The soil as an ecosystem

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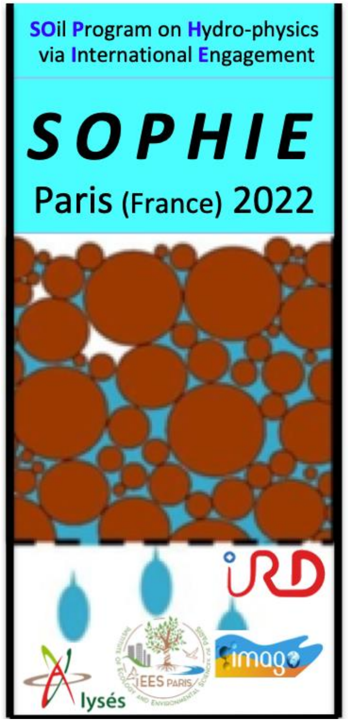
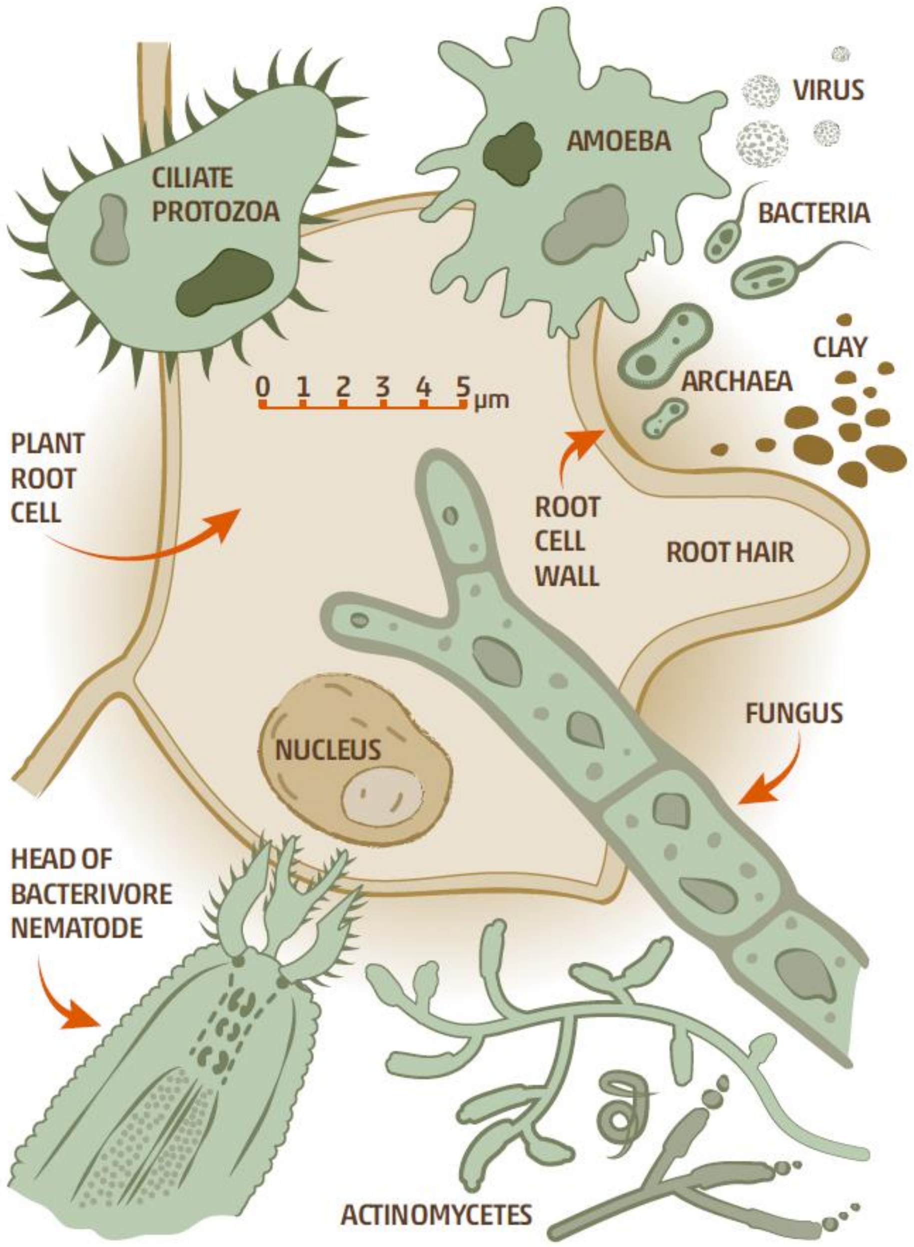
Source: FAO



20 January 2022



1.6 – 9.4 mm /day *(Juyal et al. 2018)*

1 – 7 mm /day *(Otten et al., 2001)*

< 1 cm /day (Ojala and Huhta, 2001; Lehmnitz et al., 2012)

8 mm /day *(Ackermann et al., 2016)*

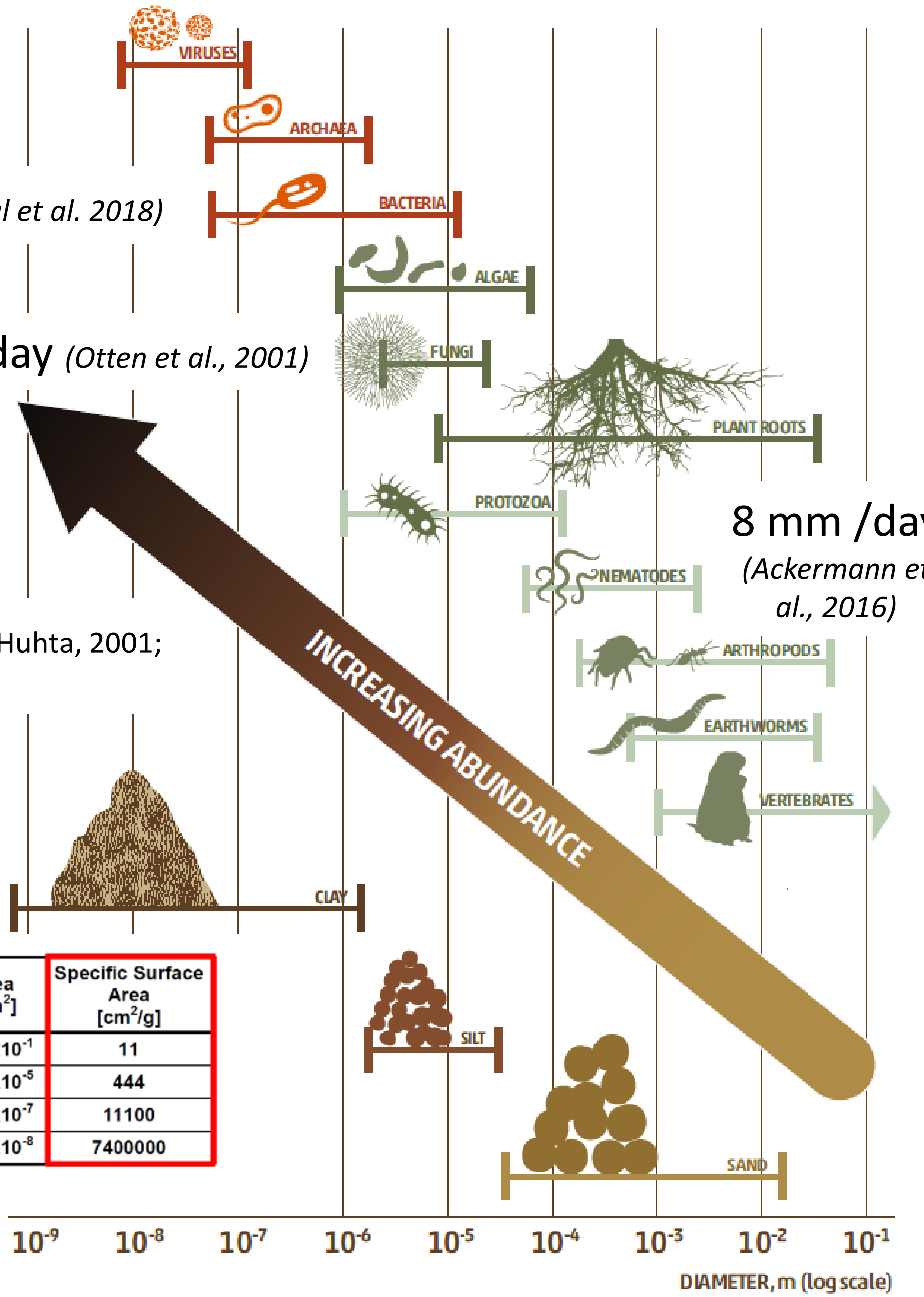


Table from Mohsen Zare (Uni. Bayreuth)

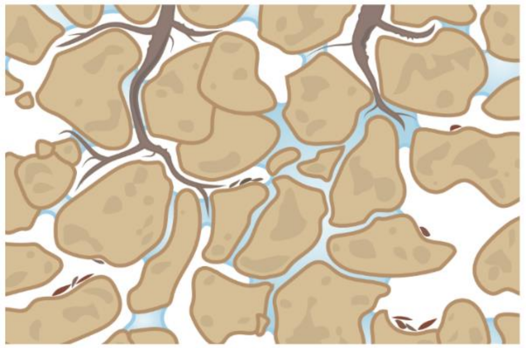
Particle	Idealized Shape	Effective Diameter [cm]	Mass [g]	Area [cm^2]	Specific Surface Area [cm^2/g]
Gravel	Sphere	$2x10^{-1}$	$1.13x10^{-2}$	$1.26x10^{-1}$	11
Sand	Sphere	$5x10^{-3}$	$1.77x10^{-7}$	$7.85x10^{-5}$	444
Silt	Sphere	$2x10^{-4}$	$1.13x10^{-11}$	$1.26x10^{-7}$	11100
Clay†	Disk	$2x10^{-4}$	$8.48x10^{-15}$	$6.28x10^{-8}$	7400000

† Thickness ≈ 10^{-7} cm

Source: https://doi.org/10.4060/cb1928en

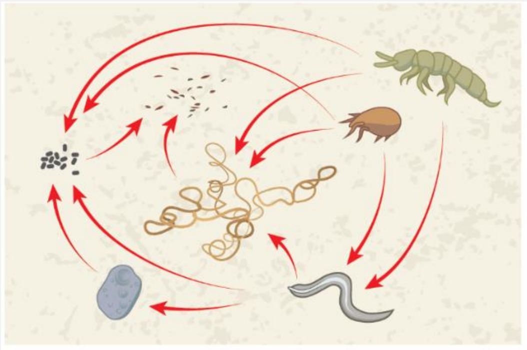
Soil structure as a determinant of trophic interactions

