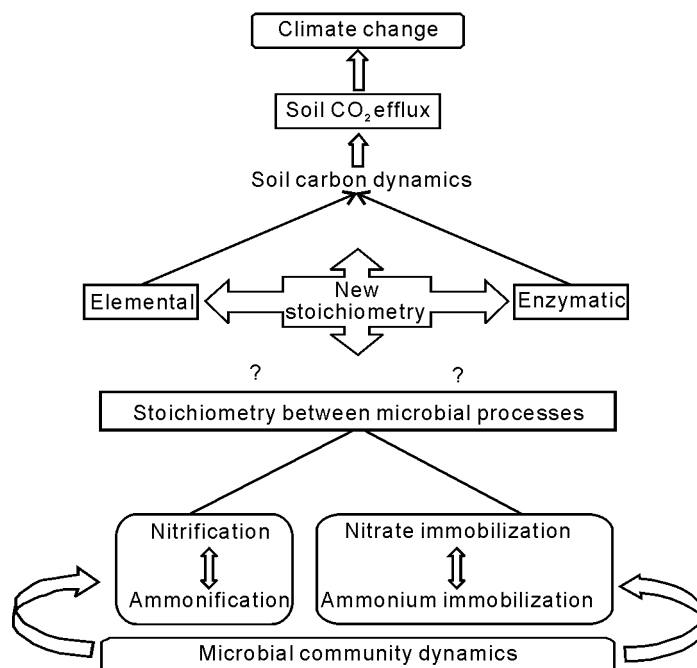


Fig. 2 A mechanistic representation of microbial-mediated interactions between soil nitrogen availability and carbon dynamics by developing new stoichiometric relations under present climate change scenarios.

shift the NH_4^+ -N to NO_3^- -N ratio in soil, which may consequently affect ecosystem properties such as SOC turnover (Bijlsma *et al.*, 2000). These two inorganic N pools variably influence the rate of SOC cycling, and thus, soil CO_2 efflux *via* bringing chemical and biological changes in soil (Min *et al.*, 2011; Yang *et al.*, 2014; Srivastava *et al.*, 2015, 2016a, d). The change in nutrient stoichiometry may drive a shift in bacterial diversity and composition in soil (Delgado-Baquerizo *et al.*, 2013). Thus, such changes in soil nutrient properties may directly as well as indirectly (*via* affecting microbial abundance) affect soil CO_2 efflux. In Cruz *et al.* (2003), the relative shifts in soil NH_4^+ -N and NO_3^- -N availabilities under the changing environmental regime were suggested to affect ecosystem functions in different ways. For example, they may significantly affect SOC dynamics, owing to their contrasting effects on SOC turnover (Currey *et al.*, 2010; Luo *et al.*, 2016).

The physiological alteration in specific microbial functional groups in soil may have significant effects on soil nutrient dynamics. It has been observed that changes in soil microbial community under changing moisture-temperature interactions may affect soil nitrification process (Delgado-Baquerizo *et al.*, 2016), which may hold crucial significance under changing climate. For example, a shift in soil microbial community associated with nitrification has been identified as a mechanism behind an exotic plant invasion (Hawkes *et al.*, 2005). Invasive plant species alter the ecosystem N

budget in soil by: i) increasing gross nitrification and ii) increasing the abundance and changing the composition of ammonia-oxidizing bacteria (Hawkes *et al.*, 2005). This suggests that a comprehensive understanding of the relative availability of inorganic N pools in relation to changes in soil microbial community and linked processes may have a significant role in soil ecological functioning, such as soil C dynamics.

MANAGEMENT OF MICROBIAL BEHAVIOR FOR IMPROVED SOC DYNAMICS

Recent studies advocate that biological controls predominate over chemical recalcitrance (*i.e.*, molecular structure) with regard to SOM stability and dynamics (Schmidt *et al.*, 2011). Soil organic matter variations are highly related to microorganisms, as they have a primary role in nutrient cycling and SOM turnover in soil (Paul and Clark, 1989; Trasar-Cepeda *et al.*, 1998; Fließbach and Mäder, 2000; Chu *et al.*, 2007; Ryan *et al.*, 2009). It is proposed that we may potentially manage our future climate and soil multi-functionality, if we holistically understand how soil C and N dynamics would respond to changing moisture-temperature interactions in soil. In this regard, the relative availability of inorganic N pools and associated microbial processes (*i.e.*, nitrification and immobilization) in soil might play crucial roles (Fig. 1). In an incubation experiment, the variations in NO_3^- -N and NH_4^+ -N availa-

