

Opening the black box of
decomposition relationships
between microbial communities and
detritivores.

Relationships between litter, microbial communities and detritivores in the decomposition process

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Summary

Decomposition is an ecosystem process, mainly important in the carbon and nitrogen cycles. When looking at what drives decomposition, there are three major drivers. These are plant litter quality, microbes and soil animals (detritivores). A large problem in understanding the decomposition process is that the remaining drivers all affect each other. When describing a single driver, the state of the other drivers should always be considered. When the interactions between the drivers is understood, it can be used to manage an ecosystem appropriately.

The most important relationship between litter and microbes is the ability of the microbes to alter the chemical composition of litter (even condition litter for detritivores). The litter also has effect on the microbial community, for a microbial community is adapted to the litter that they have been given historically.

The most important relationship between litter and detritivores, is the shredding of litter by detritivores. This increases the surface area and decomposition rate. However, it is still up for debate if detritivores feed on the litter or the microbes on the litter. This may also differ between species of detritivore. It is known that detritivores still prefer higher litter quality overall.

The most important relationship between detritivores and microbes, is the influence of bioturbation and faeces on the microbial community. It increases microbial activity (especially in systems with low quality litter). Microbes may be of nutritional importance to detritivores, but this is not confirmed. They also influence the gut microbes of detritivores, which define the organism functioning in the ecosystem.

In forestry, the depletion of forest soils is a major issue. With the use of the described relations between the decomposition drivers, forestry could be made more sustainable. The introduction of alder trees into commercial coniferous forests leads to many positive effects on the decomposition drivers. The overall litter quality becomes higher and therefor increases decomposition speed. This causes the turnover of nutrients into the soil to be faster. The difference in litter causes an increase in microclimate diversity, leading to a higher diversity of soil fauna. This increases the stability and resilience of a forest. While alder trees also have a second benefit in their Nitrogen fixating abilities, compensating for the N lost in harvesting.

Samenvatting

Decompositie is een ecosysteem proces, vooral belangrijk in de koolstof en stikstof kringlopen. Als er wordt gekeken naar wat decompositie aanstuurt, zijn er drie belangrijke drivers. Dit zijn plant strooiselkwaliteit, microben en bodemfauna (detritivoren). Een groot probleem bij het begrijpen van het decompositie proces is dat al deze drivers op elkaar inwerken. Bij het beschrijven van een enkele driver moet de staat van de andere drivers altijd worden meegenomen. Wanneer de interactie tussen de drivers is begrepen, kunnen ze gebruikt worden om een ecosysteem op een gepaste wijze te managen.

De belangrijkste relatie tussen strooisel en microben is het vermogen van microben om de chemische compositie van strooisel aan te passen (mogelijk het te preluderen voor detritivoren). Het strooisel heeft effect op microben in de vorm dat microbiële gemeenschap is aangepast op strooisel dat ze historisch hebben ontvangen.

De meest belangrijke relatie tussen strooisel en microben, is de versnippering van strooisel door detritivoren. Dit zorgt voor een toename in oppervlakte en decompositiesnelheid. Echter, het is nog ter discussie of detritivoren zich voeden met de microben of het strooisel zelf. Dit zou ook kunnen verschillen per soort detritivoor. Wel is bekend dat detritivoren een voorkeur hebben naar strooisel met hogere kwaliteit.

De meest belangrijke relatie tussen detritivoren en microben, is het effect van de bioturbatie en uitwerpselen op de microbiële gemeenschap. Dit verhoogt de microbiële activiteit (vooral in systemen met een lage strooiselkwaliteit). Microben zijn mogelijk een belangrijke voedselbron voor detritivoren, hier is echter geen zekerheid over. Microben kunnen ook effect hebben op de darmflora van detritivoren, welke de functie van het organisme binnen het ecosysteem bepalen.

In de bosbouw, is de uitputting van de grond een groot probleem. Met de beschreven relaties tussen de decompositie drivers kan bosbouw duurzamer worden gemaakt. De introductie van elzen in bossen leidt tot vele positieve effecten op de decompositie drivers. In het algemeen wordt de strooiselkwaliteit hoger en daarmee de decompositiesnelheid. Dit zorgt voor een snellere turnover van nutriënten in de bodem. Het verschil in strooisel zorgt voor een toename van microklimaat diversiteit, wat leidt tot een hogere diversiteit van bodemfauna. Dit zorgt voor een betere stabiliteit en veerkracht van het bos. Hiernaast hebben elzen een voordeel dat ze stikstof fixerend zijn, wat compenseert voor het verlies van stikstof bij de houtoogst.

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1. Introduction

Decomposition process

Decomposition of plant litter is a major component in the carbon and nitrogen cycle. Carbon and nutrients are bound into plant tissue. These nutrients have to be released into the soil for future plant growth. For plants to absorb the nutrients, decomposition of dead plant material is needed, altering the chemical structure and thus making it available again for plants. A large variety of organisms is responsible for this litter decomposition process. However, our understanding how plant litter and its characteristics, the main decomposers (microbes), their consumers and litter-feeders (soil fauna such as isopods and earthworms) interact and combined degradation of litter is poorly understood.

Plant Litter consists of multiple compounds, rich in carbon and nitrogen. The most important of forms carbon in litter are cellulose and lignin. The ration of cellulose and lignin differs between species and environments. This causes litter to have different properties in different locations. In current times anthropogenic sources bring a significant amount of carbon in the atmosphere, increasing global warming. Likewise, pollution is causing an increase in nitrogen levels. These additional sources of carbon and nutrients, as well as the rising in air temperature have an impact on litter decomposition. Therefore, it is important to understand what the major drivers are in decomposition to limit the consequences (Den Ouden, Muys, Mohren, & Verheyen, 2010).