Soil physical structure



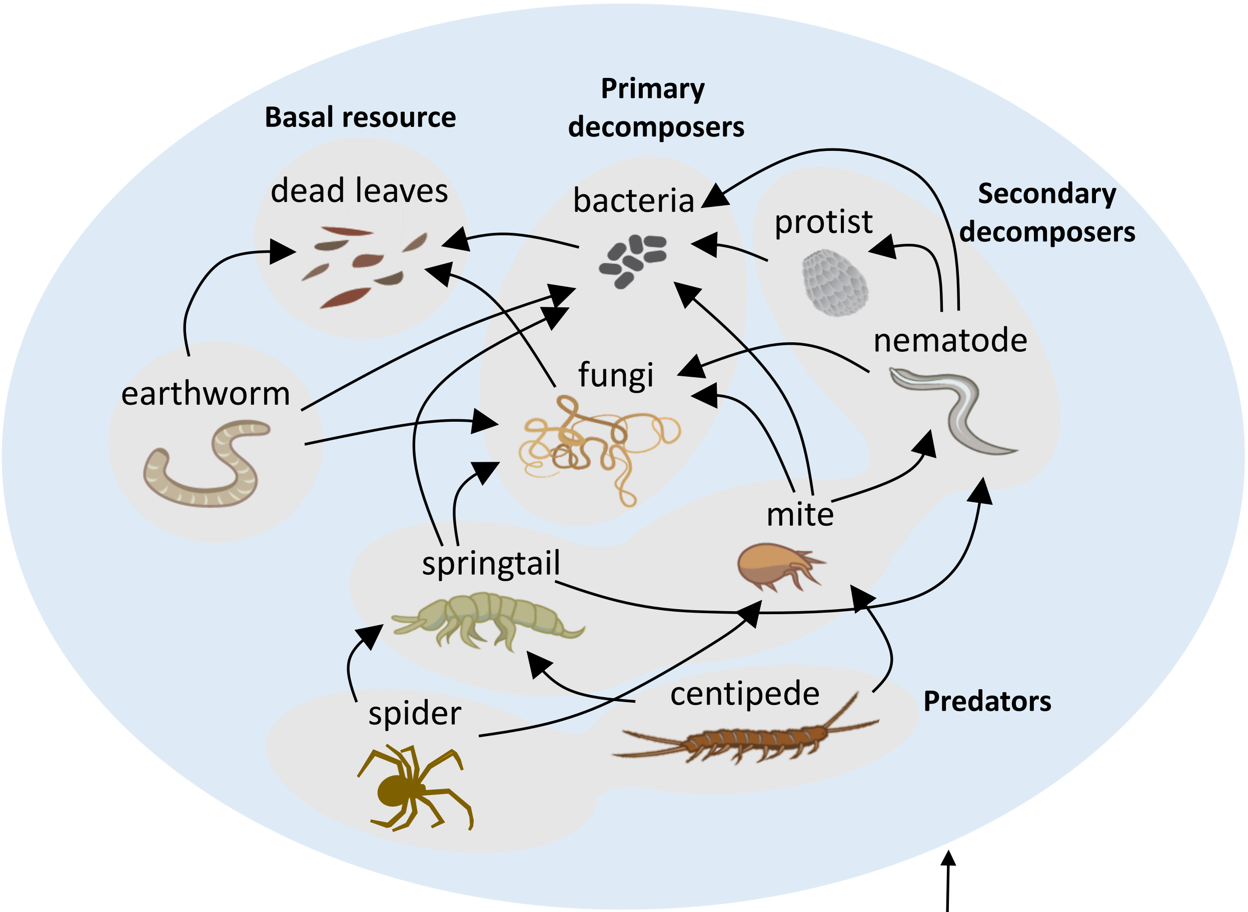
Soil physics

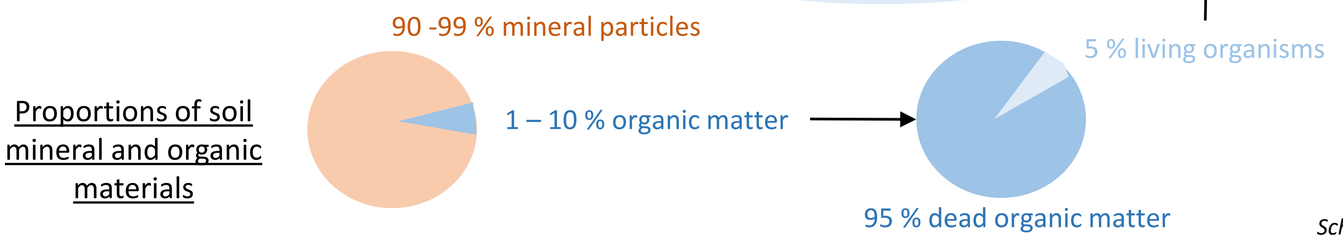
Trophic interactions



Soil food web ecology

Introduction





Scheme adapted from Basile-Doelsch et al. (2020)
https://doi.org/10.5194/bg-2020-49

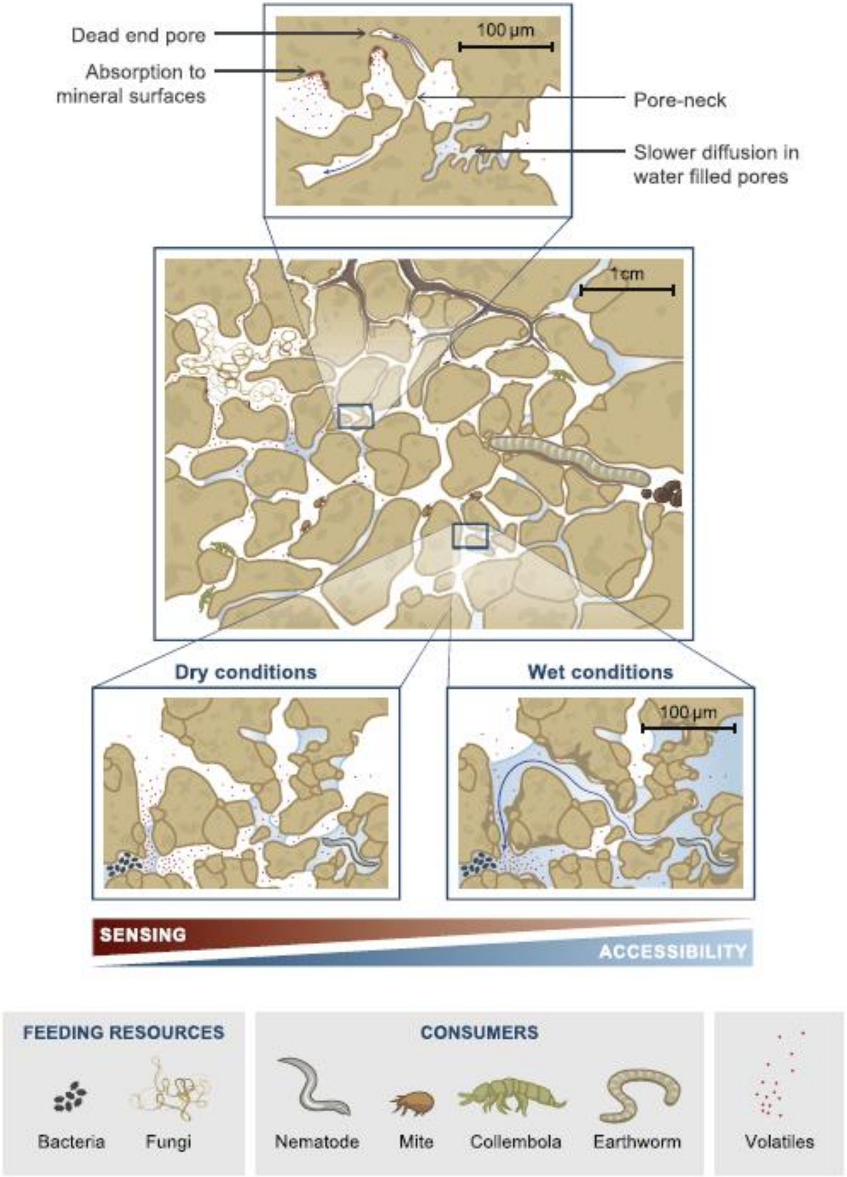
Main hypothesis and objective

- Hypothesis: Restrictions imposed on soil organisms' ability to sense and access food resources/prey by soil physical structure essentially shape trophic interactions in soil, while affecting soil biodiversity.

- Main goal: Reviewing mechanisms underlying the effect of soil physical structure on soil food webs.

