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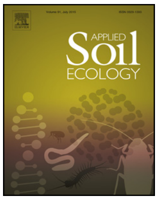

Conversion of grassland to arable decreases microbial diversity and alters community composition

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ABSTRACT

The rapid global conversion of biodiverse landscapes to intensively managed arable fields may decrease microbial diversity and threaten the long-term fertility of native soils. Previous laboratory and experimental studies provide conflicting results: some have recorded declines in overall microbial diversity and certain beneficial microorganisms under intensified cultivation while others report no change (or even increased) diversity. However, few studies have been carried out in actual agricultural fields. We analysed the soil metagenomic communities of 36 current and former grasslands in Oxfordshire, England using Illumina sequencing of the bacterial 16S and fungal ITS1 regions to examine how agricultural intensification alters native microbial communities and whether arable reversion can reverse these processes. We demonstrate that land-use change did not affect bacterial diversity or specific beneficial taxa (nitrogen-fixing bacteria and mycorrhizas). However, fungal diversity declined and certain microbiota known to be plant pathogens (e.g. *Olpidium*) were significantly more abundant on agriculturally improved fields. On sites where arable reversion took place, microbial communities were similar to those from unimproved grasslands although overall vegetation diversity and fungal richness were lower. The conservation of species-rich grasslands and their associated microbial diversity could therefore be a key resource for sustainable agriculture in the future.

1. Introduction

Soil is the basis of agricultural productivity; and yet agricultural soils are heavily degraded worldwide. For example, many agricultural soils are thin and extremely low in organic matter (Jones et al., 2012; Matson et al., 1997). However, the biotic component of soil is equally important and often overlooked. Given that just one gram of soil contains over 50,000 bacteria and fungi, which play a key role in plant health, soil fertility, and wider ecosystem functioning (Chaparro et al., 2012; Garbeva et al., 2004; Salles et al., 2006; Singh et al., 2014; Zak et al., 2003), protecting and restoring soil fauna on agricultural lands will be key to supporting sustainable food systems in the future (Brussaard et al., 2007; Mendes et al., 2013).

Natural ecosystems are the main reservoir of soil microbial diversity (Lee and Lee, 2013). For example, the microbiota from highly biodiverse ecosystems have been used in the development of new antibiotics, biofertilizers and even pigments (Balser et al., 2010; dos Reis Celestino et al., 2014). However, natural ecosystems around the world are being replaced by agricultural systems threatening this diversity and the potential for future products (Chapin et al., 2000). Certain processes associated with intensification, such as the use of inorganic fertilizers, are already known to affect microbial diversity. For example, previous research suggests that microbial diversity generally and the diversity of highly beneficial arbuscular mycorrhizal fungi (which provide their plant hosts with phosphorus) specifically, decline with the application of nitrogen (N), phosphorus (P) and potassium (K) (Gosling et al., 2006; Kiers et al., 2002; Oehl et al., 2010; Verbruggen et al., 2013). Addition of nutrients to the soil may also reduce the effectiveness of microbiota associated with plant-defence and nitrogen-fixation (Salles et al., 2006; Fox et al., 2007). However, to better understand the changes in microbial communities that take place under intensification, more detailed studies of specific systems in the field are needed that reflect the changes taking place in real landscapes.

In northern Europe agricultural intensification poses a particular threat to species-rich grasslands. Intensification usually

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involves changes in land use and the application of inorganic fertilizers and pesticides on fields. Species-rich 'unimproved' grasslands have developed over thousands of years of human management, specifically through regular livestock grazing and cutting for hay. Unimproved grasslands are known to contain exceptional levels of plant and animal diversity (Yeates et al., 1997). Several studies have also reported that unimproved grasslands contain exceptional levels of microbial diversity, although most only focus on mycorrhizal fungi and not entire microbial communities (Douds and Millner, 1999; Gosling et al., 2006; Van Der Heijden et al., 2006). Since the 1950s, farmers have increasingly ploughed up unimproved grasslands and replaced them with arable crops, or with 'improved' grasslands – where a single species of grass is grown as an annual or bi-annual crop—leading to a loss of over 97% of unimproved grasslands in lowland England alone (Blackstock et al., 1999). In certain conservation areas, arable fields have also been part of 'reversion schemes,' where land owners and managers have attempted to restore species-rich grasslands on former arable land. This system offers an ideal opportunity to compare the soil biota of different fields before and after conversion to arable and to quantify the effectiveness of reversion on restoring the soil microbial community to its pre-arable state.