Decomposition of plant matter consists out of three processes; leaching, fragmentation and chemical alteration (Chapin, Matson, & Vitousek, 2011). Leaching is the primary flux of soluble materials from decomposing material into the soil (Chapin et al., 2011). This is the first step in the decomposition progress (figure 1) and is dependent on water fluxes like rainfall (Berg & McClaugherty, 2008; Chapin et al., 2011). When labile compounds leach through the soil they are broken down further by chemical alteration (Berg & McClaugherty, 2008; Chapin et al., 2011). Fragmentation is the shredding of large organic materials into smaller ones by a huge variety of soil fauna (Chapin et al., 2011). This process increases the total surface of the litter available for micro-organisms and increases access to more easily consumable compounds of the litter (Chapin et al., 2011). This enhances the degradation of litter. Chemical alteration is the transformation of large chemical structures that cannot pass membranes to smaller molecules (Chapin et al., 2011). This transformation is entirely done by fungi and bacteria, together they are named microbes (Chapin et al., 2011). The action of microbes takes place within the soil matrix, or takes place in the gut of animals. Most animals cannot assimilate nutrients from litter, unless they get help from their gut microflora (Bouchon, Zimmer, & Dittmer, 2016). These three processes are influenced

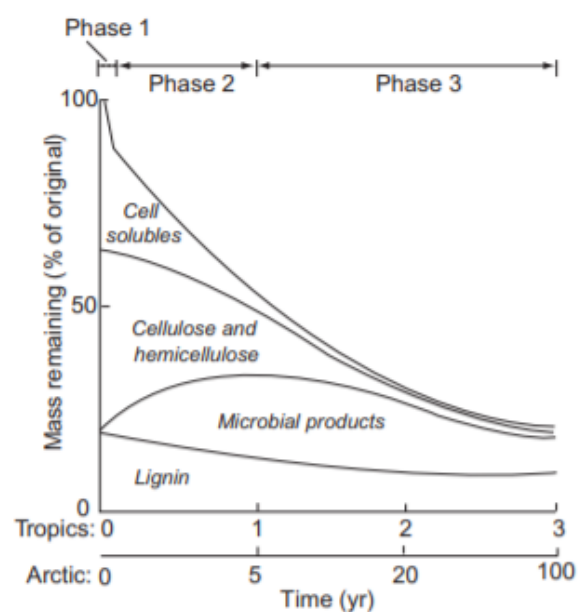


Figure 1: Litter degradation rate as a function of time. Three phases are recognized. In phase 1 most cell solubles are lost due to leaching. In phase 2 fragmentation by soil animals and chemical alteration by microbes are the key drivers. In phase 3 the leftover organic material is mixed with the soil and slowly broken down and leached into deeper layers. Components such as lignin take a long time to degrade while cell solubles have a short degradation time (Chapin et al., 2011).

by three major factors on three different spatial scales. On global scale climate influences litter decomposition, while on a more regional scale the quality of the litter is of importance, and on a local scale, when climate and litter quality are constant the decomposing organisms are the main driver (Couêteaux, Bottner, & Berg, 1995). Below the effect of the three drivers of litter decomposition will be explained in more detail.

Climate

Climate is an independent controlling variable in the decomposition process, influencing nearly all factors of decomposition. Therefore it is called a state factor (Chapin et al., 2011). It determines major water fluxes, as well as temperature and soil water content, all of which have an effect on the total decomposition rate by influencing microbial (or total biological) activity (Liang, Das, & McClendon, 2003; Sierra, Müller, & Trumbore, 2012). An increase in temperature and precipitation usually stimulate decomposition rates. Chapin et al (2011) mentions that depending on litter quality and climate the decomposition rate varies a lot. In the arctic it can take up to a hundred years to reduce total mass by 75% while in tropics it only takes 3 years. Especially in colder climates, global warming is affecting vegetation, microbial activity and soil fauna ultimately leading to increased decomposition rate (Aerts, 2006). Dryness is a major limiting factor in this, therefore a high annual precipitation is of importance for a high decomposition rate (Aerts, 2006). However, very high temperatures and low precipitation have a negative effect on the activity of microbes and soil fauna (Thakur et al., 2017) or shift community composition of soil animals with consequences for litter degradation (Bokhorst et al., 2011). Overall climate change has many direct and indirect effects on decomposition mostly causing an increase in decomposition rate (Allison & Treseder, 2011).

The increased carbon content of the air and global warming causes shifts in the C/N ratio in litter and thus effects the litter quality (Couêteaux, Bottner, & Berg, 1995; Gavazov, 2010). An increase in CO₂ levels causes concentrations in litter to alter; in Trembling aspen (*Populus tremuloides*) the phenolic compounds, lignin levels, and C:N ratio are increased while foliar nitrogen was decreased with higher CO₂ levels (Tuchman, Wahtera, Wetzel, & Teeri, 2003). Eventually leading to a decrease in decomposition rate. To limit the thesis, and climate being an independent driver, the thesis will focus on the other (interacting) drivers of the decomposition process.

Litter quality

Dead plant litter and other dead organic material is collectively called detritus (Chapin et al., 2011). At a regional scale, where climate is more or less stable, litter quality becomes the strongest driver that affects litter decomposition. Specifically the plant functional traits are the predominant control on litter quality (Cornwell et al., 2008). For example, on average eudicot litter decomposes four times faster than bryophyte litter, because they are different functional groups of plants (Cornwell et al., 2008). This is mostly caused by the different chemical composition of the different groups. The chemical makeup of the litter has strong effects on decomposition rate (Valiela et al., 1985; Chapin et al., 2011; Wickings, Grandy, Reed, & Cleveland, 2012). The litter quality is commonly assessed by the ratio of

lignin (or Carbon) to nutrients (especially nitrogen) (Valiela et al., 1985; Taylor, Parkinson, & Parsons, 1989; Cornwell et al., 2008) but other compounds such as phosphor are also of importance (Berg & McClaugherty, 2008). A large driver in litter degradation is the ratio of lignin/nitrogen in the litter (Figure 2) (Chapin et al., 2011). Litter with a high lignin/nitrogen ratio such as pine will degrade much slower compared to litter with a lower lignin/N ratio such as pin-cherry (Chapin et al., 2011). This could cause an accumulation of litter in various degradation stages. However, there may also be other components that could be important for decomposition, like Ca, Na and Mn content should also be considered (Hobbie, 2015). Calcium (Ca) is an important element for the functioning of soil fauna such as woodlice (Wood & Russell, 1987) and earthworms (Reich et al., 2005). Sodium (Na) has just like Calcium positive effects on soil fauna, an increase of Na shows an increased density in termites (Kaspari, Clay, Donoso, & Yanoviak, 2014). Manganese (Mn) in the form of Mn-peroxidase is used by fungi to break down lignin and could be a limiting factor in the process (Perakis, Matkins, & Hibbs, 2012; Berg, 2014). Litter quality not only influences organic matter decay, but also mineralization and nutrient immobilization (Aber & Melillo, 1982; Valiela et al., 1985).