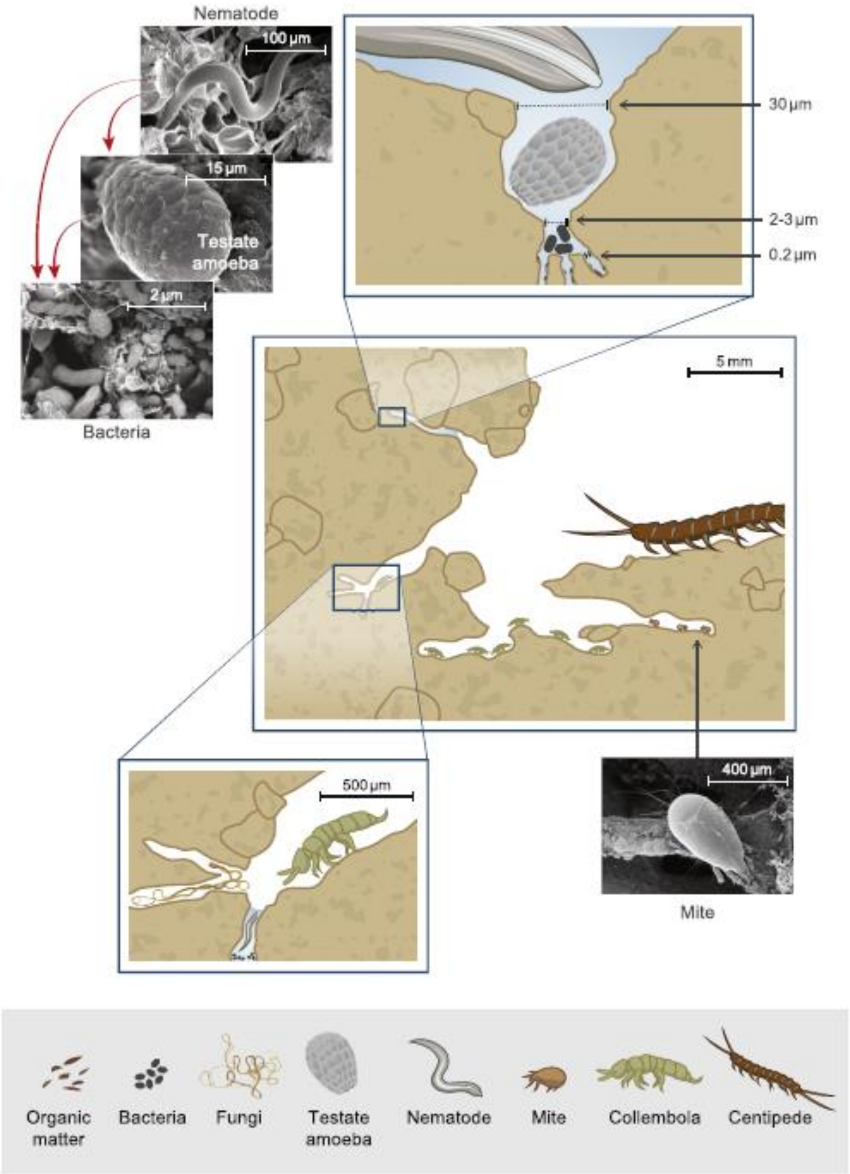
Erktan et al., (2020) SBB

Sensing food resources/prey in the opaque soil labyrinth



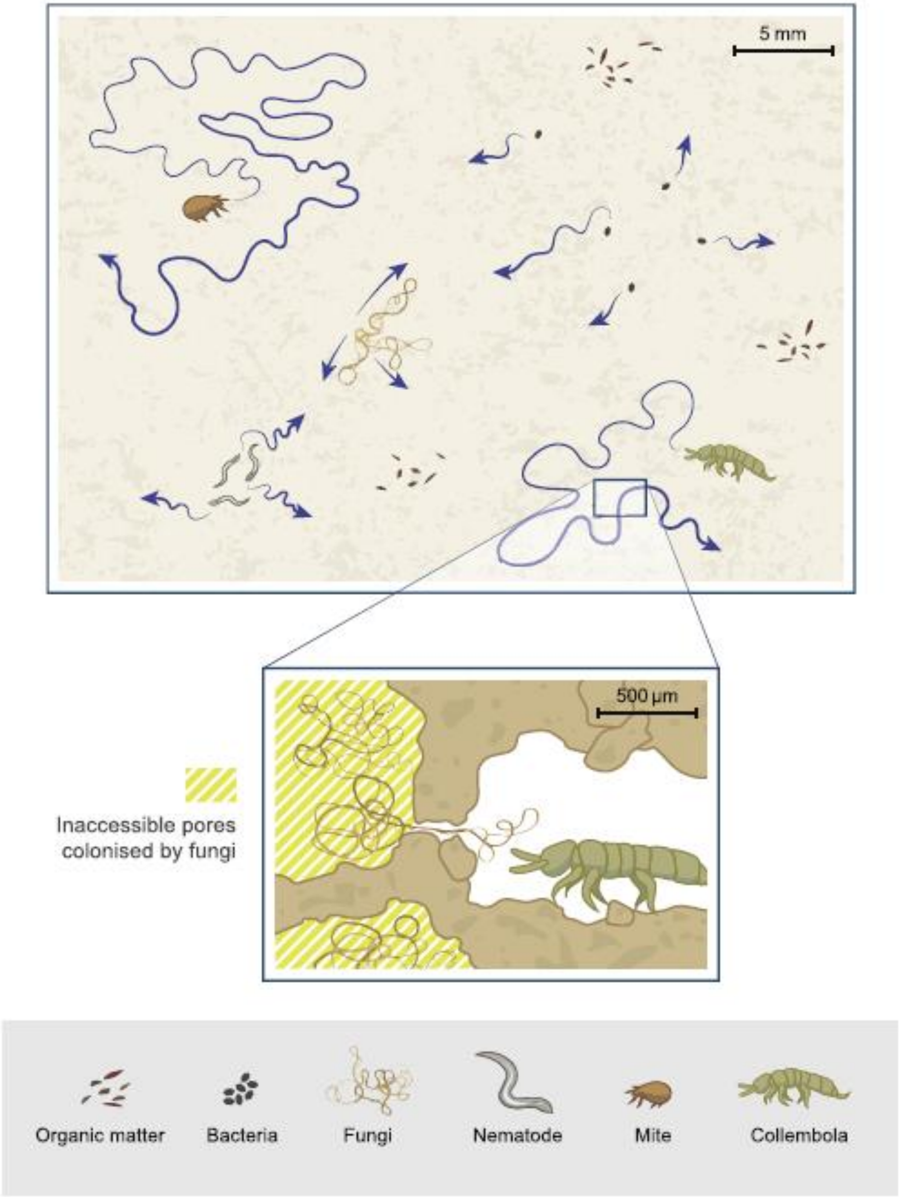
Erktan et al., (2020) SBB

Small pores protect resources/prey from consumers/predators



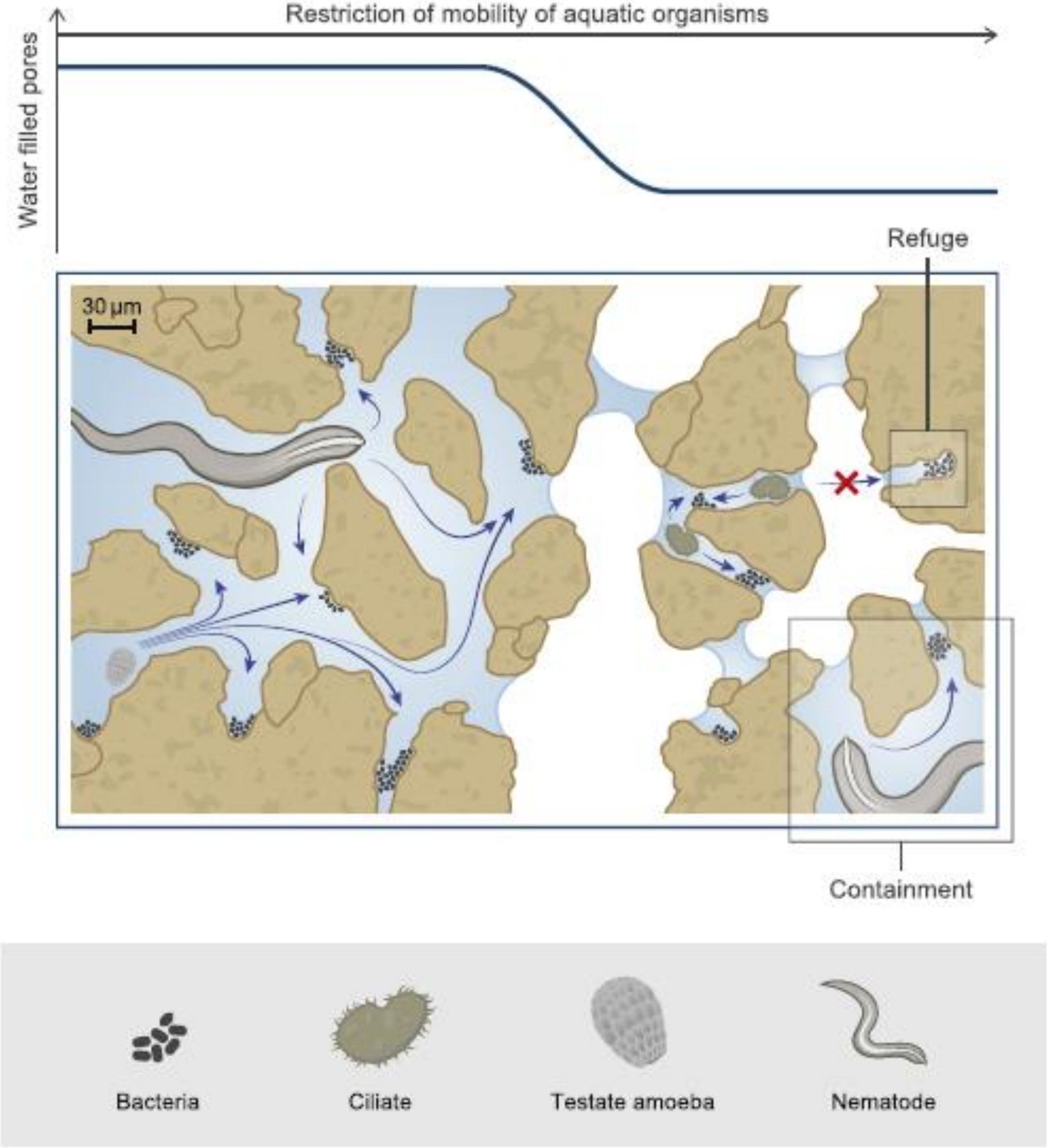
Erktan et al., (2020) SBB

Soil pore space restricts the movement of soil organisms and shapes interactions between consumers/predators and food resources/prey



Erktan et al., (2020) SBB

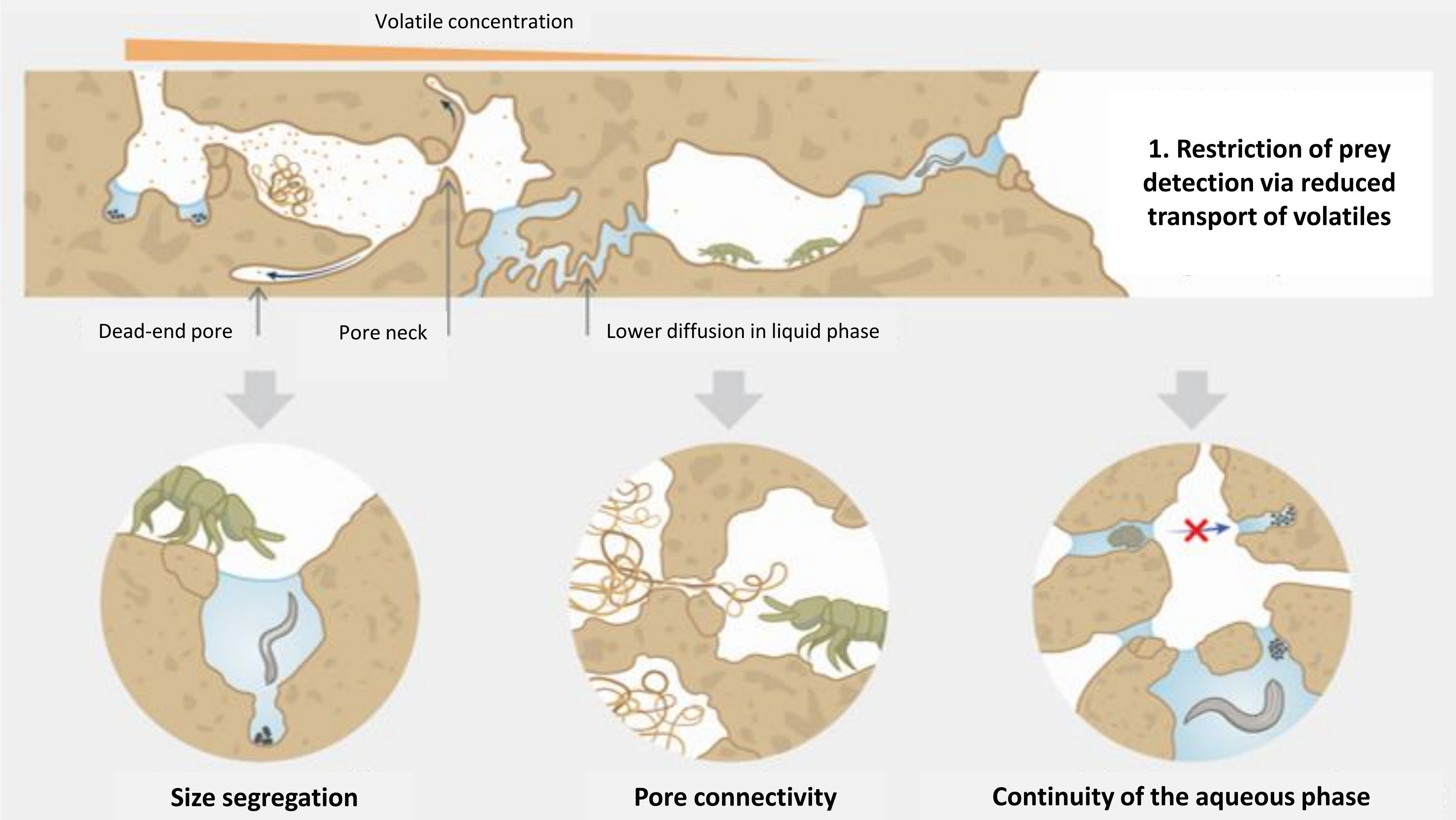
Water in soil drives trophic interactions



Erktan et al., (2020) SBB

Overall restrictions on accessibility to food resources

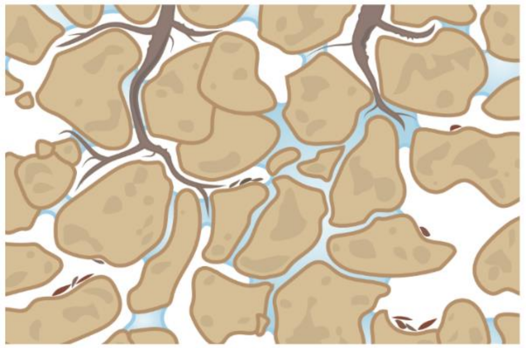
2. Restriction of prey accessibility



2

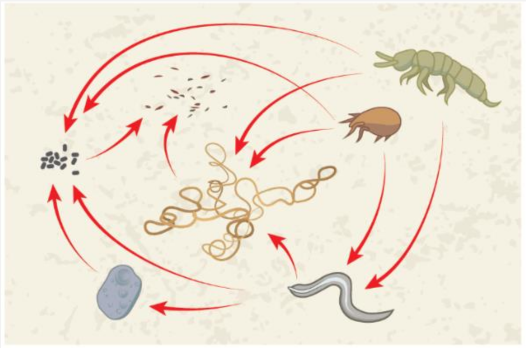
Soil structure as a consequence of trophic interactions

