Distribution patterns – Soil biodiversity at aggregate scale

Soil aggregates

Soil is an incredibly complex and diverse organisation of pores and particles, which influence the organisms that live within. These particles, known as 'soil aggregates', consist of mineral and organic materials bound together, and are generally defined by their size and their stability in water. These aggregates are typically classified into three main size fractions: macroaggregates (> 250 µm), microaggregates (50 - 250 µm) and clay- and silt-sized aggregates (< 50 µm). Different soil organisms live in the network of pores between and within aggregates. [93]

The vast variation in the size of aggregates, as well as their physical-chemical properties, results in a huge diversity of microhabitats for organisms living within the soil. For example, small pores found in clay- and silt-sized aggregates will protect microorganisms (e.g. bacteria – see pages 33-35) against predation from larger organisms, which are restricted to larger pores in meso- and macroaggregates or between aggregates, and also restrict the flow of water and air and the input of new nutrients. Therefore, clay- and silt-sized aggregates are more stable habitats, with reduced competition and predation, and less variation in water influx (due to the capacity of small pores to better hold water), and are less sensitive to mechanical breakdown and influx of environmental pollutants.

Microaggregates are intermediate habitats, mainly populated by microfauna (e.g. nematodes – see pages 46-47). Macroaggregates are considered to be less stable habitats due to greater fluctuations in water and gas flow, increased competition and predation, and their sensitivity to mechanical breakdown (e.g. due to soil tillage, rain and drought cycles – see pages 15, 122-123). Macroaggregates are mostly populated by ecosystem engineers (see box on page 95), such as earthworms and termites (see pages 55, 58).

Microorganisms and soil aggregates

The abundance of microorganisms varies with the size of soil aggregates, and is directly related to the specific environmental conditions of each size. Bacterial biomass is often higher in clay- and silt-sized aggregates, especially in fine soil fractions (< 20 µm), where it can reach levels that are 30 - 80 % higher than in macroaggregates, due to more stable environmental conditions. Aerobic (life in the presence of oxygen) bacteria dominate macroaggregates, as oxygen concentration is higher; clay- and silt-sized aggregates generally contain a mix of aerobic and strict anaerobic (oxygen not needed to live) bacteria. By contrast, fungi (see pages 38-41) are mainly found in macroaggregates where their biomass and hyphae length can be up to 80 % higher than in microaggregates. The small size of pores in microaggregates prevents fungi from growing inside them, limiting the fungal presence to their surface.

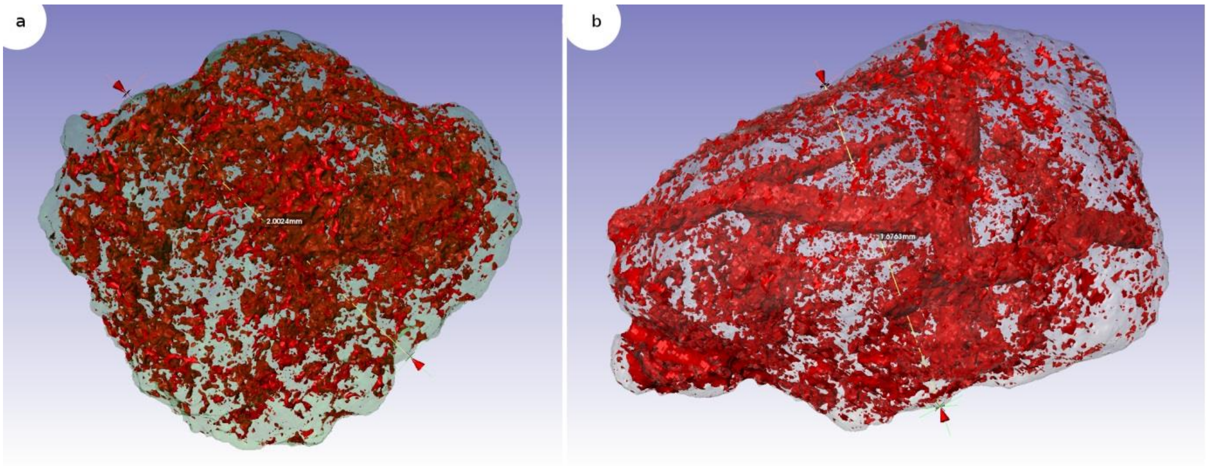
The size of soil aggregates plays a role not only in microbial abundance, but also in diversity. For instance, bacterial diversity is often higher in microaggregates than macroaggregates. There is no general pattern in the distribution of bacterial phyla associated with a specific size of soil aggregates across different soils; however, Alphaproteobacteria (see page 34) are more often found to be associated with macroaggregates, Actinobacteria (see page 35) with microaggregates and species of the genus *Acidobacterium* with the fine soil fraction. The variation in bacterial diversity between sizes of soil aggregates has been suggested to be driven by the quality of soil organic matter in each size, rather than by its quantity. However, knowledge and understanding of the microbial diversity at the scale of soil aggregates remains limited and requires further research.