Litter chemical composition is determined by many different factors. Most notably chemical makeup differs between plant species. For instance, there are large differences between coniferous and broadleaf species (Figure 2) (Sariyildiz, Anderson, & Kucuk, 2005; Chapin et al., 2011). In general, deciduous species breakdown faster than coniferous species (MacLean & Wein, 1978; Cornelissen, 1996; Chapin et al., 2011). But even within

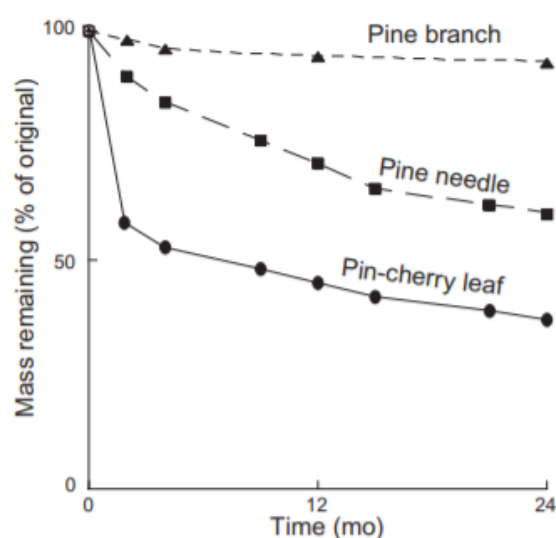


Figure 2: The effect of litter quality on decomposition rate. Pine branches have a high lignin/N ratio and are thus lower quality and decomposition rate than the low ratio pin-cherry leaf (Chapin et al., 2011; original: MacLean & Wein, 1978).

Table 1: Nutrient concentration in different coniferous needle litter. Edited version from (Berg & McClaugherty, 2008).

Litter	Concentration of nutrient (mg g ⁻¹)						
	N	P	S	K	Ca	Mg	Mn
Coniferous needles							
Scots pine ^a	4.8	0.33	0.55	1.07	4.4	0.49	0.79
Lodgepole pine ^b	3.9	0.34	0.62	0.56	6.4	0.95	1.79
Maritime pine ^c	6.8	0.54	1.01	1.95	3.1	1.90	0.59
Red pine ^c	6.0	0.36	0.73	1.40	8.9	2.00	0.73
White pine ^c	5.9	0.21	0.68	0.70	7.2	1.10	0.80
Jack pine ^c	7.8	0.64	0.77	2.30	4.0	2.10	0.25
Limber pine ^c	4.3	0.43	0.52	1.10	5.3	1.10	0.21
Norway spruce ^d	4.9	0.45	0.73	0.72	17.9	0.65	-
Stone pine ^e	3.0	0.57	1.36	5.9	7.1	2.4	0.19
Corsican pine ^f	4.7	0.54	0.71	3.5	7.8	1.3	0.5
Monterey pine ^f	5.6	0.22	0.7	1.3	1.9	0.93	0.47
Aleppo pine ^g	4.3	0.38	1.3	1.73	25.2	2.33	0.03
Average	5.2	0.42	0.81	1.85	8.3	1.43	0.58

functional groups there are differences between species. Berg & McClaugherty (2008) summarised data from nine studies and 20 litter species both coniferous and deciduous. Table 1 shows the concentrations of different elements in twelve different coniferous species.

Next to plant species, litter quality is also dependent on location characteristics where a plant grows (Sariyildiz et al., 2005). For example, altitude and the slope orientation of mountains have significant effects on litter quality, such as total N or lignin concentration (Sariyildiz et al., 2005). Litter properties can also vary annually (Johansson, Berg, & Meentemeyer, 1995). In the period 1973-1988 Johansson et al. (1995) measured Scots pine (*P. silvestris*) litter properties and found annual deviations in all ten properties measured. For example the lignin concentration had a lowest of 223 mg/g in 1973 and the highest lignin concentration was 288 mg/g in both 1979 and 1984. However, when looking at a global scale litter quality depends on the eye of the beholder, depending on the home biome of litter. Makkonen et al. (2012) used a total of 26 litter traits to measure litter quality. By using four representative species in four different biomes, they showed that different litter traits are of importance in different biomes for the total decomposition rate. For example in Temperate biomes the N concentration is of high importance in the decomposition rate, while in a Mediterranean biome the concentration of Phenols is more important (Figure 3).

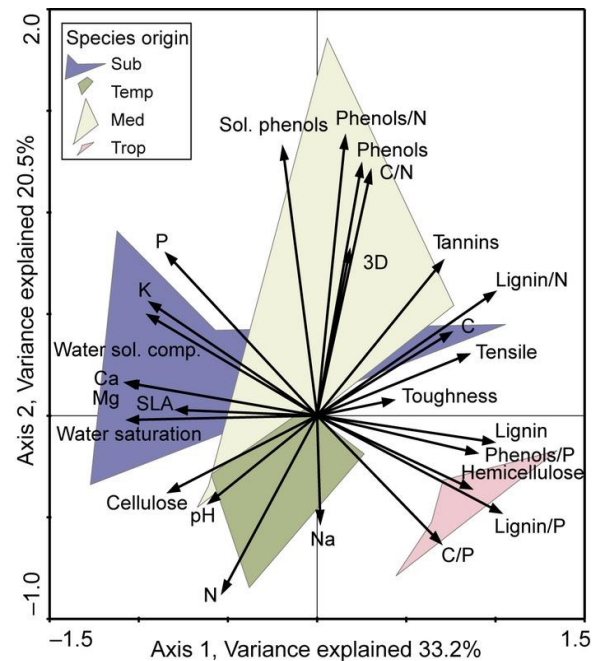


Figure 3: variance of decomposition rate in 4 different biomes. Subarctic (blue), Temperate (green), Mediterranean (yellow) and tropical (red). The corners of the polygons are 4 representative species of the biomes. The arrows represent the variance a specific traits has on the total decomposition rate. (Makkonen et al., 2012).

When looking at a longer time scales, decomposition rate slows down with litter age (Berg & Ekbohm, 1991; Chapin et al 2011). Fresh fallen litter has a higher quality resulting in a rapid decay in the early stage of decomposition but the remaining litter has a lower decomposition potential because carbon is respired and the remaining N compounds are more recalcitrant and difficult to decompose (Berg & Ekbohm, 1991; Chapin et al 2011).