Soil physical structure



Soil physics

Trophic interactions

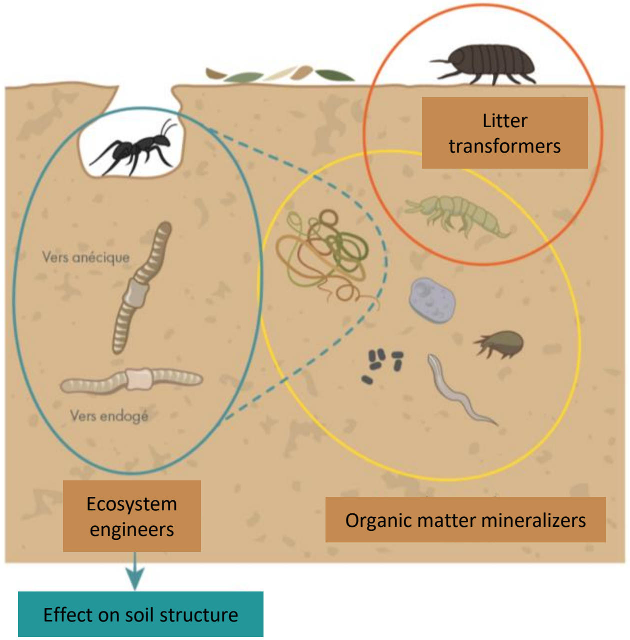


Soil food web ecology

Feedbacks of trophic interactions on soil physical structure

Jones (1994, 1997)
Lavelle et al. (1997)

Ecosystems engineers as a class of organism

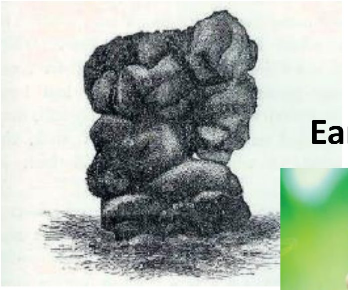


“Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials.”

Erktan et al. (submitted at EGS)

Feedbacks of trophic interactions on soil physical structure

Jones (1994, 1997)
Lavelle et al. (1997)

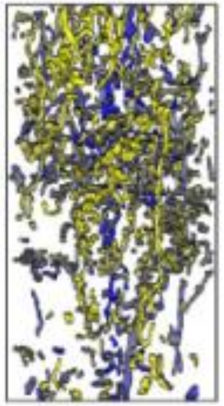


Darwin (1809-1882)

Earthworms

Source: Soil Biodiversity Atlas

control

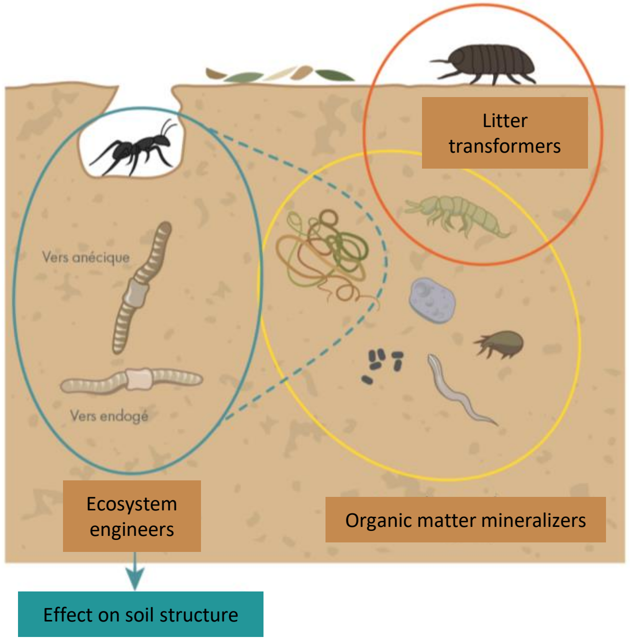


compacted soil

Capowiez et al. 2012

Earthworms

Ecosystems engineers as a class of organism



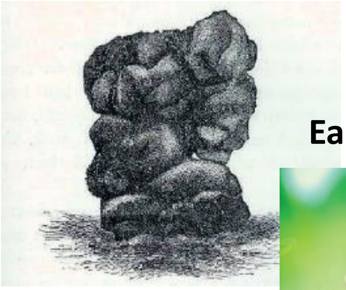
Ants

Burrowing bees

Erktan et al. (submitted at EGS)

Feedbacks of trophic interactions on soil physical structure

Jones (1994, 1997)
Lavelle et al. (1997)

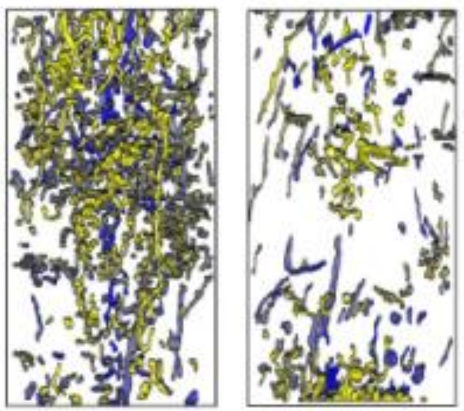


Earthworms

Darwin (1809-1882)

Source: Soil Biodiversity Atlas

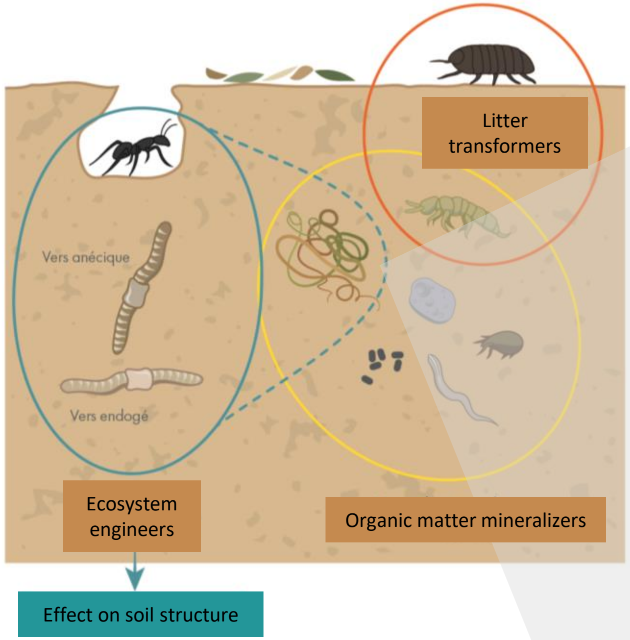
control   compacted soil



Capowiez et al. 2012

Earthworms

Ecosystems engineers as a class of organism

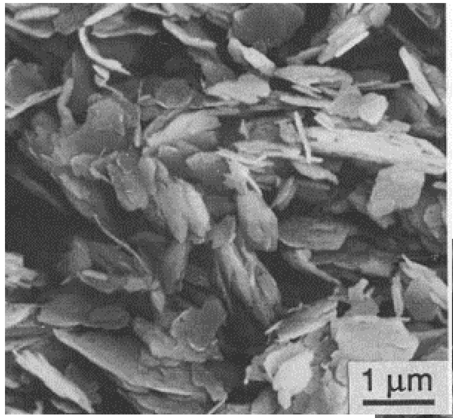


Ants

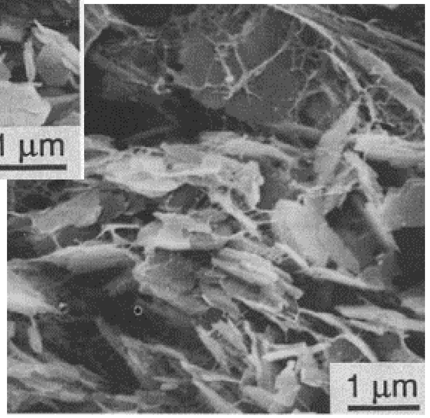
Burrowing bees

Fungi

Chenu et al. 1993

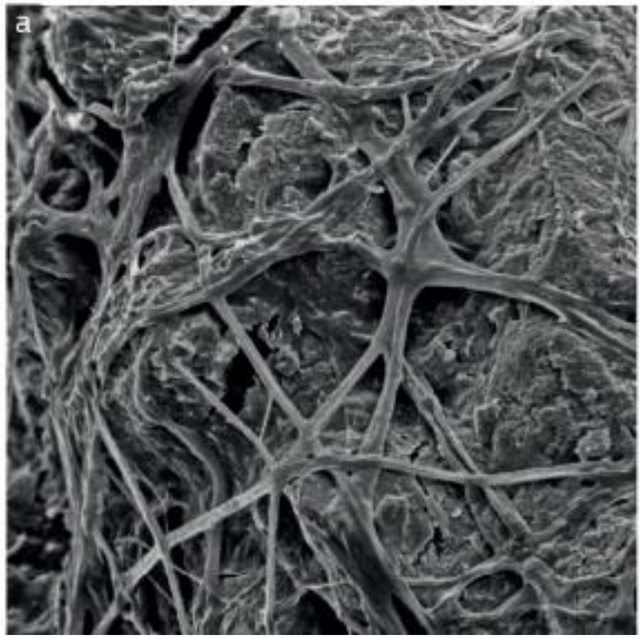


Cryo-SEM kaolinite



Cryo-SEM kaolinite-xanthan; EPS content 2,5% w/w clay

Brussaard et al. (2012)

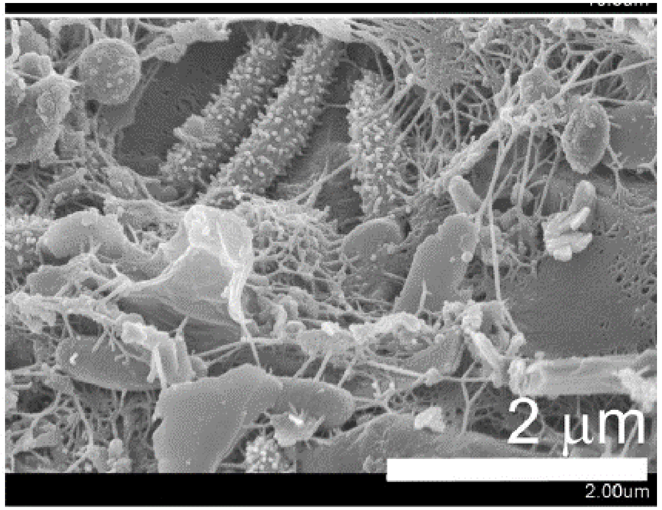


Erktan et al. (submitted at EGS)

