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Land-use and management practices affect soil ammonia oxidiser community structure, activity and connectedness

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ABSTRACT

Factors affecting community structure and connectivity within systems are crucial for provision of microbial ecosystem-services (e.g., soil nitrogen cycling), but what these factors are and how they are affected by land-use and management is poorly understood. Biogeochemical cycles are disrupted in agricultural-systems, providing an excellent opportunity to investigate the roles of management and land-use in shaping microbial communities and ecosystem function. We investigated soil ammonia oxidisers under different cropping practices and within a nearby grassy woodland; representing a gradient of physical/chemical disturbance. Land-use and management practices resulted in significant differences in community structure. Major differences in system connectivity were observed between land-uses, but not within management practices, indicating that land-use change is the major driver of ecosystem change, rather than management within land-uses. Agricultural ammonia oxidiser communities appeared to be less well connected and rely less on biotic interactions than those in natural systems, perhaps a reflection of the extent to which natural feedback loops are disturbed in managed systems. Smaller, but significant, differences were also evident between management treatments. Despite differences in community structure and connectivity there was, however, no significant effect on potential N-cycle rates, indicating that although land-use and management impacts may drive community changes, these do not necessarily translate into changes in functional capacity.

1. Introduction

Soil biota are responsible for many fundamental ecological processes occurring in both natural and managed systems (Reynolds et al., 2003). Anthropogenic activities can influence these processes. Elucidating links between biological community composition and functional capacity is therefore important to understanding and managing ecosystem service provision. Agricultural systems are managed to optimise production conditions, and as such natural biogeochemical cycles are often altered by specific management interventions. For example, nutrients (fertiliser pulses) are added, water-cycling is disrupted and resources are removed from the system (crops harvested), resulting in potentially greater imbalance in highly managed systems. Such imbalance may be caused by removal of the need for specific components of otherwise naturally connected steps in biogeochemical cycles, when these steps are circumvented by agricultural additions (e.g., N fertilizers). Such imbalance may present as reduced connectivity between system components (Raes and Bork, 2008). Connectivity between ecosystem parts may be imputed by associations between organisms (e.g., competition and mutualisms may present as negatively or positively correlated associations), between organisms and nutrients/metabolites (e.g., associations between organisms and biogeochemically cycled substances) and between organisms the system's physical and geographical heterogeneity (e.g., associations between organisms and soil edaphic factors) (Raes and Bork, 2008). Despite the type of interventions outlined above, intensively managed systems are still subject to a range of

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microbially mediated processes influencing C and N flow and, therefore, overall sustainability (Johansson et al., 2004; Brussaard et al., 2007; Osler and Sommerkorn, 2007). Previous studies have reported contrasting findings with respect to effects of long term agricultural practices on soil microbial communities (Bissett et al., 2011), resulting in a lack of clarity about how constant disturbance, including specific management interventions, in intensively managed ecosystems impacts soil processes.

Nitrification (the oxidation of ammonium to nitrate via a two-step process ($NH_4 \rightarrow NO_2 \rightarrow NO_3$)) is important in both managed and natural systems, and is often tightly connected to other components of the nitrogen cycle (e.g., denitrification). The initial step in the nitrification pathway is completed by ammonia oxidisers (AO), comprising ammonia oxidising bacteria (AOB) and archaea (AOA). In natural systems nitrification may be beneficial for the supply of nitrate to plants as a preferred form of N, decrease N loss by reducing ammonia volatilization, lower ammonium toxicity and increase the release of fixed NH_4^+ via the removal of exchangeable NH_4^+. In many managed systems, however, nitrification is often seen as a non-beneficial process that may, for example, directly by increasing soil acidification or indirectly facilitating significant N loss via leaching of nitrate or increased N_2O or N_2 emissions through denitrification. In managed systems, therefore, the N cycle is managed by N additions and measures to either decrease or slow N conversions that may result in N loss.

Previous studies have suggested that AOB populations are found in greater abundance in agricultural soils (soils with N fertiliser inputs, higher soil disturbance) (Bruns et al., 1999; Enwall et al., 2007; Cavagnaro et al., 2008; Di et al., 2010; Hayden et al., 2010), while AOA populations are numerically more important in lower N (Martens-Habbena et al., 2009), acidic and undisturbed soils (Nicol et al., 2008). In previous surveys of AOB in Australian soils both Colloff et al. (2008) and Hayden et al. (2010) found that AOB amoA copy number was often, but not always, higher in managed sites, with Hayden et al. (2010) further suggesting that this result was dependent upon soil type. It has also been suggested that potential nitrification rates are dependent upon substrate availability and edaphic factors, rather than AOA or AOB dominance (Norton et al., 2011).