Soil organisms

When climatic conditions are stable and the litter layer is composed on a fixed combination of litter species, the third driver in litter degradation becomes important: soil decomposers. When looking at a local scale, soil organism species composition and abundance play a large role. The diversity of the decomposers community is large (Figure 4). However, it is hard to group all soil organisms in a single group. There are three major groups that are defined by body size. These three groups are microbes (split up into bacteria and fungi) and microfauna, soil mesofauna and macrofauna (Figure 4) (Chapin et al., 2011). Microflora and microfauna consists out of organisms up to 100 μm these are mostly bacteria and fungi but most nematodes, protozoans and rotifers also fall into this group. Mesofauna range from 100 μm to 2 mm and consists mostly of Acari, Collembola, Dipluran and small termites (Isoptera) and millipedes (Diplopoda). Macrofauna ranges from 2 mm to 20 mm and consist of Isopods, Amphipods, earthworms, beetles (coleoptera) and most millipedes, modern spiders (Araneida) and molluscs. Next to the groups shown in figure 4, there is also megafauna which consists out of vertebrates like moles and some rodents (European Commission. Joint Research Centre & Global Soil Biodiversity Initiative, 2016). Megafauna has the ability to alter the ecosystem in the form of borrowing systems but have little effect on decomposition and will thus not be mentioned further. The diversity of soil fauna within and across groups is of importance, showing a reduced decomposition rate with a lower functional diversity (Handa et al., 2014). Below more detail will be given on how these different groups of organism affect litter decomposition.

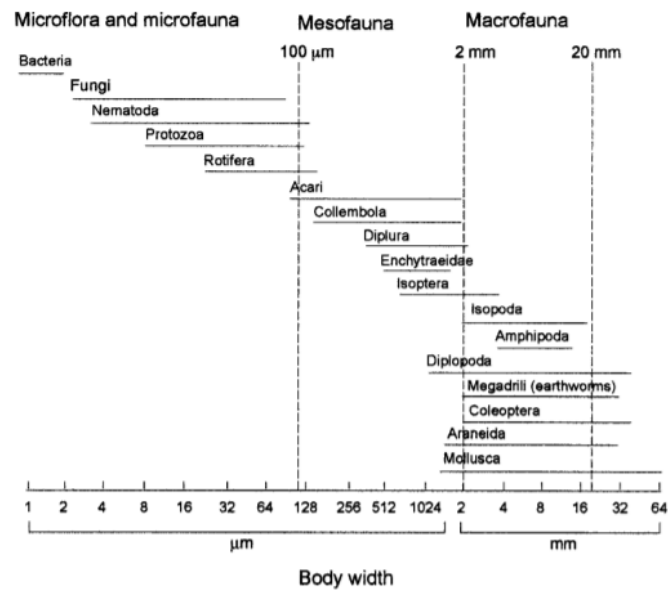


Figure 1: The body width of different groups of soil organisms. Microflora and microfauna < 100 μm , Mesofauna > 100 μm and < 2 mm, Macrofauna > 2 mm and < 20 mm. (Chapin et al., 2011; Original: Swift, Heal, & Anderson, 1979). Detritivores are mostly mesofauna or Macrofauna.

Microbes

While litter species together with the location where a plant grows may be responsible for the initial chemical composition of litter, microbes are primarily responsible for the chemical alteration of litter during degradation (Chapin et al., 2011). The two major groups of microbes are the fungi and the bacteria (Chapin et al., 2011). They differ in body size, bacteria being a factor smaller than fungi. They each have their own function in the decomposition process as they break-down different components of litter (Schneider et al., 2012). Bacteria are the main group of the digestion and chemical alteration of soluble organic substances such as sugars (Berg & McClaugherty, 2008; Chapin et al., 2011). Bacteria can create extracellular material that increases the capability to absorb more nutrients. This structure is called biofilm (Chapin et al., 2011). This allows the secretion and use of exoenzymes (Chapin et al., 2011). Exoenzymes break down larger molecules that are unable to pass the membrane of the bacteria cell (Chapin et al., 2011). However, since they do not have the capability to break down cell walls, fungi are needed to break down lignin in cell walls, this gives access to the cellulose molecules (Hatakka, 1994; Bugg, Ahmad, Hardiman, & Rahmanpour, 2011; Chapin et al 2011). Although there are also some bacteria that have the ability to break down lignin,

this process is mostly associated with fungi (Bugg et al., 2011). The composition of the microbial community has a significant impact on the decomposition rate, even an invasive species can alter community composition on micro- and macroscale and even ecosystem functioning (Hahn, 2003; Strickland, Lauber, Fierer, & Bradford, 2009; Litchman 2010). As example, a single fungi reduced tree growth in the USA causing a constraint on succession from grassland to forest (Rudgers, Holah, Orr, & Clay, 2007).

Soil fauna

Soil fauna is a very diverse group of organisms and are divided in different groups (Den Ouden et al., 2010). One way of grouping is based on body size, resulting in three groups; micro-, meso- and macrofauna. Microfauna has some indirect impacts on the decomposition process, because they feed on microbes and as such determine the density, activity and species composition of microbes. All three can have an effect on litter decomposition. However, their impact is believed to be negligible compared to the effects of macrofauna and will therefore mostly be excluded (Chapin et al., 2011). The many types of soil fauna as seen in figure 4, have different roles and habitats they reside in. A more functional way of grouping is using the diet of species. Based on diet soil fauna can be divided into microbivores, fungivores, detritivores (litter eating), (sapro-) xylophagous ((dead) wood eating), root eaters, carnivores and omnivores (Den Ouden et al., 2010). For species that belong to the same group the diet seems to be relatively the same. It is still debated what is causing the huge biodiversity of soil fauna and high species richness in soils (Bardgett, Yeates, & Anderson, 2005).

When litter decomposition is concerned the focus will be on detritivores. Detritivores are fauna that feed solely on detritus and the microbes that grow on the litter and are thus important in the decomposition process. Detritivores do not have the capability to digest organic matter on their own. They rely on a symbiotic relationship with their gut microflora. The gut microflora are able to digest dead plant material (Bouchon et al., 2016). The main influence of detritivores is not the digestion of litter, they only account for 5% of the total soil respiration, but their effects are mostly indirect (Chapin et al., 2011). The importance of detritivores lays in the fragmentation of litter and as ecosystem engineering (Chapin et al., 2011). Fragmentation of litter causes an increase in surface area in litter and accelerates the decomposition process (Chapin et al., 2011). Ecosystem engineers have the capability to alter their habitat. Macrofauna are mostly the ecosystem engineers (Chapin et al., 2011). Many detritivores are bioturbators, altering the physical properties of the soil (Howison, Olff, van de Koppel, & Smit, 2017) or mix litter with the mineral soil (Frouz et al., 2008). While mesofauna are the primary fragmentation organism, some macrofauna like amphipods do it as well (Chapin et al., 2011).