Feedbacks of trophic interactions on soil physical structure

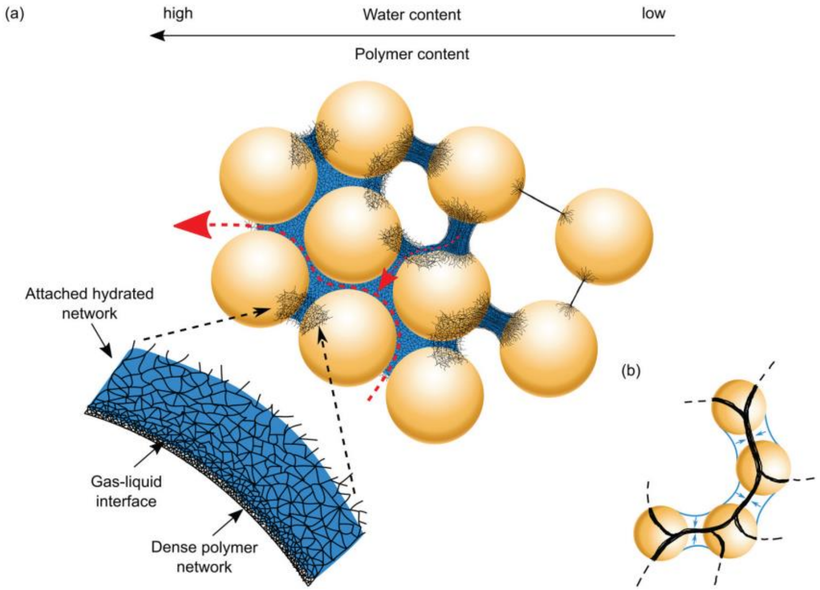
Bacteria

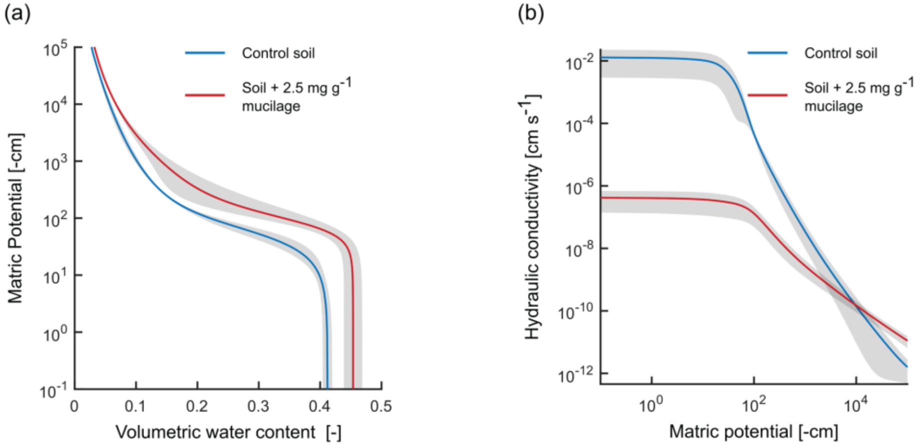
Tecon and Or, (2017)



Scanning electron microscopy images of bacterial cells attached to solid surfaces by exopolysaccharides (filamentous mesh).

- Extra polymeric substances (EPS) glue soil particles together (Chenu, 1993)
- They have many roles in bacterial ecology (Costa et al., 2018)
- EPS production and type depends on bacterial strains (Caesar Tonthat et al., 2014)





Benard et al. (2019)

Sensing food resources/prey in the opaque soil labyrinth

Protist

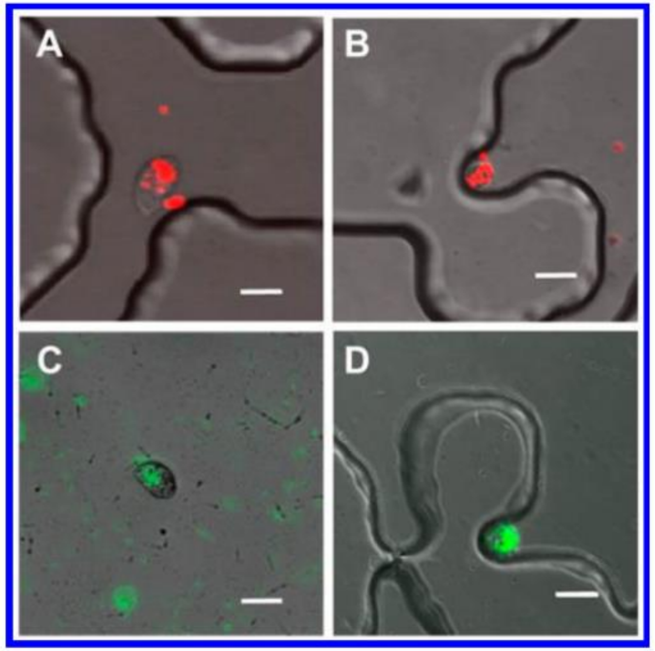


Figure 2. (A) Active *Colpoda* sp. carrying fluorescent red beads. (B) Encysted *Colpoda* sp. with fluorescent red beads. (C) Active *Colpoda* sp. in an unstructured microfluidic device, carrying unfixed GFP-expressing *P. fluorescens*. (D) Encysted *Colpoda* sp. in a soil-patterned microfluidic device carrying fixed GFP-expressing *P. fluorescens*. All scale bars are 20 μm.

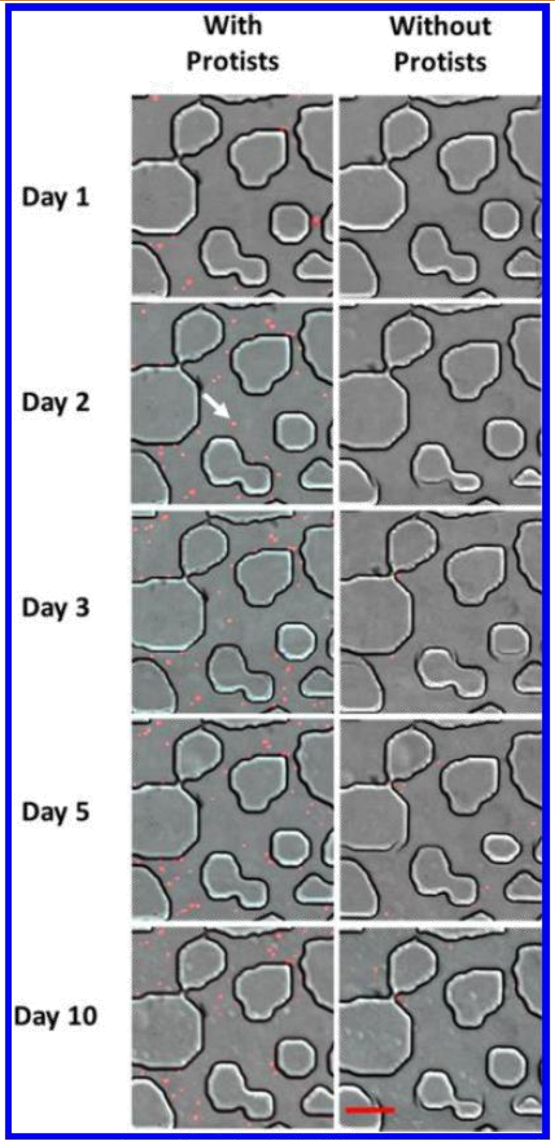
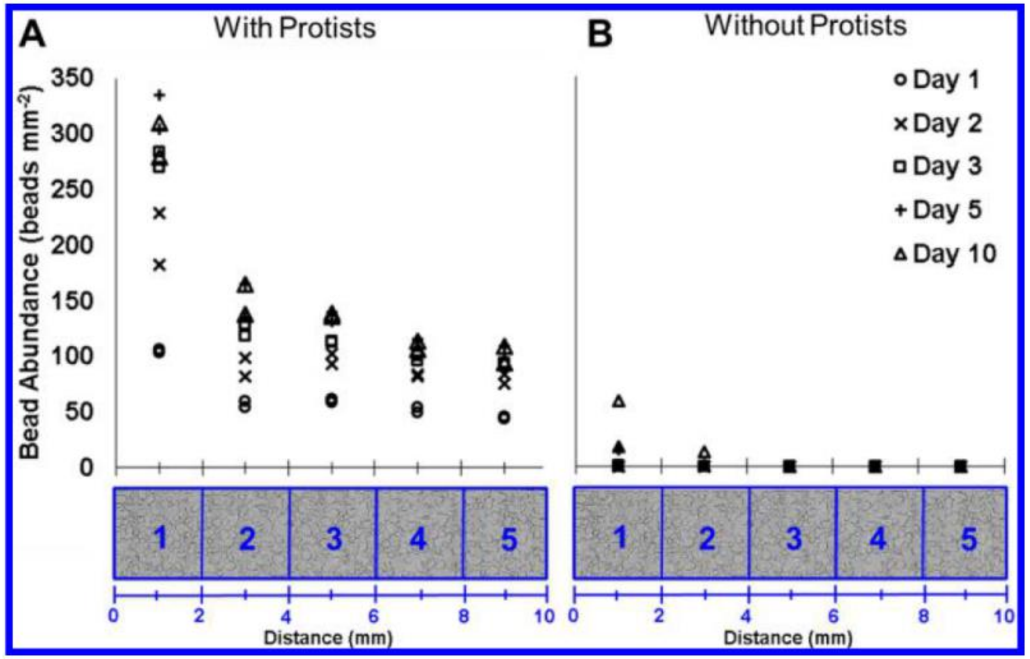


Figure 3. Beads in a small portion of region 1 with treatment and time. The arrow indicates a single fluorescent bead. The scale bar is 100 μm.



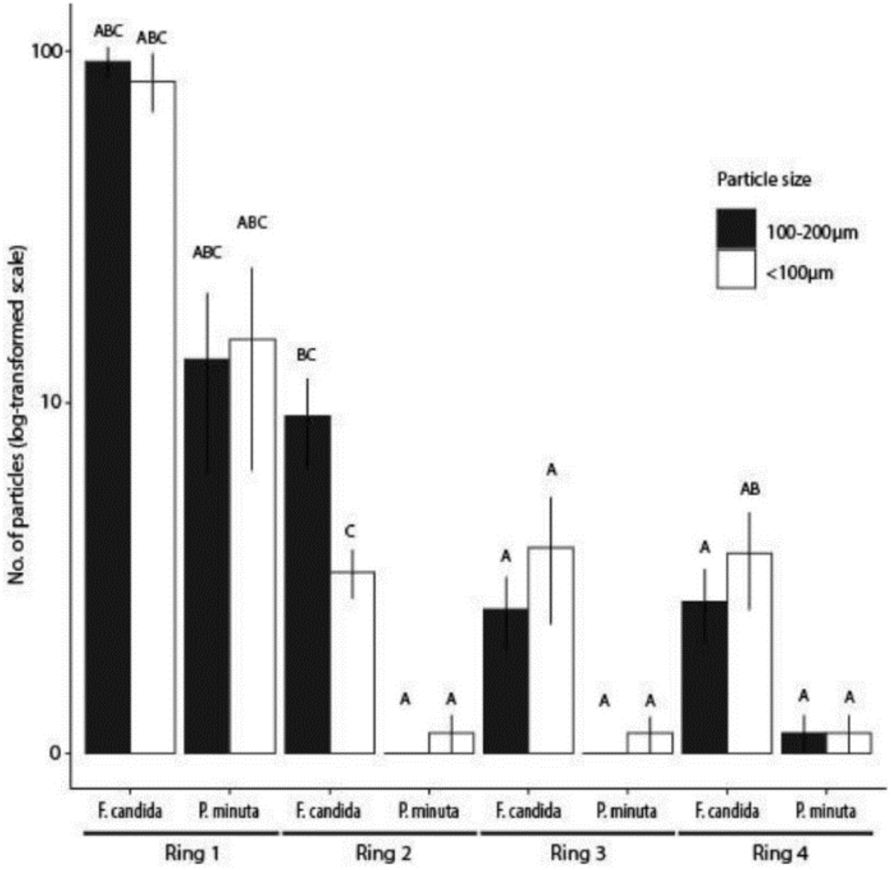
Rubinstein et al., (2015)

- Protists carry clay particles and bacteria

Sensing food resources/prey in the opaque soil labyrinth

Collembolan

Fig. 1. Examples of image analysis with four concentric circles of 1, 2, 3 and 4 cm diameter placed around the feeding station (left: initial photo, right: day 5). The amount of particles was counted in each ring and used for analysis. (photos: D. Daphi).