bilities in soil over time were significantly affected by soil moisture and temperature and their interactions (Kowalenko and Cameron, 1976). This indicated that the often-neglected interactions between soil moisture and temperature might affect microbial processes related to the availabilities and dynamics of NH_4^+ -N and NO_3^- -N in soil. The optimum soil moisture for the activity of a nitrifying population was found to be temperature-dependent (Kowalenko and Cameron, 1976). Srivastava *et al.* (2015) observed that the relative availabilities of NH_4^+ -N and NO_3^- -N in soil might represent the integrative effects of moisture-temperature interactions on soil microbial community dynamics under long-term organic management. Interestingly, varying NH_4^+ -N to NO_3^- -N ratios in soil have shown their impacts on soil nitrification processes (Lang and Elliott, 1991)

NITRIFICATION AND IMMOBILIZATION PROCESSES IN SOC DYNAMICS

Nitrification process could be a critical control point in SOC accumulation and dynamics under changing climate. It appears to primarily determine soil ecological functioning than ammonification (Luo *et al.*, 2016). This might be attributed to its relatively higher sensitivity to changes in soil moisture and temperature than that of ammonification (Jha *et al.*, 1996). Moreover, the response of nitrification process to moisture depends on its interaction with temperature. The higher rate of nitrification potentially increases soil N loss *via* leaching and denitrification, which affect soil quality as stable/less mobile soil NH_4^+ -N is converted to mobile NO_2^- -N and NO_3^- -N (Müller *et al.*, 2003). Additionally, higher nitrification rate and consequent nitrate availability in soil increase SOM decomposition and CO_2 emissions from soil (Srivastava *et al.*, 2015, 2016a, b; Luo *et al.*, 2016), and detrimentally affect agro-ecosystem functioning (Subbarao *et al.*, 2013). This suggests that microbe-mediated regulation of nitrification or NO_3^- -N availability in soil might be of considerable importance to SOC dynamics under changing climate or moisture-temperature interactions.

It is advocated that nitrification process in soil could be managed through appropriate land use and management (Srivastava *et al.*, 2015). A significant negative effect of organic fertilizers has been observed on the microbe-mediated nitrification process and, consequently, on NO_3^- -N availability in soil (Wang *et al.*, 2015). Srivastava *et al.* (2015) also proposed that long-term organic fertilization regulates SOC dynamics by efficiently moderating nitrification and NO_3^- -N availability in soil, even under increased warming conditions. This is attributed to the fact that organic fertiliza-

tion promotes adaptive changes in soil microbial functional community, particularly those associated with the nitrification process. Biochar amendment has also been found to reduce the NO_3^- -N availability in soil (Zheng *et al.*, 2012). It has been reported that a change in land use considerably alters soil ecological processes, affecting specific bacterial groups (*e.g.*, those associated with nitrification) in soil (Rampelotto *et al.*, 2013). A continuous decrease in the net nitrification rate (to reduce soil N loss) after 20 years in a C-accumulating ecosystem indicated the inverse relationship between nitrification and soil C dynamics (Piccolo *et al.*, 1994). Land use change was found to alter soil NH_4^+ -N to NO_3^- -N ratio by possibly affecting microbial functional groups associated with nitrification, with higher values indicating the improved soil C dynamics (Srivastava *et al.*, 2016a). Some observations provide us with a crucial insight into the biogeochemical processes, with a global pattern in ecological stoichiometry and SOM storage (Sinsabaugh *et al.*, 2008). Also, their linkage has been found affected by soil pH and substrate availability. For example, the enzymatic potential for labile C decomposition has been observed to be linked to the stoichiometry of soil microbial nutrient demands, substrate availability, and soil pH (Sinsabaugh *et al.*, 2008); however, that of recalcitrant C which is primarily responsible for SOC accumulation was strongly related to soil pH (Sinsabaugh *et al.*, 2008). This strengthens our assumption that the microbe-mediated nitrification process, which is also primarily determined by soil pH, might play a major role in SOC dynamics.