In the sections above, the role of climate, litter quality and soil organisms in litter decomposition are described. All these factors are of importance, and their relative impact depends on the spatial scale of resolution. From a global to a local scale the importance of climate decreases, while the importance of soil organism increases (Makkonen et al., 2012). However, at the local scale these drivers have the ability to interact with each other and this interaction is very important to understand how these factors drive litter degradation rates. Each of these drivers has the ability to alter the functioning of the others, and could either enhance or decrease activity depending on the driver and the aspects of that driver. Therefore, we need a better understanding of how these drivers interact with each other and how these interactions are important for litter degradation.

1.2 Relationship between decomposition drivers

While each component of the decomposition process has its own value, they interact with each other. Each driver has potentially the ability to alter the functioning of the other drivers, or is reliant on the driver to some extent. This is further explained in figure 5, it indicates the potential interactions between the drivers of litter decomposition. For instance, local climatic conditions determine the composition of plant species, which results in certain litter combinations, with certain litter properties and thus qualities.

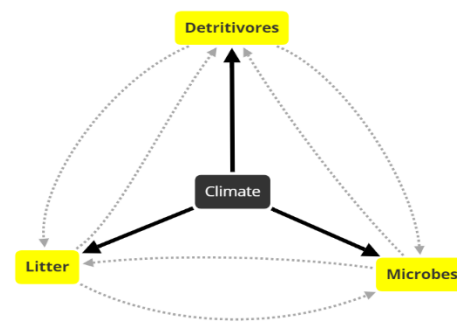


Figure 5: Scheme of relationships between climate, litter and microbes and detritivores that have to be described.

After litter quality, microbe activity becomes the most important driver in litter accumulation, causing tropical regions to barely have any plant litter because of the extreme degradation speed compared to other regions enabled by the climate (Olson, 1963; Chapin et al., 2011). Temperature and soil moisture are steering factors in microbe activity (Chapin et al., 2011). However, this is still limited by litter quality (Chapin et al., 2011). The litter quality has an impact on the microbial community composition and the same goes for vice versa (Wickings et al., 2012; Schneider et al., 2012; Cleveland et al., 2013). Soil fauna species composition is also dependent on local climatic conditions, with a change in species composition from dry to moist soils (Lindberg, Engtsson, & Persson, 2002). Soil fauna and microbes have (depending on the species) multiple relations including competition and predation (Sampedro & Domínguez, 2008; Domínguez, Aira, & Gómez-Brandón, 2009). But they also have some positive effects on the microbial community by altering the soil structure, creating a favourable habitat for microbes (Chapin et al., 2011). While there is also plenty of research on the effects microbes have on detritivores for example by facilitating the passage of food through the gut or colonisation of the gut (Ihnen & Zimmer, 2008). Litter gets shredded by detritivores, this increases the total surface area and makes more litter available for microbes (Chapin et al., 2011). High litter quality also has an effect on detritivore species composition, abundance and activity as physical attributes of litter (Yang & Chen, 2009; Cothran, Stoler, & Relyea, 2014) or chemical composition affect soil fauna (Loranger-Merciris, Imbert, Bernhard-Reversat, Ponge, & Lavelle, 2007).

To summarise; in figure 5 a scheme can be seen that shows the relations between the three drivers, with climate being a control factor. Microbial communities have a major impact on the change of chemistry in litter and the decomposition rate (Wickings et al., 2012), but this also affect the quality of litter as a food source for detritivores (Foucreau, Puijalon, Hervant, & Piscart, 2013; Ihnen & Zimmer, 2008; Quadros, Zimmer, Araujo, & Kray, 2014). These examples indicate that litter decomposition rate is heavily affected by the interactions between all three components (Vos, van Ruijven, Berg, Peeters, & Berendse, 2010). However, the details of these relationships are poorly described and sometimes an indirect effect is disregarded in research.

The focus of the literature research is on specific aspects and details of the scheme of network interactions. Therefore the main research question is: What is known about the interactions between the drivers of litter decomposition and where are the gaps in our knowledge?

Therefore the research question is divided in a number of sub-questions:

- Do litter traits influence microbial composition and activity?
- Do microbial communities influence decomposition rate and products of litter?

- Do microbial communities influence the physical properties of detritivores?
- Do detritivores influence the microbial composition and activity?
- Do litter traits influence the physical properties of detritivores?
- Do detritivores influence the decomposition rate and products of litter?

Answering these questions will give greater insight in the interactions between drivers of litter degradation affect the decomposition process. This could create a foundation for decisions within forestry or nature management. In commercial forestry the afterlife effect of trees, via dead branches, twigs and leaves that reach the ground where they are decomposed, determines indirectly soil fertility and the conditions for tree growth. The choice of tree species has major impacts on the litter quality and with that on tree growth and yield. However, climate change, via heat waves and dry spells, also determines the growth conditions for plants. Under climate change different tree species may be successful, resulting in a shift in species composition, hence, litter quality. This affect the soil and its organisms, with potential changes in the feedbacks to litter decomposition. Since climate change is a phenomenon nature management and forestry should react to, it is important to focus on the factors that are in human control. This would maximise nature conservation and forestry profit. This thesis could also serve as an introduction to someone that is not familiar with these relations and would like to have deeper understanding of these factors in the decomposition process.

1.3 Hypothesis

It is hypothesised that the relationship between microbial communities and litter are described at a high level since it is easy to leave out detritivores in an experiment. However, there is probably less information available on the effect of microbial communities on litter for microbial communities could fluctuate a lot and it is therefore hard to standardise. Information of effects of detritivores on microbial communities or litter is widely available and should not be a major unknown in the black box. It would be quite hard to measure indirect effects from microbial communities and litter on detritivores. Which means that it is hard to say what the effect is of either microbes or litter without taking the other in consideration since the exact diet of detritivores might be controversial in literature. The effects of litter quality or microbe abundance may be either a direct or an indirect effect on detritivore. Causing an expectation that the effects of microbes/litter on detritivores will be the biggest missing link.