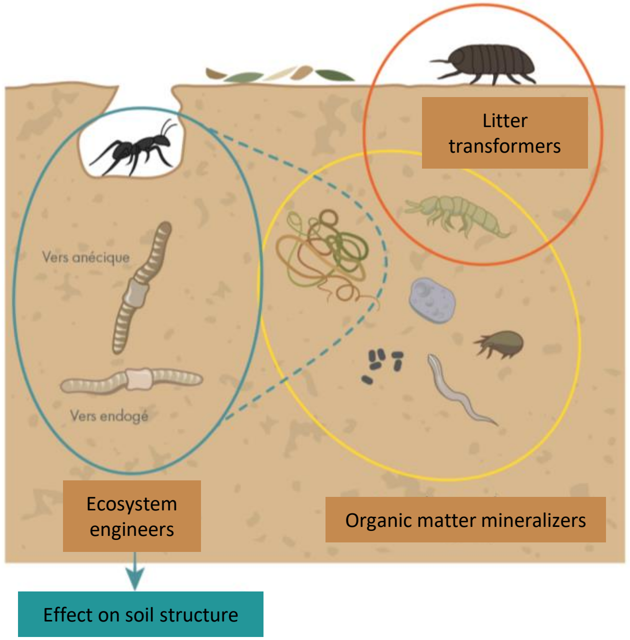


- Collembolans transports particles up to 200 µm diameter

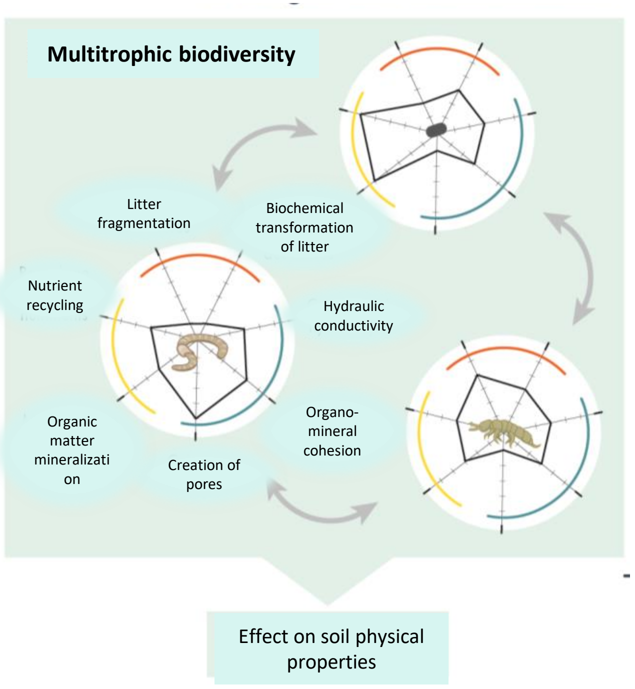
Maaß et al., (2015)

Feedbacks of trophic interactions on soil physical structure

Ecosystems engineers as a class of organism



… toward multifunctional organisms

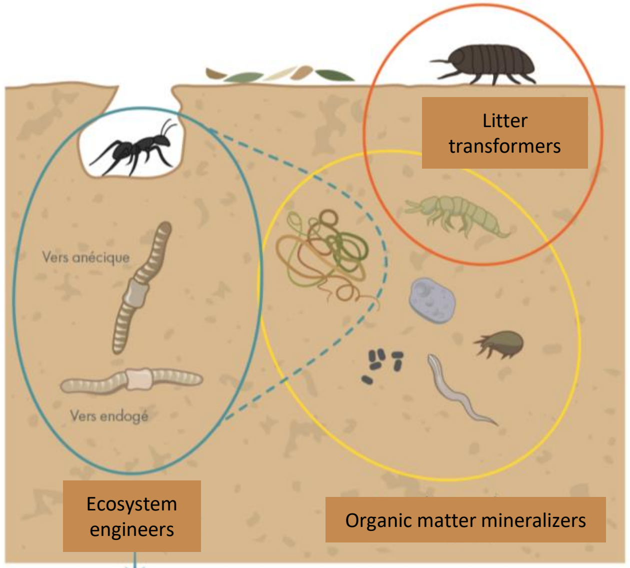


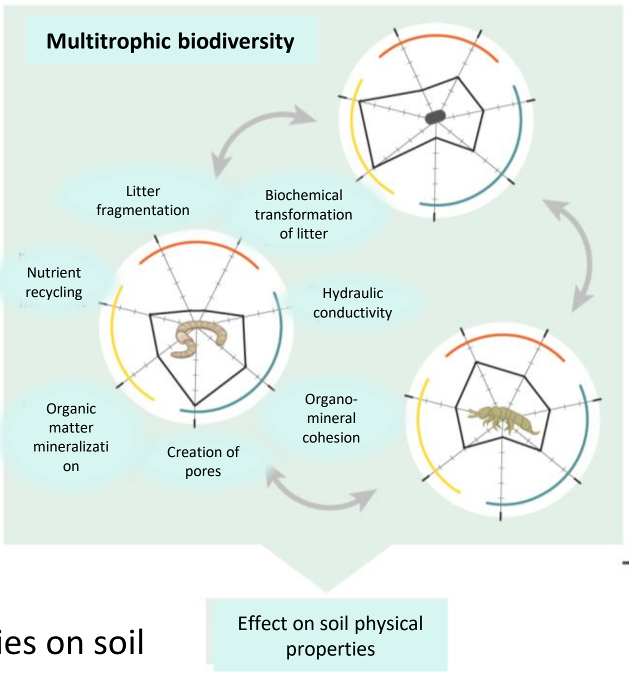
Erktan et al. (submitted at EGS)

Feedbacks of trophic interactions on soil physical structure

Ecosystems engineers as a class of organism

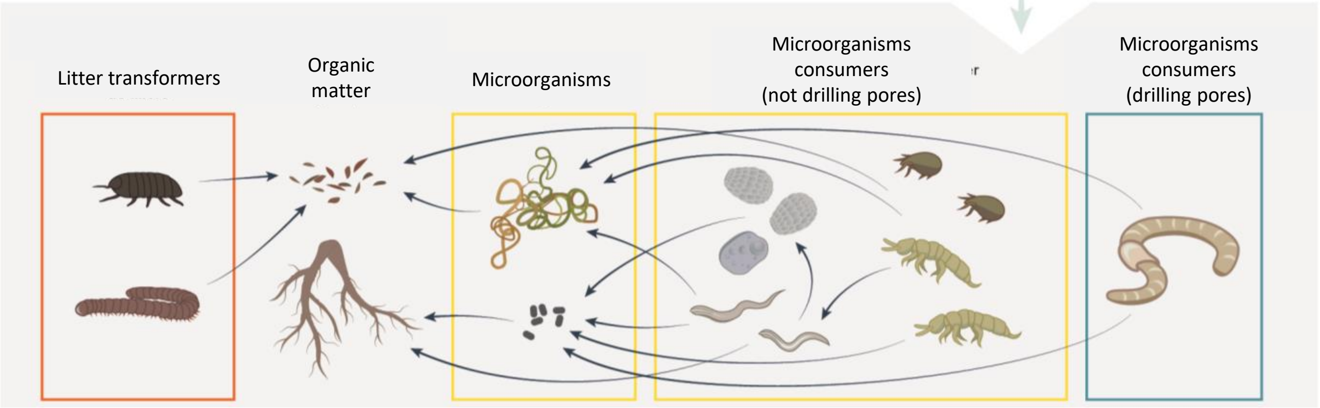
... toward multifunctional organisms





Effect on soil structure

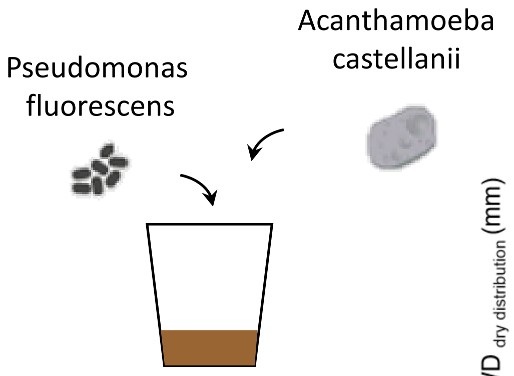
Quantification of the effect of soil communities on soil structure



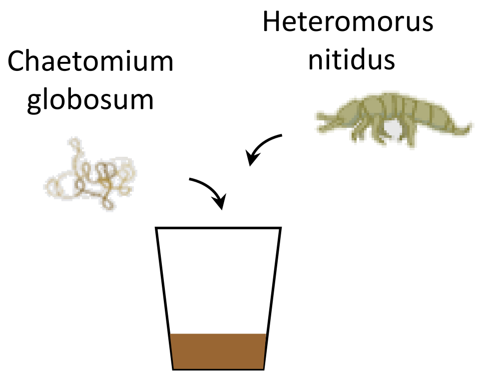
Erktan et al. (submitted at EGS)

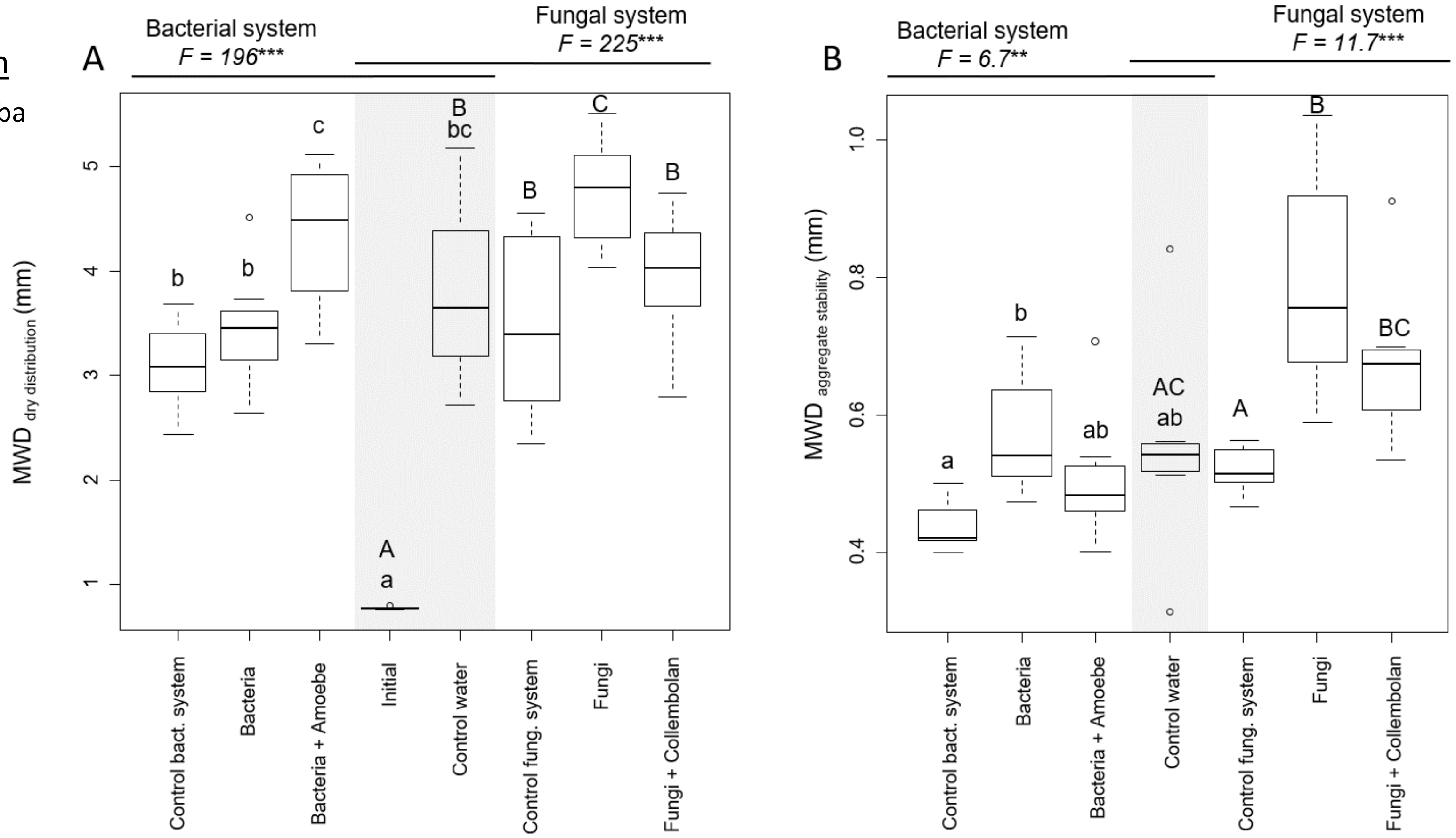
Feedbacks of trophic interactions on soil physical structure

