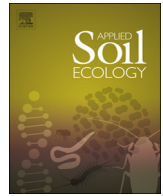




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Spatial structuring of soil microbial communities in commercial apple orchards

Greg Deakin¹, Emma L. Tilston¹, Julie Bennett, Tom Passey, Nicola Harrison, Felicidad Fernández-Fernández, Xiangming Xu*

NIAB EMR, East Malling, West Malling, Kent ME19 6BJ, UK

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ABSTRACT

Characterising spatial microbial community structure is important to understand and explain the consequences of continuous plantation of one crop species on the performance of subsequent crops, especially where this leads to reduced growth vigour and crop yield. We investigated the spatial structure, specifically distance-decay of similarity, of soil bacterial and fungal communities in two long-established orchards with contrasting agronomic characteristics. A spatially explicit sampling strategy was used to collect soil from under recently grubbed rows of apple trees and under the grassed aisles. Amplicon-based metabarcoding technology was used to characterise the soil microbial communities. The results suggested that (1) most of the differences in soil microbial community structure were due to large-scale differences (i.e. between orchards), (2) within-orchard, small-scale (1–5 m) spatial variability was also present, but spatial relationships in microbial community structure differed between orchards and were not predictable, and (3) vegetation type (i.e. trees or grass and their associated management) can significantly alter the structure of soil microbial communities, affecting a large proportion of microbial groups. The discontinuous nature of soil microbial community structure in the tree stations and neighbouring grass aisles within an orchard illustrate the importance of vegetation type and allied weed and nutrient management on soil microbial community structure.

1. Introduction

Ecologists have long sought to understand the factors underlying the distribution and abundance of species. This is particularly true for the microorganisms in soil, where differences in soil chemistry give rise to large differences in the composition of soil microbial communities (Fierer and Jackson, 2006). Similarly, the type of overlying vegetation is important, with soil under trees supporting very different communities from those under grass (Rich et al., 2003). Until the early 1990s spatial variability in the distribution of soil organisms was often considered to be ‘random noise’, but slowly the interactions of a hierarchy of environmental factors, intrinsic population processes and disturbances are being described at scales ranging from millimetres to hundreds of metres (Ettema and Wardle, 2002). Improving our understanding of the factors that regulate the spatial distribution of soil biota in agroecosystems has relevance to many agronomic issues including nutrient cycling, the management of soil-borne plant pathogens and the efficacy of various microbial inoculants.

Two mechanisms are frequently proposed to account for differing

spatial patterns of soil microbial diversity. The first is a more nuanced version of the generalisation that ‘...everything is everywhere, but the environment selects...’ (Baas Becking, 1934) and is predicated on the assumption that spatial patterns of microbial diversity are driven by environmental heterogeneity, rather than dispersal limitation. Thus, the composition of a given microbial community is dependent upon deterministic processes for the environmental filtering of component species, according to their ecological fitness for specific niches. Where deterministic processes operate, increasingly dissimilar microbial communities can be expected to develop under concomitantly different environmental conditions (Martiny et al., 2011); or along an environmental gradient (Green and Bohannan, 2006). The second mechanism is that dispersal processes determine the similarity of microbial communities. The physical structure of the soil matrix is assumed to limit migration of microorganisms and consequently, similar communities develop at neighbouring sites irrespective of any environmental differences. At small spatial scales, habitat heterogeneity declines and stochastic processes exert a greater influence on community composition than deterministic processes (Chase, 2014), but at larger spatial

* Corresponding author.

E-mail address: Xiangming.Xu@emr.ac.uk (X. Xu).

¹ Both authors contributed equally to this paper.

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scales this can produce pronounced spatial structuring of microbial communities in soil (Ettema and Wardle, 2002).

One commonly reported spatial patterning of ecological communities is the negative relationship between community similarity and spatial distance, known as distance–decay of similarity (Nekola and White, 1999). Distance-decay of similarity is believed to result from a combination of deterministic processes (environmental filtering), and stochastic or neutral processes (dispersal limitation and ecological or evolutionary drift) (Bahram et al., 2015). Although environmental filtering is an obvious underlying mechanism for the emergence of distance-decay relationships, they can also arise where the environmental conditions are comparable, but there is significant drift (Bell, 2010). Other factors that influence the distance decay of community similarity include environmental periodicity, which, depending on the scale of observation relative to the periodicity, can either result in a lack of distance decay, or facilitate its detection.

Microorganisms are the most diverse and complex component of soil biodiversity and participate in many of the ecological interactions and processes required for the regulation of pests and diseases, water and nutrient retention, and maintenance of soil structure (Barrios, 2007). Managing soil biodiversity, and the community-level processes therein, has been highlighted as a major challenge in the transition to more sustainable agricultural systems (Lemanceau et al., 2015). It is therefore surprising that, in contrast with natural habitats, the distance-decay of similarity for microbial communities in cropped soils has received little attention. As a multi-layer assemblage of plants in a long-term complex spatial arrangement (Simon et al., 2017), commercial apple orchards are an interesting agroecosystem in which to study plant-soil-microbial interactions. The perennial nature of the plant communities in the rows of trees and the grass aisles means that soil management is constrained by time and space, and above- and below-ground ecosystems have greater stability than that associated with annual cropping. The low frequency of physical disturbance also means there is ample opportunity for the development of multiple bi-directional plant-soil-microbial interactions.