1.4 Reading guide

Chapter 2. Method describes the process of the research and how the results come to be. In 3. Planning and organisation the management of the research is presented, regarding time, organisation and quality control. In 4. Results the results from the literature research can be viewed, all sub questions being answered in order as described. In 5. Discussion, discusses all results by making a short recap of the most important findings. After this the main research question will be answered and a conclusion will be presented.

2. Method

The main part of the research consists out of literature research. Since decomposition is a process of all ecosystem around the world, it would have been hard to describe every effect of all factors for different ecosystem types. Therefore, only universal effects were described. To show all the relationships in decomposition a flow chart was made with all components of decomposition (figure 3). This relationships in this figure was described and the figure was expanded to get a grip on the main factors on decomposition. To answer the sub questions the relationship was described and be made clear with a scheme like in figure 3 but only the two that are being discussed were connected and their direct relations and influences.

The literature research was mainly done by using google scholar. All scientific literature found on google scholar will be used. However, if a statement is made with a source older than 2005 it must be either backed up by another source newer than 2005, must be a mechanistic phenomenon or will be disclosed as an uncertainty. An article was considered scientific when the it is double peer reviewed or comes from a university. All literature in the results will be scientific. If the source describes a direct relationship between detritivores, litter and microbes it will be used. If an article does not bring new information compared to already used articles, it will be dismissed.

All search terms were kept track of, found in Appendix I: search terms. Sometimes when researching a sub question a relevant source for another can be found, in that case the original search term was used regardless of sub question. A combination of backward and forward research was used when looking at citations. How an article is found can be seen in Appendix I: Literature. Appendix I: Literature consists out of all sources used in the results section in APA style, their respective keywords and how the source was acquired.

Next to online research, Matty P. Berg and James T. Weedon from the Vrije Universiteit, Amsterdam were asked for literature on these relationships. Matty P. Berg has an expertise in soil fauna ecology, community ecology and extensive knowledge of *Orchestia* and its food. He is also specialist in decomposition studies and the role of soil fauna. James T. Weedon also has an expertise in decomposition, and especially in the role microbes play in the degradation of litter and how litter quality plays a role. They will also review the thesis periodically to check for inaccuracies.

The last section of the results consists of a description of a model system will be used as an example of how these relationships work in practice. *Orchestia Gammarellus* (Amphipoda) in north-west European salt marshes acts as a good model since there is extensive research on the ecology of this species. Matty P. Berg has extensive knowledge of the ecology of *Orchestia Gammarellus* while also taking apart in research on this species.

In *Appendix I: search terms* all used search terms will be presented. This will be sorted per sub question. *This list will be expanded during the research since more terms will be useful when going deeper into research.* In *Appendix II: received articles* all articles received from Matty P. Berg and James T. Weedon will be presented.

4. Results

4.1 Litter and microbes

Effect of litter traits on microbial

The main effects the litter can have on microbial communities regard the abundance, composition, diversity, activity and function of microbes. When talking about the microbial community composition, it can be divided into two main groups: the fungi and the bacteria. Next to the fungi and bacteria are the archaea and other non-fungal unicellular microbial eukaryotes (protists). Most studies focus on the fungi and bacteria. These each have their own role in the decomposition process. Within fungi and bacteria there are many more different groups. The composition and ratio between these groups can differ greatly depending on litter quality and vegetation origin (Strickland, Lauber et al., 2009; Urbanová, Šnajdr, & Baldrian, 2015). A community is adapted to their environment and the litter type they have historically received (Strickland, Lauber et al., 2009; Urbanová et al., 2015). The dominant vegetation, most notably that between coniferous and broadleaf (and thus the litter), seems to be the dominant factor influencing microbe diversity, especially in fungi (Urbanová et al., 2015, Prescott & Grayston, 2013).

As an example of how litter can influence microbial community, Strickland, Lauber et al (2009) used three different inoculum soils as starting microbial communities and used three different types of litter to show that over time the microbial communities diverge and adapt. The full table can be seen in appendix III, in table 3 some of the data is presented to show how different litter can have an effect on the same starting composition (Rhododendron). The measuring point after 300 days is presented to show as much divergence as possible.

Table 2: Strickland, Lauber et al (2009) difference in microbial community composition after 300 days from a Rhododendron inoculum on three different types of litter. (Data derived from Strickland, Lauber et al (2009)).

Litter type	Day	Bacteria %	Fungi %	Proteobacteria %	Acidobacteria %	Actinobacteria %	CFB %	Firmicutes %	Other Bacteria %	Ascomycota %	Other fungi %
Rhododen	300	82,7	17,3	30	36,6	3,6	4,4	0	8	11,6	5,7
Pine	300	93,3	6,7	50	40	0	0	0	3,3	6,7	0
Grass	300	100	0	76,7	6,7	3,3	3,3	0	10	0	0

However, Prescott & Grayston (2013) pointed out that even though there is a difference in microbial communities over time, the stage of litter decay may differ. Rather than just the incubation time, C loss and mass loss also have to be considered to determine the phase of litter decay (Prescott & Grayston, 2013). The effect litter has on microbial community might not be directly plant-species dependent but drifts more towards the physical properties of the litter, for example the pH and the C/N ratio (Siles & Margesin, 2016). Over time, the microbial community composition changes during the decomposition process (Bray, Kitajima, & Mack, 2012).

The accumulation of litter causes different phases of litter to stack on top of each other. Being buried, the environmental factors will change and will thus have a different effect on the microbial community. The soil depth has massive influences on the microbial community composition and abundance (Fierer, Schimel, & Holden, 2003; Kramer & Gleixner, 2008; Baldrian et al., 2011). While going deeper, the age of the litter increases and therefore the microbial community alters. However, at a certain point, the organic matter transforms from litter to humus or soil organic matter (SOM) (Chapin et al., 2011; Berg & McClaugherty, 2008). At this point the soil composition starts to play a role (Chapin et al., 2011). In coniferous forests and other soils where most of the decomposition takes place above the mineral layer, the soil properties have a much smaller impact (Chapin et al., 2011). While soil properties thus have little effect on litter decomposition aboveground, it should still be kept in mind when describing the relationships.

Litter mixing has great effects on the abundance, diversity and the composition of the microbial community (Chapman & Newman, 2009). Chapman & Newman (2009) looked at the effects of mixing litter, while most studies look at the decomposition of a single species. They found that when mixing litter from different species (aspen and conifer), the total phospholipid fatty acid microbial biomass increased by more than 40% on both species. Furthermore the composition changed significantly and diversity increased.