- Bacterial-based interaction



- Fungal-based interaction

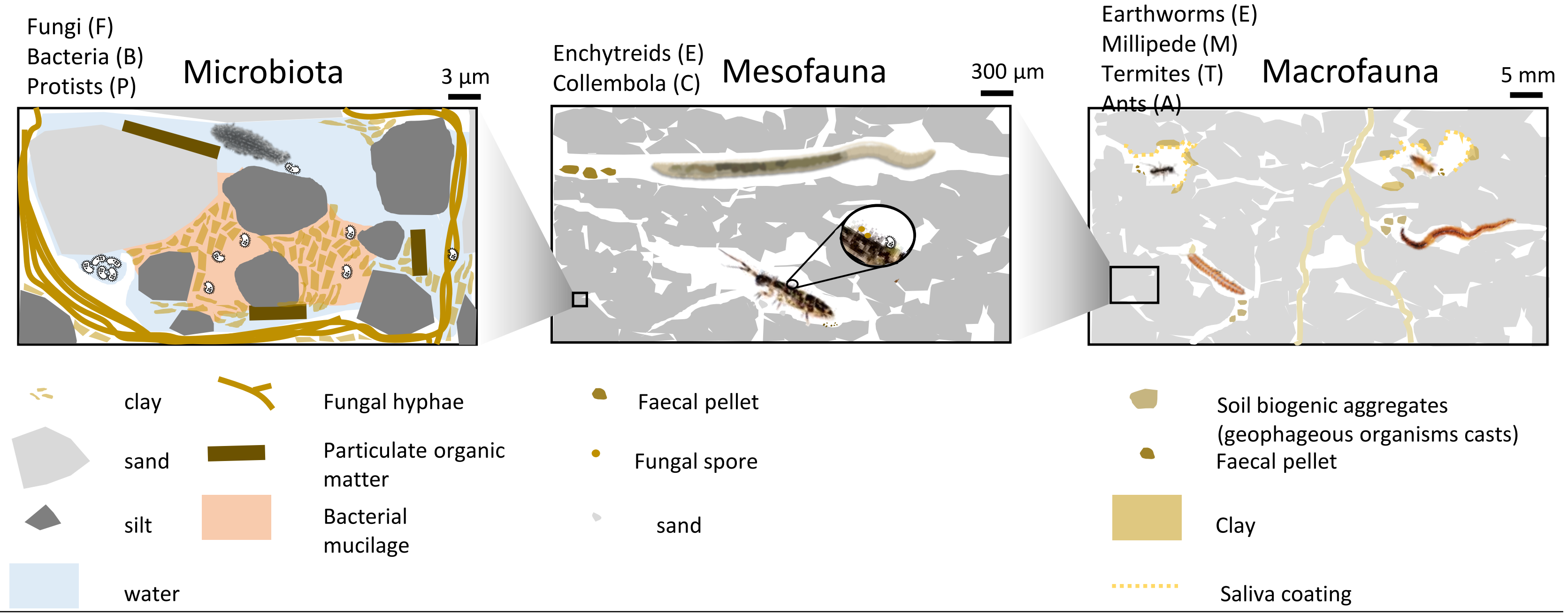




- Adding microbial predators modified soil aggregation

Erktan et al., (2020) Biogeosciences

Feedbacks of trophic interactions on soil physical structure



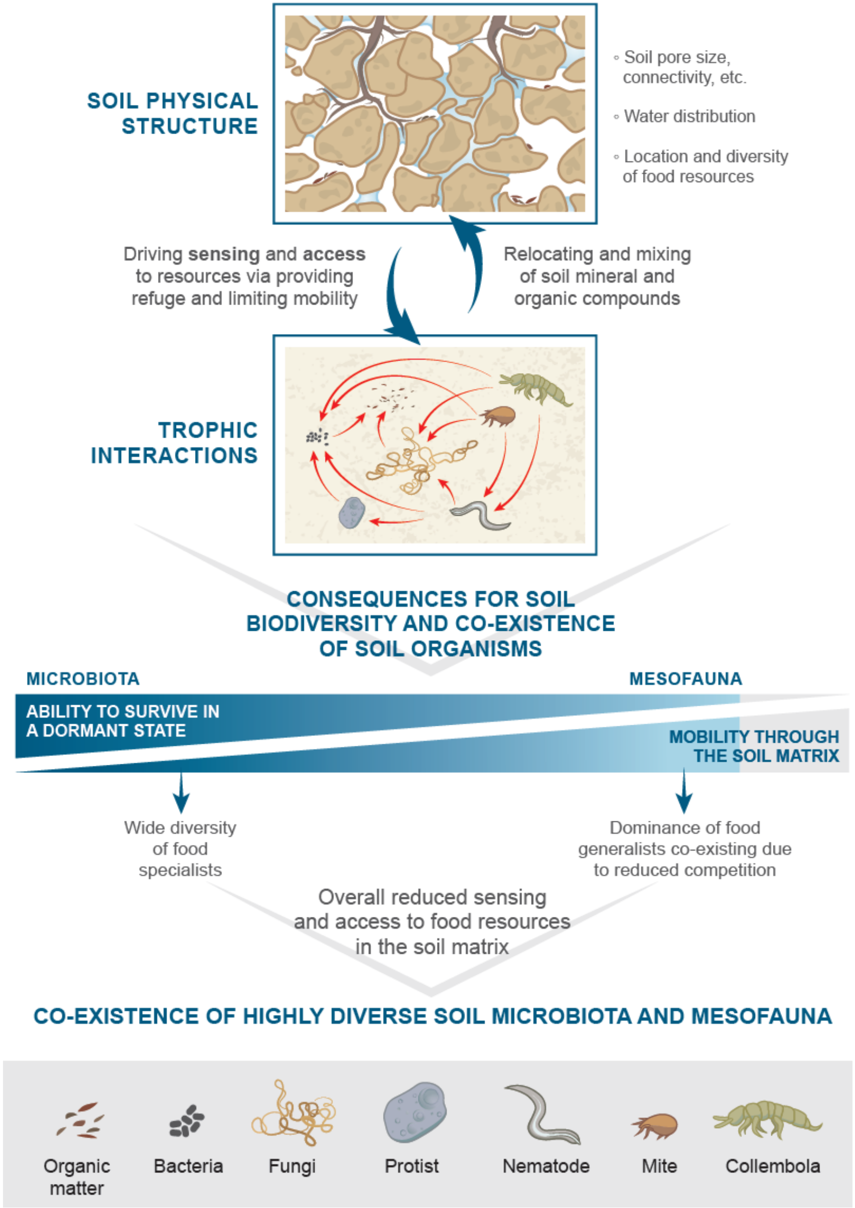
		Microbiota	Mesofauna	Macrofauna
Direct effects	Physical effect	- Gluing effect of mucilage on clay, leading to microaggregate formation (B, F) - Particle enmeshment (mainly F) - Redistribution (P) and realignement (F) of clay sized particles	- Create mesopores (E ?) - Move small sand particles (± 100 µm) within existing pore space (C) - Form (and break) microaggregates (enchytreids faecal pellet)	- Create macropores (mm) (E, T, A) - Move mineral particles via ingestion (E, M) or transport in mandibules (A, T) - Release of mucus (E) or saliva (A, T) cementing soil particles (macroaggregate)
Indirect effects	Redistribution of soil organisms	- Fungal highway for bacteria (F) - Fungal spore and bacteria dispersal via actively mobile bacteria or protists (B, F)	- Disperse fungal spores attached to their cuticle within pore space (C) - Redistribute organic matter and microbes via faecal pellets within pore space (C) - Move soil organic matter via molting, egg and necromasse	- Mix organic debris and microbiota by ingestion and release of faeces (E, M), transport of organic matter in their mandibules (A) and transport of fungal spores, bacteria or microarthropods eggs on their cuticle (E, T, A)
	Trophic effects	- Predator-prey interaction influence the microorganisms abundance and composition - Influence higher trophic level as being their food source	- Modify the abundance and composition of the microbiota through predatory interactions - Influence higher trophic level as being their food source	- Modify the abundance and composition of the mesofauna and microbiota through predator-prey interactions

Conclusions

Soil physical structure influences trophic interactions by e.g.:

1. Limiting sensing of food sources (via restricting the transport of volatiles through soil pores)
2. Restricting the overall mobility of organisms and the accessibility of resources / prey in small pores

- Feedback effect on soil organisms, and their interactions, on various aspects on the soil physical structure
- These restrictions promote soil biodiversity and select for specific adaptations for feeding in the dark soil labyrinth while allowing survival of weak competitors by reducing the strength of biotic interactions.
- Quantitative incorporation of effects of physical structure on trophic interactions requires interdisciplinary efforts for merging food web ecology and soil physics.