In this paper we report an investigation of the spatial similarity, specifically distance-decay, for microbial communities in soil under the two plant communities present in two long-established orchard sites with contrasting agronomic characteristics. We used a spatially explicit sampling strategy to collect soil from under recently grubbed rows of apple trees and under the grassed aisles. Culture-independent next generation sequencing techniques were used to profile soil microbial communities in soil. We hypothesized that (1) there would be coupling between vegetation composition and soil microbial assemblages, (2) the presence of environmental gradients would favour the development of distance-decay of similarity in soil microbial communities, and (3) distance-decay of similarity would be modified by management decisions such as the intensity of operations and tree spacing (i.e. environmental periodicity).

2. Materials and methods

2.1. Study design

Soil microbial communities were profiled in soil samples taken from two geographically and agronomically distinct apple orchards. Within each orchard, soils were sampled from two **vegetation types**: former tree stations and the adjacent grassed aisles; which were divided into three **blocks** of ca. 20 m long, each with eight consecutive trees (i.e. eight pairs of tree and aisles samples). The spatial location (i.e. the distance between sampling points within each orchard) was also recorded to enable calculation of spatial autocorrelation. At each sampling point (tree station or adjacent grassed aisle), three analytical replicate soil samples were taken.

Table 1
Selected geographical information and climate statistics for both sites.

	Dessert Orchard	Cider Orchard
<i>Geographical information</i>		
Latitude	51.210596	52.251020
Longitude	0.601664	-2.301711
Altitude (m a.s.l.)	80	65
Slope (° and orientation)	7, south-facing	2, south-facing
Soil type [†]	Eutric Luvic Planosol	Chromic Vertic Luvisol
<i>Regional climate statistics</i> [‡]		
Minimum monthly mean air temperature (°C)	1.4	0.9
Maximum monthly mean air temperature (°C)	22.6	21.6
Ambiental air temperature range (°C)	6.4–14.7	5.9–14.1
Minimum mean soil temperature, 10 cm (°C)	−1.9	−1.0
Maximum mean soil temperature, 10 cm (°C)	26.5	20.0
Ambiental soil temperature range, 10 cm (°C)	5.0–17.7	6.8–13.7
Minimum monthly mean soil temperature, 30 cm (°C)	0.7	No data
Maximum monthly mean soil temperature, 30 cm (°C)	24.4	No data
Ambiental soil temperature range, 30 cm (°C)	6.1–16.5	No data
Air frost (days)	47.5	49.3
Sunshine (hours)	1634	1554
Rainfall (mm)	673	665

[†] Soil nomenclature is in accordance with the recommendations of the [IUSS Working Group WRB \(2015\)](#).

[‡] Regional climate statistics are mean values for the period 1981–2010 (2000–2015 for soil temperature), as measured by UK Meteorological Office weather stations within 10 km and 35 km of the dessert and cider orchards, respectively.

2.2. Orchards

The two orchards sampled represented the contrasting rootstock and scion combinations typical for the production of dessert/culinary and cider apples (*Malus pumila* Miller) in the UK. The first orchard, planted with dessert/culinary varieties, was located in south-east England on Wickham series soil (Table 1). Between 1992 and the winter of 2014–15 this site was planted with ‘Bramley’s seedling’ and ‘Golden Delicious’ on ‘M.9’ rootstock. Prior to grubbing, the trees had been grown in north–south orientated rows 3.75 m apart, with an in-row tree spacing of 1.6 m. Groundcover in the aisles between the tree rows was mainly grasses (e.g. *Lolium perenne* L., *Poa pratensis* L., *Agrostis* spp. and *Festuca* spp.), with occasional weeds, which was kept short by periodic mowing during the growing season. The soil directly under the trees was kept mostly free of vegetation by regular application of herbicide.

The second orchard was located in the West Midlands of England, approximately 230 km to the north-west of the dessert orchard, on Whimple series soil (Table 1). Since 1988 the orchard had been planted with cider apple varieties, the most recent planting prior to sampling was the cultivar ‘Katy’ on two different rootstocks: ‘M.M.106’ and ‘M.M.111’. The trees were planted in north–south orientated rows 5.5 m apart, with an in-row tree spacing of 2.75 m. The planting of ‘Katy’ was grubbed after 12 years in 2014. Before 2002, the site had been planted with the cider apple variety ‘Bulmer’s Norman’ on seedling rootstock at planting distances of 6.6 m between rows, and 2.6 m within rows. The former rows of the ‘Katy’ planting, sampled for this study, had been aisles in the ‘Bulmer’s Norman’ planting. There was no record of soil sterilization or the application of organic amendments to the land, either before or since 1988. A mixture of herbaceous plants (mainly grasses) was present in the aisles and a vegetation-free ‘herbicide strip’ was maintained under the rows as described above.

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