Functions at aggregate scale

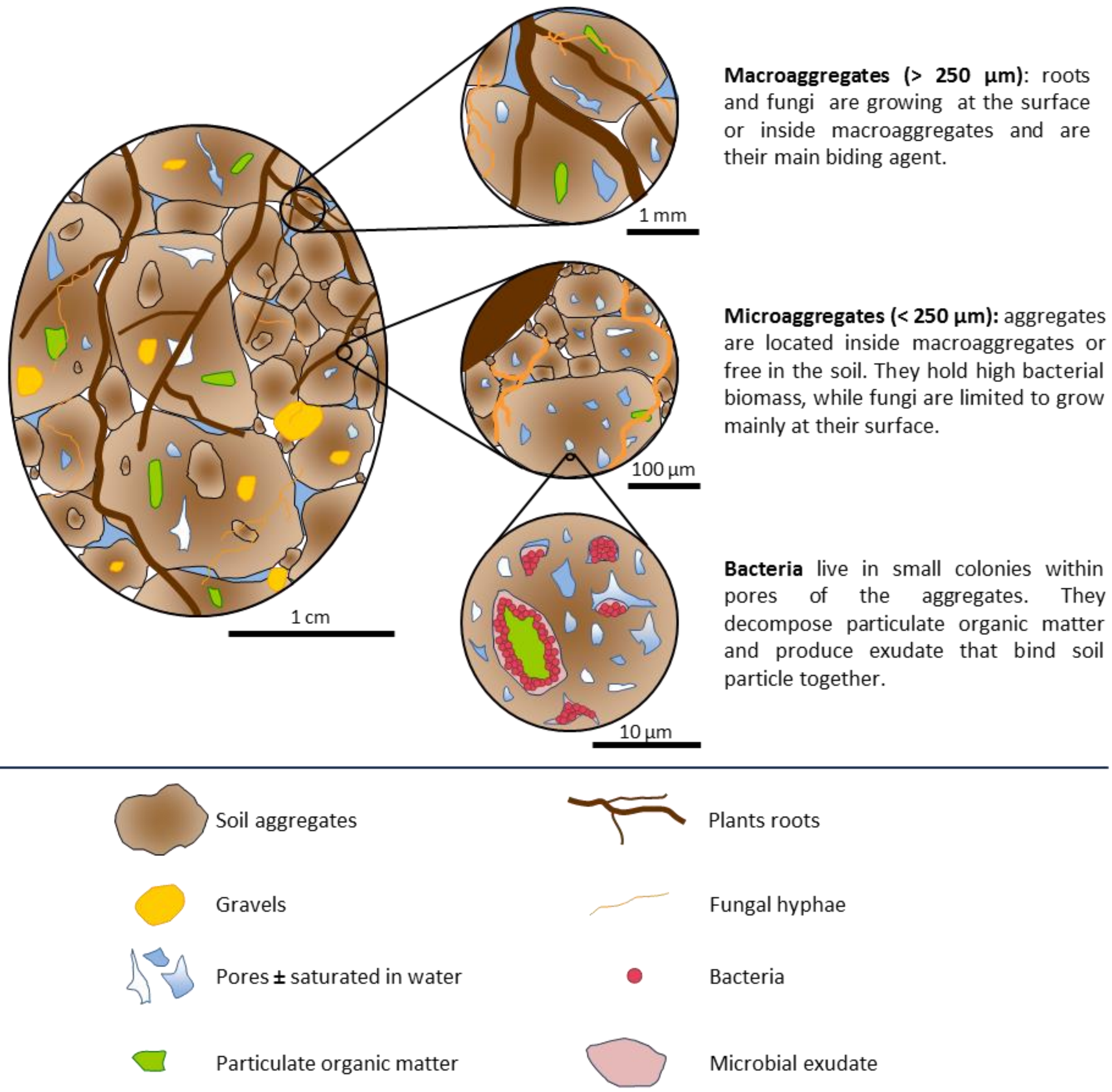
In addition to microbial diversity and distribution, variation in soil aggregates also affects the functions carried out by microorganisms. For example, the composition of free-living bacteria that fix atmospheric nitrogen into soils (so-called diazotrophs – see page 99), differs with the size of soil aggregates. Macroaggregates have a greater diversity and activity of diazotrophs, yet microaggregates can carry between 30 % and 90 % of the diazotrophic population. These different diazotroph communities exploit specific anaerobic niches within the different sizes of aggregates, creating the conditions required for the fixation of nitrogen.

Similarly, denitrifiers, which reduce nitrate by releasing it back into the atmosphere (in a process called denitrification), are not present and active in all sizes of soil aggregates, but occur mainly in microaggregates, where nearly 90 % of the potential denitrification activity can occur. Furthermore, microbial diversity and functions can differ in relation to the location of microorganisms in the exterior or interior parts of aggregates. The process of nitrification (i.e. conversion of ammonium into nitrate) can be 50 % higher on the exterior of the aggregates (first mm) than in the interior, due to the aerobic conditions which are required for this process. Conversely, the interior of soil aggregates can provide anaerobic conditions favourable for processes that require low levels of oxygen, such as nitrogen fixation, denitrification or methane production. The interior of aggregates can also protect bacteria against pollutants, such as heavy metals, whereas the bacteria on the exterior of aggregates generally show more resistance to pollutants.

The different sizes of soil aggregates. Soil structure is determined by how individual soil granules bind together and aggregate and, therefore, by the arrangement of soil pores between them. (ABL)



X-ray microtomography images of soil aggregates (~ 2 mm in size), from (a) cropland and (b) grassland. The pores, in red, where microorganisms live and develop, are small and fragmented in cropland aggregates. They are larger in grasslands due to the higher presence of roots. (MME)



Overview of soil aggregates and the distribution of organisms at the aggregate scale. Due to the small sizes, the main inhabitants at aggregate scale are microorganisms, namely bacteria and fungi. (ABL)