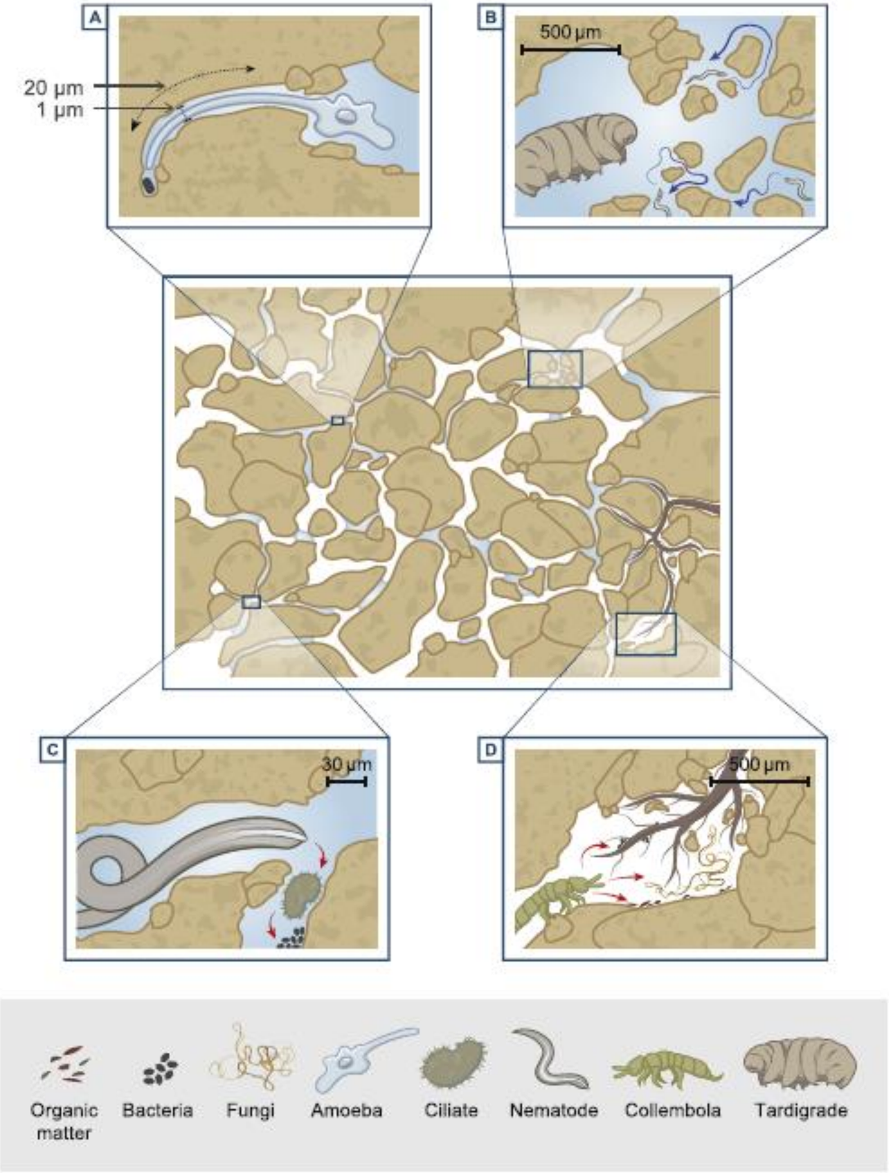


We thank Audrey Marville for drawing the schemes

Thank you for your attention

Source: FAO

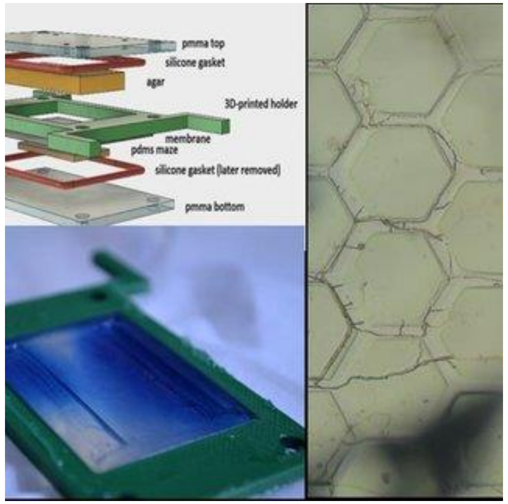
Adaptations of consumers and prey to feeding constraints inherent to the opaque and labyrinthine nature of soil



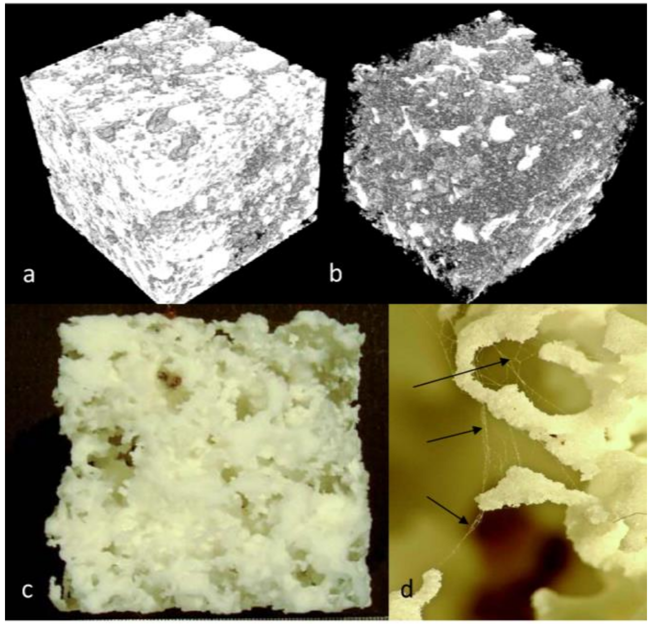
- The soft body of amoebae allowing them to adopt virtually any shape is an adaptation enhancing prey accessibility in the soil (or sediment) matrix and thereby the fitness of these organisms.
- For nematodes, that are larger than protists, tri-partite interactions between bacteria, protists and nematodes may be considered as adaptation allowing them to benefit from the access to hidden bacterial prey by protists.
- The dominance of omnivory and food flexibility among microarthropods may as well be viewed as an adaptation to the scarcity and discontinuous accessibility of food resources in space and time in the soil matrix.
- Adaptations also concern prey species by increasing protection from predators. For example, soil structure can induce changes in prey mobility resulting in enhanced avoidance of predators.

Erktan et al., (2020) SBB

Outlook: integrating soil food web ecology and soil physics



Soil Chips
(Edith Hammer)



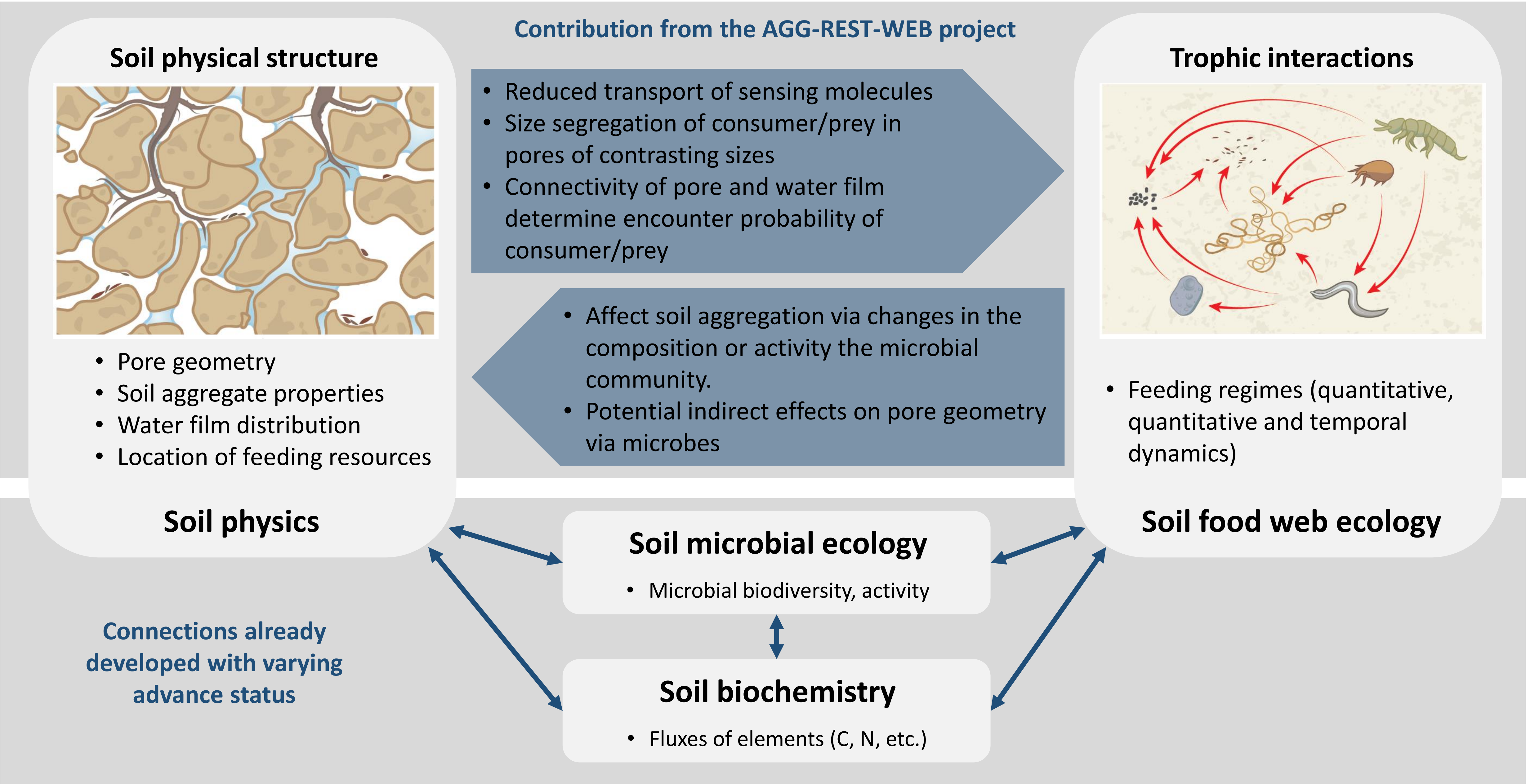
3D printing soils
(Wilfred Otten)

- Need for (i) improved knowledge on small-scale habitats of soil organisms, especially for those unable to modify or create their own pore space, and (ii) laboratory studies to experimentally explore how soil physical structure drives trophic interactions within and among micro-, meso- and macrofauna.

- Soil food web ecologists need to include descriptors of the characteristics of soil physical structure as standard parameters in the analysis of soil food webs: partnering with soil physicists and ecohydrologists.

- Linking the composition of soil microbial hotspots to the microbial gut content of microarthropods

- Experimental studies will be indispensable for improving the mechanistic understanding of the role of soil physical structure for trophic interactions (ex: Soil chips, 3D printing, etc.)


Contribution from the AGG-REST-WEB project
Soil physical structure
• Pore geometry
• Soil aggregate properties
• Water film distribution
• Location of feeding resources
Soil physics
• Reduced transport of sensing molecules
• Size segregation of consumer/prey in pores of contrasting sizes
• Connectivity of pore and water film determine encounter probability of consumer/prey
• Affect soil aggregation via changes in the composition or activity the microbial community.
• Potential indirect effects on pore geometry via microbes
Trophic interactions
• Feeding regimes (quantitative, quantitative and temporal dynamics)
Soil food web ecology
Soil microbial ecology
• Microbial biodiversity, activity
Soil biochemistry
• Fluxes of elements (C, N, etc.)
Connections already developed with varying advance status

Feedbacks of trophic interactions on soil physical structure

- Soil structure is dynamic and strongly influenced by the activities of soil organisms. However, most studies considered organisms in isolation and the role of trophic relationships and interactions on soil structure has rarely been in focus of scientific studies.

- Even though often not considered as such, the effect of earthworms and more widely geophageous organisms in general feeding on microbes by ingesting soil is a trophic interaction with major consequences for the physical structure of soils. For example, the feeding activity of earthworms result in compaction

- Soil micro- and mesofauna species typically cannot drill into the soil and form pores for their own habitat. Nevertheless, however, they may substantially affect the physical structure of soils, notably because many of them feed on microbes that are key players in forming soil physical structure (consumption, physiological changes, transport, etc..).

- Altogether, microbial consumers, such as protists, nematodes and microarthropods, are thought to impact soil physical structure mainly by modifying microbial communities, either directly via trophic interactions or through associated non-trophic interactions, such as the transport of microbial propagules on their body surface. While their effect is undoubtedly less strong than that of ecosystem engineers (and roots), we argue that they may be substantial and are currently largely negelected.