However, it should be noted that the microbial community is extremely dynamic and vulnerable. For example, Purahong et al (2014) found that the microbial community structure is influenced by differences in forest management. While receiving litter from the same species, the community compositions diverged significantly. Yet, he did not find any difference in enzymatic activity, meaning the function of the different microbial communities stayed the same (Purahong et al., 2014). Purahong et al (2014) explains this with functional redundancy, as there is a widespread of some enzymes in the microbial groups. To illustrate how dynamic and vulnerable the microbial community composition is, they could be influenced by themselves. For instance, fungal growth is reduced by the presence of bacteria while bacterial growth is stimulated by fungal presence (Schneider et al., 2010). Therefore, it should not always be taken for granted that a difference in microbial community composition causes a difference in microbial functioning, especially when historical litter is much alike. Of course, the difference between functional diversity and taxonomic diversity should not be neglected.

The most obvious effect of litter on microbial activity is the positive correlation between respiration rate and litter quality (Cleveland et al., 2013). However, when looking at the functioning of microbial communities, the litter chemical composition may have an effect on the use of exoenzymes. Allison & Vitousek (2005) found that (depending on available nutrients in the soil) an increase in complex molecules such as cellulose can increase the use of exoenzymes if the economical exchange is worth it for the microbes. However, this was done without litter, measuring enzyme production from microbes on the large molecules solely. There is some research about the effect of litter on enzyme production, showing it is mostly limited by N. However, these are old studies and were done under very specific circumstances (Sinsabaugh, Carreiro, & Alvarez, 2002). The effect on real litter is thus relatively unknown and has not been recently studied. The use of exoenzymes is not only determined by the litter quality but also by the decomposition phase. It also influences which type of exoenzyme is used (Šnajdr et al., 2010).

Effect of microbes on litter decomposition rates and products

There are three ways how microbial communities can affect litter decomposition: they influence the decomposition rate, the chemical conversion and the chemical product.

When discussing the decomposition rate, the microbial community has the ability to regulate the speed. Litter quality is perceived differently by microbial communities, a so-called home-field advantage (HFA) or perceived litter quality (Figure 6) (Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009; Strickland, Lauber, et al., 2009). This is mostly dependent on what the microbes historically received (See: *Effect of litter traits on microbial community*). The HFA effect does not necessarily always occur, if the litter is chemically alike, the advantage will not occur (Cleveland et al., 2013). Moreover, if the quality of litter is high enough and easy to decompose, the HFA effect is smaller (Strickland et al., 2009). Even though the HFA is of high importance on the decomposition rate, the overall decomposition rate is still mostly influenced by litter quality (64%), while the microbes are responsible for a much smaller proportion (25%) (Cleveland et al., 2013). However, the relative importance of the microbes increases over the decomposition process (Cleveland et al., 2013).

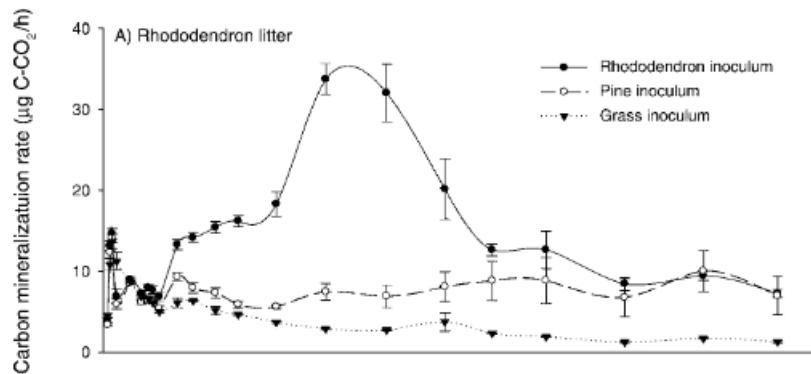


Figure 2: Different microbial communities breaking down Rhododendron litter. The homefield advantage (HFA) of the Rhododendron inoculum allows it to break down Rhododendron litter faster because they are adapted to it (Strickland, Lauber, et al., 2009). (all graphs in appendix III: full graphs and tables)

When looking into HFA with more detail, the HFA effect is sometimes unable to explain decomposition rates when there is a high diversity in litter quality within a specific area (Freschet, Aerts, & Cornelissen, 2012). Freschet et al. (2012) provided an alternative hypothesis that fills in this gap. Freschet et al. (2012) argue how the composition of the mix of litter is the main driver of the microbial community, causing the microbial community to be adapted to what the main resource of litter is. This is called the substrate quality–matrix quality interaction (SMI) hypothesis (Freschet et al., 2012). The difference between HFA and SMI is that HFA assumes that the matrix quality drives the microbial community and thus has an effect on all litter decomposition rates (Freschet et al., 2012). SMI explains that the dominant substrate quality defines the microbial community. This causes a difference in specific litter species decomposition rate (figure 7) (Freschet et al., 2012). However, this hypothesis is not yet fully confirmed as it was shown to only have moderate impact on the overall decomposition rate in an ecosystem (Freschet et al., 2012).