To examine whether agricultural intensification in grasslands threatens native microbial diversity, we conducted vegetation surveys, soil analysis, and metagenomic research at 36 current and former grasslands in Oxfordshire, UK. All sites are part of active, working farms. We assessed: (1) how agricultural intensification affects microbial diversity and community composition; and (2) whether arable reversion can reverse any observed effects. Specifically, we compared five land-use types that reflect real changes affecting the local landscape and environment within the study area. These land-use types were: (1) unimproved grasslands which had never been ploughed or used for arable cultivation; (2) improved grasslands which receive high levels of inorganic inputs and are sown with commercial ryegrass (*Lolium perenne* L.) and clover-based seed mixes (*Trifolium pratense* L. and *T. repens* L.); (3) 'conservation grasslands' which are former arable fields which have undergone arable reversion; and two arable crops grown on former grassland sites: (4) oilseed rape (*Brassica napus* L.) and (5) poppy (*Papaver somniferum* L.). We selected these crop types because of concerns that growing non-mycorrhizal crops will negatively impact soil fungal diversity. At each site we determined the soil metagenomic profiles using Illumina sequencing of the bacterial 16S and fungal ITS1 regions and we compared differences in bacterial and fungal taxonomic diversity among the land-use types. We also looked for changes in two groups of microbiota with well-established functions, nitrogen-fixing bacteria and mycorrhizas, to determine whether agricultural intensification decreases the abundances of these agriculturally-important microbiota.

2. Materials and methods

2.1. Study area and site selection

The county of Oxfordshire is located in south-east England, UK. It has a maritime temperate climate with an annual rainfall of between 570 and 750 mm (depending on elevation) (Killick et al., 1998). The daily average temperature in winter (November–February) ranges from 4.9–7.6 °C and the daily average temperature in summer (May–August) ranges from 12.5–17.6 °C. The three main soil types are alluvial, sandstone, and chalk. The primary crops are wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), and oilseed rape. Poppy is not a major crop but is increasingly grown due to demand for UK-derived codeine and morphine. Farmers also raise cattle and sheep for meat and dairy production.

Between June–July 2015, we conducted fieldwork at 36 sites in the region (Supplementary materials Table 1 and Fig. 1). These sites fell under five major land-use categories (Table 1, Fig. 1). Unimproved grasslands are pastures and meadows managed by farmers (for fodder) or by conservation groups (to maintain rare plant species located there). All unimproved sites, as far as we know, have never been ploughed. Conservation grasslands are former intensively cultivated arable fields that have undergone arable reversion. This is achieved by (1) soil amendment (where soil is stripped to reduce soil nutrients) and (2) re-sowing former arable fields with plants characteristic of unimproved grasslands. Improved grasslands are leys sown with legume-based seed mixtures and treated with fertilizers (inorganic and organic). These fields are ploughed and re-sown every year or every other year depending on the yield of the first season and if a rotation system is used. The rapeseed and poppy fields were converted from grassland to arable within the past 30 years. All agriculturally improved arable fields receive inorganic N and P (and in one case, digestate from an anaerobic digester). None of these fields are tilled and all undergo rotation. In north Oxfordshire, farmers rotate rapeseed with wheat, barley, oats and peas (*Pisum sativum* L.). In south Oxfordshire, farmers rotate the rapeseed and poppy fields together along with wheat and barley.

2.2. Soil sample collection and vegetation surveys

We conducted a systematic program of soil sampling at each site to ensure the soil samples reflected local grassland vegetation and soil diversity. We collected soil samples at each site at the same time of day (early morning), season (early summer), and weather (no rain) in order to ensure comparability between sampling units. This is particularly important because microbial abundance can decline during certain seasons (particularly winter) and increase under certain environmental conditions (e.g. rainfall) or

Table 1
Description of Land Use Categories. The study sites are divided into five land use categories: unimproved grasslands, conservation grasslands, improved grasslands, poppy fields, and rapeseed fields. Each category is characterized by type of land use (grassland or arable), function (agriculture or conservation), vegetation (unsown (i.e. natural) or sown), seed source (local or commercial), application of inorganic inputs (N, P, and K), use of rotation, and whether the field is grazed (G), mown (M), mown and grazed (MG), or cut.

Description	Unimproved grassland (n = 14)	Conservation grassland (n = 10)	Improved grassland (n = 6)	Poppy field (n = 3)	Rapeseed field (n = 3)
Land Use	Grassland	Grassland	Grassland	Arable	Arable
Function	Agricultural	Conservation	Agricultural	Agricultural	Agricultural
Vegetation	Unsown	Sown	Sown	Sown	Sown
Seed source	Local	Local, commercial	Commercial	Commercial	Commercial
Application of inorganic N, P, K	No	No	Yes	Yes	Yes
Rotation	No	No	Yes	Yes	Yes
Grazed, Mown, or Cut	G, M, MG	G, MG	Cut	Cut	Cut