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The impact of crop rotation on soil microbial diversity: A meta-analysis

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ABSTRACT

Agricultural intensification can involve the simplification of agroecosystems to crop monocultures while the practices of crop rotation, intercropping and companion planting maintain some crop diversity over time and space. It is generally postulated that reduced diversity can have an impact on ecosystem function. Here we determine whether decreased aboveground crop diversity affects belowground microbial biodiversity by conducting a meta-analysis of studies comparing monocultures and crop rotations. We based taxonomic richness and diversity indices on both molecular and biochemical fingerprinting methods. Soils under a higher diversity of crops in rotation produced higher microbial richness (+15.11%, n = 26) and diversity (+3.36%, n = 43) scores. This effect was significantly influenced by the proxy and methodology used where pyrosequencing produced higher richness scores compared to fingerprinting methods. Longer study trials produced larger increases in microbial richness, although the opposite was true for microbial diversity. The addition of legumes to rotation had no consistent effects on microbial diversity or richness. Whether the overall rotation-effect on microbial diversity promotes ecosystem functioning in terms of nutrient cycling and resilience to stress remains unclear. Future studies that incorporate next-generation sequencing techniques will help to elucidate complex microbial community structures and specific functional niches in agroecosystems.

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1. Introduction

The intensification of conventional agricultural practices is threatening ecosystem services and agroecosystem sustainability through soil erosion, agro-chemical pollution of groundwater,

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release of green-house gases and biodiversity loss (Tilman et al., 2001). This is causing a paradigm shift toward sustainability, characterized by practices and concepts such as organic agriculture (Badgley et al., 2007), agroecology (Rosset and Altieri, 1997; Thomas and Kevan, 1993), functional agrobiodiversity (Wood and Lenné, 1999) and conservation agriculture that includes crop rotation (Hobbs et al., 2008). The historical adoption of crop rotations was largely motivated by the associated yield increase in the cash crop (Bullock, 1992) attributed to enhanced agro-ecosystem function in terms of increased soil fertility (particularly when leguminous plants are used in rotation), maintenance of soil structure, disruption of pest cycles and weed suppression (Smith et al., 2008). These processes are mediated largely by soil microorganisms through their complex biochemical processes (Kennedy and Smith, 1995; Kennedy, 1999; Parkinson and Coleman, 1991).

Within the broader context of diversity-ecosystem function theory, an increase in plant species number within a crop rotation system may result in a concomitant increase in agroecosystem function (Smith et al., 2008; Vitousek and Hooper, 1994). However, the mechanism behind this positive effect may be attributed to singular key-stone species such as N_2-fixing legumes (the selection effect) or due to the facilitation and niche differentiation associated with a number of species (the complementarity effect) (Hooper et al., 2005). It is often the case that both these mechanisms are at work which gives support for the decoupling and coupling of biodiversity with function. It is less well known whether aboveground crop diversity is coupled to belowground microbial biodiversity and how this affects function.

The primary drivers of microbial diversity include edaphic variables such as soil pH and moisture, yet plant diversity is also now recognised as an important driver of soil microbial diversity (Berg and Smalla, 2009). It has been posited that management practices such as crop rotation, through increasing aboveground biodiversity, can result in corresponding increases in diversity belowground (Hooper et al., 2000). Soil microbial communities in the rhizosphere respond differently to root exudates associated with various crops (Costa et al., 2006; Wardle et al., 2004) and these rhizosphere communities can have an impact on the bulk soil microbiome (Kent and Triplett, 2002). In addition, crop rotations lead to a greater abundance and diversity of plant litter, which in turn can support a greater diversity of microbial decomposers (Kennedy, 1999). Thus increases in microbial diversity may not only be a direct effect of plant diversity, but due to the associated increases in soil organic matter caused by increased ground cover in rotations (Zak et al., 2003).

There is conflicting evidence in the literature addressing the relationship between above and belowground biodiversity in agroecosystems. A number of studies have shown microbial diversity to increase, not change, and decrease under crop rotations. For example, Lupwayi et al. (1998) discovered that microbial diversity, based on community level substrate utilisation, was significantly higher under a rotation of wheat and clover or field peas than under continuous wheat. However, Navarro-Noya et al. (2013) found that crop management (continuous maize versus maize-wheat rotation) had no effect on soil microbial diversity. Finally, Yin et al. (2010) found that incorporating soy beans into rotation with wheat decreased richness and Shannon's diversity indices in conventional tilled plots when compared to continuous wheat.

Here we assess whether increased crop diversity leads to increased soil microbial diversity and richness using a meta-analysis of the literature. A problem in reviewing independent studies is that differences between study conditions and abiotic factors may obscure the question of interest. The advantage of meta-analyses is that a relative measure of effect size (the treatment relative to a control or other comparison) allows for comparisons across varying geographical regions, experimental and abiotic conditions. (Hedges et al., 1999). Although originally developed for medical and social science reviews, meta-analysis has been adapted for application to many ecological and agricultural datasets in the literature (e.g., Johnson and Curtis, 2001; McDaniel et al., 2014; Tonitto et al., 2006).

2. Methods and materials

2.1. Meta-analysis criteria

The analysis requires that a treatment and control are defined in order to calculate a response ratio. For the purposes of this analysis, the control was defined as any annual cash crop that is grown in monoculture every season. The experimental treatment/s were defined as any crop rotation including the same cash crop and at least one other rotation crop. Studies were included that recorded taxonomic (using genetic fingerprinting methods) or functional proxy measures (using biochemical fingerprinting methods) of soil (free-living) microbial (bacterial and/or fungal and/or archaeal) diversity, including the Shannon's diversity index (Shannon and Weaver, 1969) and/or richness (Hill, 1973). These are the most commonly used measures of soil microbial diversity in agricultural studies (Spellerberg and Fedor, 2003). Species richness is defined as the number of unique taxonomic sub-units, and diversity as the richness and relative abundance of these sub-units as calculated with the Shannon's diversity index. Many studies were excluded because they did not (1) contain the control, experimental treatment/s and diversity measures as listed above, (2) contain purely agricultural cash crops, or (3) metadata was not available upon request. From the rejected studies, those that reported some measure of microbial diversity were collated according to whether they detected significant increase, decrease or no change in microbial diversity with an increase in crop diversity over time.

2.2. Literature search and data extraction

The literature was searched using electronic databases, including Google Scholar, AGRIS, ScienceDirect, Elsevier and Wiley by entering the following search terms used in various combinations: crop rotation, microbial diversity, microbial richness. The Boolean operators 'AND' and 'OR' were used to combine two separate searches and include alternative search terms. The following criteria were used to select studies: (1) only peer reviewed articles in journals; and (2) studies with sufficient sample size to determine both a mean and standard error. In addition, studies were also identified through a 'snowballing' technique where reference lists of acquired studies were searched for additional relevant studies. For some studies, Data Thief® (Tummers, 2006) software was used to extract values from figures within studies. In cases where diversity measures or variances were not reported, the corresponding authors were contacted to request this information.

A total of 20 studies met the selection criteria and were entered into a database containing the following categorical moderating variables: microbial analysis method (biochemical fingerprinting, molecular fingerprinting and pyrosequencing), number of crops in rotation (2 or 3), use of legume (yes or no), use of cover crop (yes or no), and trial length (1–5, 6–15 and >15 years) (S-1 in Supplementary material). Here cover crop is defined as a crop that is not harvested but produced to enrich some aspect of soil health. To account for differences between next generation sequencing and other microbial analysis methods, studies using biochemical fingerprinting [fatty acid methyl ester analysis (FAME) analysis, community-level physiological profiling (CLPP) and plate

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