Nitrogen immobilization may also be important when determining ecological functioning in addition to denitrification, as it is also responsible for the disappearance of NO_3^- -N from soil (Khalil *et al.*, 2004). Lower NO_3^- -N immobilization in agro-ecosystems has been proposed to reduce soil C storage and increase greenhouse gas emissions due to faster C mineralization (Mariano *et al.*, 2016). The differential immobilization of NH_4^+ -N and NO_3^- -N may determine their relative availabilities in soil, depending on the management. It has been observed that amendment with indigenous plant residues induces N immobilization in most soils (Karyotis *et al.*, 2006), depending on the amount of application. Agro-ecosystems receiving variable organic input have both variable rates of N transformation and fates of NH_4^+ -N and NO_3^- -N in soil (Burger and Jackson, 2003). Interestingly, the high-input agro-ecosystems release NH_4^+ -N gradually and support a relatively active microbial biomass with greater N demand, which is met primarily by soil NO_3^- -N immobilization in the biomass (Burger and Jackson,

2003). This shows that current models highly underestimate the role of microbial community in checking NO_3^- -N loss from soil based on its immobilization in biomass (Wallenstein *et al.*, 2006). Organic fertilizers have also been observed to increase the immobilization rate of NH_4^+ -N and, thus, prevent NO_3^- -N build-up in soil by affecting nitrifier activities *via* limiting NH_4^+ -N availability (Wang *et al.*, 2015). This indicates that immobilization processes might also be related to nitrification to a considerable extent, which is yet unexplored for its implications for soil C dynamics. Therefore, we advocate the appropriate consideration of microbial processes (nitrification and immobilization) associated with the availability of inorganic N pools in studies on soil C dynamics and management. This might resolve the enigma of complex relationships between soil N availability and SOC dynamics, particularly under variable moisture-temperature interactions.

RELATIVE SIGNIFICANCE OF INORGANIC N POOLS AND MICROBIAL PROCESSES IN SOIL C DYNAMICS

It is highly plausible that variable responses of NO_3^- -N and NH_4^+ -N under changing moisture-temperature interactions may influence their relative availabilities in soil. Most likely, the influences would be rooted in shifting microbial composition and linked functions (such as nitrification and immobilization). This indicates that a shift in the stoichiometric balance between soil microbial processes (between nitrification and ammonification and between NH_4^+ -N and NO_3^- -N immobilization) might be of crucial importance to soil C dynamics (Fig. 2). However, whether this shift may show variations depending on management, ecosystem, and climate requires exploration.

Soil microbial community may show adaptations to climate change (Singh *et al.*, 2010; Romero-Olivares *et al.*, 2017). The latter might be mediated by microbial acclimation, adaptation, and community changes in

addition to reduction in labile C, which may ameliorate the warming effects on soil respiration in the long term (Romero-Olivares *et al.*, 2017). Soil microbial adaptation to wet and dry cycles has been reported to occur even during the growing period. The changes in soil moisture due to climate warming may lead to a shift in microbial community composition, process rates, or both (Lundquist *et al.*, 1999). A change in the relative availabilities of NH_4^+ -N and NO_3^- -N in soil, in addition to their absolute availabilities, appears to be a function of interactions among soil microbial attributes, management, and climate (*i.e.*, moisture-temperature interactions) (Srivastava *et al.*, 2015). Therefore, the change could be identified as an integrative soil functional trait, which may indicate the nature of SOC dynamics in soil under climate change scenarios (Srivastava *et al.*, 2015). Its higher value has been reported to be beneficial for soil C dynamics and soil quality, as it indicates soil C protection from decomposition (Srivastava *et al.*, 2015; Luo *et al.*, 2016). Limited studies in the literature show that soil NH_4^+ -N to NO_3^- -N ratios are also related to various other soil properties (Table II). This suggests that the recovery of a specific balance between N (NH_4^+ -N and NO_3^- -N) pools might be a mechanism of conservative N cycle, which improves soil C dynamics (Pellegrini *et al.*, 2014). Therefore, a thorough assessment and validation of changes in the relative availability of inorganic N pools as potential indicators of soil C dynamics would help in the fine-tuned management of SOC dynamics in agroecosystems *via* appropriate amalgamation of management practices, which may thus help in the mitigation of climate change and the improvement of soil infertility. Furthermore, it would help explain the complex relationship between N availability and SOC dynamics, which has been primarily responsible for the dilemma associated with the impact of climate warming on SOC dynamics. Therefore, its inclusion in current climate models may refine future climate predictions and may

TABLE II

Soil properties other than CO_2 efflux showing linkage with soil NH_4^+ -N to NO_3^- -N ratio

Soil properties	Reference
Nitrification	Lang and Elliott, 1991
Moisture	Wood and Silver, 2012
Moisture, temperature, and microbial biomass C	Srivastava <i>et al.</i> , 2015
Biological processes	Liang <i>et al.</i> , 2016
Microbial biomass C, microbial biomass C/N ratio, and macro-aggregate physical stability and chemical stability	Srivastava <i>et al.</i> , 2017
Microbial biomass C, bulk density, aggregate-size distribution, labile C concentration, and stock in meso- and micro-aggregates	Srivastava <i>et al.</i> , 2016b
Phenol oxidase activity	Luo <i>et al.</i> , 2016

help in devising the accurate adaptation and mitigation measures.