Tillage has been shown to stimulate AOB and nitrification via aeration of the soil matrix (Cavagnaro et al., 2008). Effects of N fertilisation on AOB and AOA biomass and potential nitrification rates have been mixed. For example, Kelly et al. (2011) show no response to synthetic fertilisers (urea-N), but a response of AOA to biosolids, while Di et al. (2009) reported that AOB, not AOA responded to urea-N additions in managed grassland soils. It has further been suggested that within both AOA and AOB physiological diversity is sufficient to allow functional representation of both groups in most soils and that attributing dominance of one or the other to a single or few factors is difficult (Prosser and Nicol, 2012).

Current land-use practices within intensively managed systems focus on minimising soil disturbance to maximise soil health, but the true efficacy of these practices, and their impact on ammonia oxidiser communities and function, is not well understood. We utilised a long-term field trial to study effects of different land-use, and different management practices within intensively managed agricultural systems, on soil AO community structure and functional (nitrification) potential. We assessed soil physicochemical properties, AO community structure and N transformation rates in soils from two different land-uses (agricultural and non-agricultural) and three management practices within the agricultural land-use [till (Incorp), no-till (SSDD), and till plus nutrients (Incorp + N)] to address our hypotheses that both land-use and land-management would affect AO community structure and function and that the disturbance to natural cycles in intensively managed systems would result in system imbalance. Our objective was, therefore, to investigate AO abundance, community structure and function in response to land-use and management interventions (soil physical disturbance and N additions).

2. Materials and methods

2.1. Site description

Agricultural treatment samples were collected from a long-term (>20 yr) wheat tillage site at Harden, NSW, Australia (−34.523083, 148.298686) (Kirkegaard et al., 1994). Treatments comprised a randomised block design (three blocks per treatment, individual blocks 30 m × 6 m). We utilised two of the original treatments imposed in 1990 (Kirkegaard et al., 1994) and one treatment initiated in 2007 (Bissett et al., 2011). The two oldest treatments comprised Stubble Incorporation (Incorp) which used annual tillage to incorporate crop residue, and the no-till treatment, Stand Stubble Direct Drill (SSDD). The newer treatment comprised the Incorp treatment plus the addition of nutrients (Incorp + N) at the time of stubble incorporation. Nutrient addition was designed to achieve a C:N:P:S ratio thought to be required for maximum soil C sequestration (Himes, 1998) and the conversion of sequestered C into humus (Kirkby et al., 2011). This consisted of the addition of 25.6 kg N (ammonium), 21.5 kg P, 18.8 kg S to 10 tonnes/ha of wheat residue at the time (T1) of incorporation (Fig. 1).

Soil was classified as red chromosol (Kirkegaard et al., 1994) (refer to Table 1 for soil chemical characteristics). The site has been managed in a break-crop/wheat rotation since 1990; however during the period 2007 to 2009 three consecutive wheat crops were grown. Agricultural treatments were sown to wheat (87 kg/ha) in May, using a narrow tne seeder and press-wheels (18 cm row spacing) and with 120 kg/ha of starter fertiliser (Granulok® 15 Incitec Pivot, Melbourne, Australia − 20 kgP/ha, 15 kgN/ha, 15 kg S/ha).

The non-agricultural treatment (NC) comprised open woodland, dominated by eucalypts and a grassy understory. The NC site had never previously been cultivated or fertilised, but had been grazed intermittently, and was located approximately 4 km from the agricultural treatments (−34.497632, 148.316213). The NC treatment also comprised three replicate blocks. All soils experienced similar climatic and geological conditions.

2.2. Sample collection

Samples were collected as detailed in Bissett et al. (2011). Soil samples were collected at 4 times representing a full crop cycle: T1 = February 2009, crop residue incorporation for Incorp treatments and nutrient addition for Incorp + N; T2 = March 2009, pre-crop; T3 = April 2009, early crop; T4 = September 2009, mature crop (Fig. 1). The crop was sown just prior to T3. For each time-point, samples comprised 4 cores (50 × 150 mm) taken from each replicate block. These samples were then bulked to give one sample per replicate block per treatment ($n = 3$). Within four hours of collection, soils were sieved and homogenized for nucleic acid extraction (~50 g, −80 °C), soil chemical and physical properties, N-cycling "actual" and "potential" rates and, N and P determination. All assays were started as soon as possible after sample collection, within 24 h.

2.3. Soil chemical and physical properties

Soil moisture (%GWC) was measured gravimetrically (Rayment and Higginson, 1992). Soil total organic matter (OM) was approximated by the loss on ignition (LOI) method (Rowell, 1994), P