POSSIBLE NEW ECOLOGICAL STOICHIOMETRIC RELATIONSHIPS OF SIGNIFICANCE TO SOIL C DYNAMICS

Ecological stoichiometry (*i.e.*, elemental and enzymatic) is widely known for its fundamental importance in determining ecosystem processes and functioning (biogeochemical nutrient cycling, decomposition, *etc.*) (Sinsabaugh *et al.*, 2008). Climate change is proposed to change the stoichiometric balance between biogeochemical cycles of nutrients, which may potentially affect the relative availability of nutrients in soil (Delgado-Baquerizo *et al.*, 2013). More specifically, CO₂ enrichment under changing climate may increase the soil NH₄⁺-N to NO₃⁻-N ratio (Liang *et al.*, 2016). This changed NH₄⁺-N to NO₃⁻-N ratio and subsequent biological processes may result in changes in soil micro-environments, above and belowground community structures, and associated interactions, which could potentially affect terrestrial biogeochemical cycles. Therefore, it is highly plausible from the discussion in this review that the stoichiometric balance between nutrient availability (*i.e.*, N pools) and linked microbial processes in soil may have some crucial roles in determining SOC decomposition and CO₂ emissions under climate change (Fig. 2). Recently, nutrient stoichiometry has been found to be a strong predictor of soil bacterial diversity and composition at a regional scale (Delgado-Baquerizo *et al.*, 2017). Therefore, understanding the relative importance of soil physicochemical properties and associated microbial processes in determining soil multi-functionality and ecological functioning may considerably improve our future management strategies (Delgado-Baquerizo *et al.*, 2016; Srivastava *et al.*, 2016a, b, d). Moreover, the observations in the present review hold significant importance, because the relationship between microbial processes within an element's biogeochemical cycle has never been identified and discussed in relation to SOC dynamics under climate change scenarios. In some studies, however, changes in land use have been suggested to alter the stoichiometric balance of nutrient cycling processes (Davidson *et al.*, 2007). As the drivers of soil CO₂ flux in semiarid ecosystems are often similar to those observed in more humid ecosystems, the assessment of stoichiometry between soil NH₄⁺-N and NO₃⁻-N availabilities and associated microbial processes across ecosystems may be of significant importance to soil C management across the world (Sullivan *et al.*, 2015).

CONCLUSIONS AND FUTURE RESEARCH PERSPECTIVES

The transformed soil inorganic N dynamics have been at the core of changes in soil C dynamics. It is believed that SOC dynamics are going to change dramatically under changing soil moisture-temperature interactions due to climate change, most possibly due to shifting N availability in soil. However, we still have a limited understanding of the future course of the climate due to complex and ambiguous interactions between soil N availability and SOC dynamics. We can manage our soil ecosystems and future climate only if we have an in-depth understanding of the interactions among the availabilities of soil inorganic N pools (and associated microbial processes), soil C dynamics, and moisture-temperature interactions. In this regard, an in-depth literature survey suggests that climate change may affect soil C dynamics by affecting microbial community and processes associated with the dynamics of inorganic N pools under the interactive effects of soil moisture and temperature. Additionally, the relative shift in soil microbial processes (*i.e.*, ammonification/nitrification and NO₃⁻-N immobilization/NH₄⁺-N immobilization) may be of significant importance to soil C dynamics under changing climate. We observed that stoichiometric relationships between soil inorganic N pools (*i.e.*, NH₄⁺-N and NO₃⁻-N) and associated microbial processes could be used as indicators in monitoring soil C dynamics. Literature studies indicate that the stoichiometry of microbial processes, which keeps higher NH₄⁺-N and NO₃⁻-N availabilities in soil, beneficially promote soil C dynamics and sequestration. This suggests that recovery of a specific balance in N pools might be a mechanism of the conservative N cycle, which improves soil functioning. Therefore, we strongly advocate a new set of multi-faceted experiments (considering the relative roles of inorganic N pools and microbial processes, moisture-temperature interactions, SOC, and CO₂ efflux) to understand SOC dynamics. This would help to improve the management of agro-ecosystem functioning and climate stability *via* enhanced C protection in soil.

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