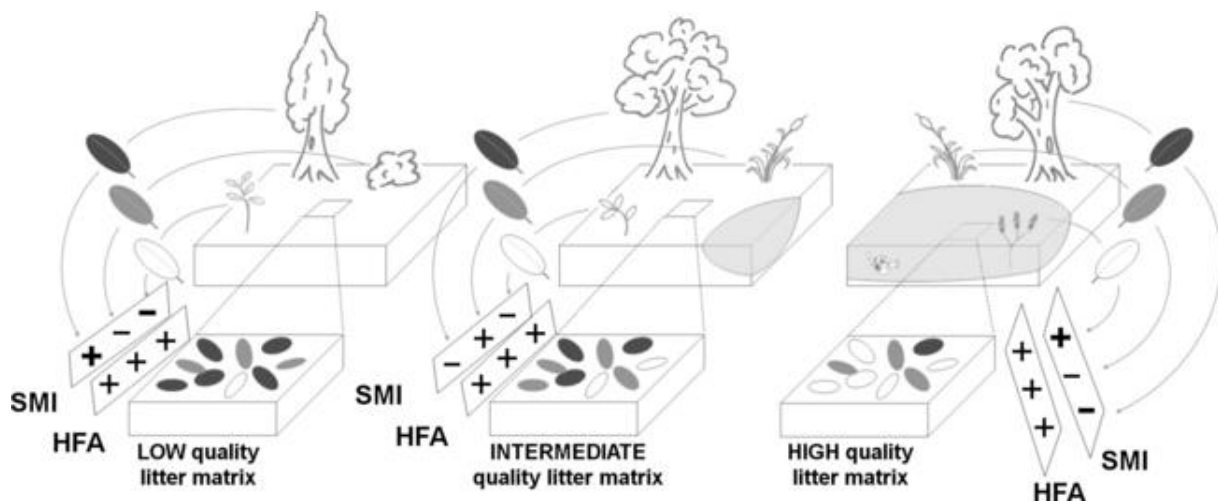


Figure 3: The difference in the home-field advantage (HFA) and the substrate quality–matrix quality interaction (SMI) hypothesis. The – or + show if it is an expected fast (+) or slow(-) decomposition rate for the different specific litter qualities shown as different colours in a low, intermediate and high quality litter matrix. White litter has a high quality, grey litter has an intermediate quality and black litter has a low litter quality. (From Freschet et al., 2012).

Wickings et al (2012) show us that there are three possible hypotheses on how microbial communities affect plant litter conversion (figure 8). The first hypothesis describes how the microbial community processes all litter into the same decomposition process regardless of the litter quality. The second hypothesis describes that the initial litter is the main factor influencing the chemistry of the end product. The third hypothesis describes that the microbial community composition has an effect on how the litter gets decomposed. However, since the initial litter quality has shown to be the most important factor on the decomposition product, the first hypothesis gets eliminated (Valiela et al., 1985; Chapin et al., 2011; Wickings et al., 2012). While the second and the third hypotheses are

not wrong, it is more likely to be a combination between the two. Wickings et al (2012) show in their research that there is a significant difference in the chemical composition of the decomposition products of grass and corn, which supports the initial litter quality hypothesis. Wickings et al (2012) also provided evidence for the decomposer control hypothesis, showing that a single litter type diverged greatly in chemical composition with different decomposer communities and stayed divergent during the decomposition process.

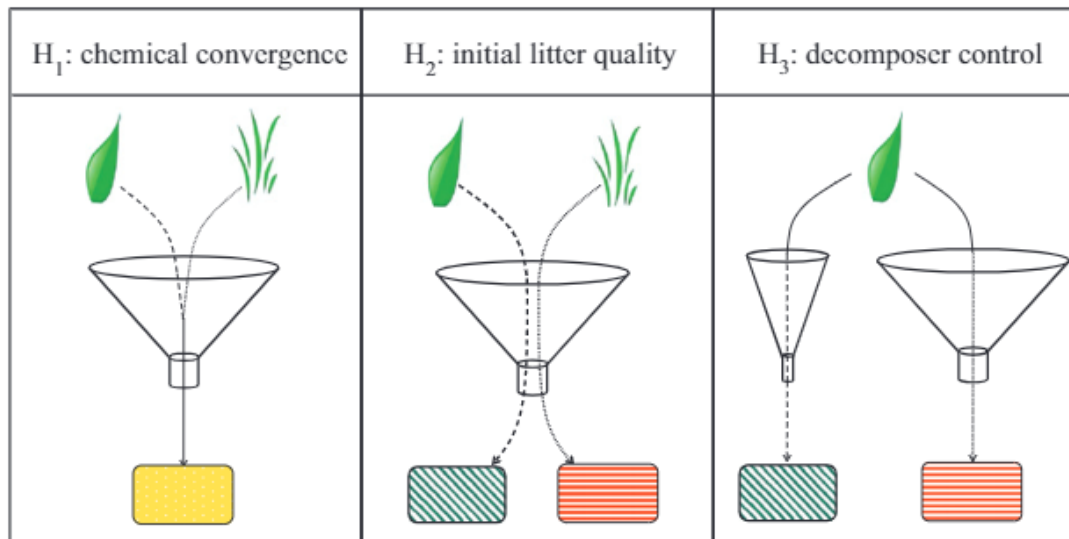


Figure 4: Wickings et al (2012) show possible hypotheses to illustrate what effect the microbial community has on litter decomposition.

Regarding decomposition products, the chemical aspects of the litter play the biggest role. The fibres and main polymers in litter (cellulose, hemicelluloses and lignin) can be broken down in different ways depending on the microbes (Berg & McClaugherty, 2008). While it is perhaps not considered litter, wood has a clear visual difference in degradation and could be considered a good model for lignin degradation.

Lignin gets degraded in several ways, this is dependent on the type of fungus it gets degraded by (Figures 9 & 10) (Berg & McClaugherty, 2008; Goodell, Qian, & Jellison, 2008; Den Ouden et al., 2010; Chapin et al., 2011). White-rot fungi are able to completely mineralize lignin (Berg & McClaugherty, 2008; Goodell et al., 2008). White-rot fungi secrete Mn-peroxidase, this is an enzyme to help decomposing lignin (Berg & McClaugherty, 2008; Goodell et al., 2008). Interestingly this causes Mn to be a possible limiting factor (Berg & McClaugherty, 2008; Goodell et al., 2008). Brown-rot fungi mainly focus on decomposition of cellulose and do not have the capability to degrade lignin as well as white-rot (Berg & McClaugherty, 2008; Goodell et al., 2008; Chapin et al., 2011). However, brown-rot fungi can make some alterations to the molecule (Berg & McClaugherty, 2008; Goodell et al., 2008). Brown-rot fungi target the methoxyl groups in lignin, leaving the altered lignin behind (Berg & McClaugherty, 2008; Goodell et al., 2008). Soft-rot can alter wood in extreme conditions, yet the mechanism on lignin degradation of soft rot is unknown (Goodell et al., 2008). The difference in lignin degradation is much higher between microbial communities than (hemi)celluloses, while fibre degradation also has great divergence between microbial communities (Berg & McClaugherty, 2008).

In figure 11, all previously described relations between microbes and litter are summarised to a scheme, showing direct and indirect relations regarding soil. Most important of these are the microbial adaptation on the litter and the chemical alteration of the litter.



Figure 6: White-rot in oakwood. By Auró - Own work, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=46955258> (Wikipedia).



Figure 6: Brown-rot on oakwood. CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=1098816> (Wikipedia).

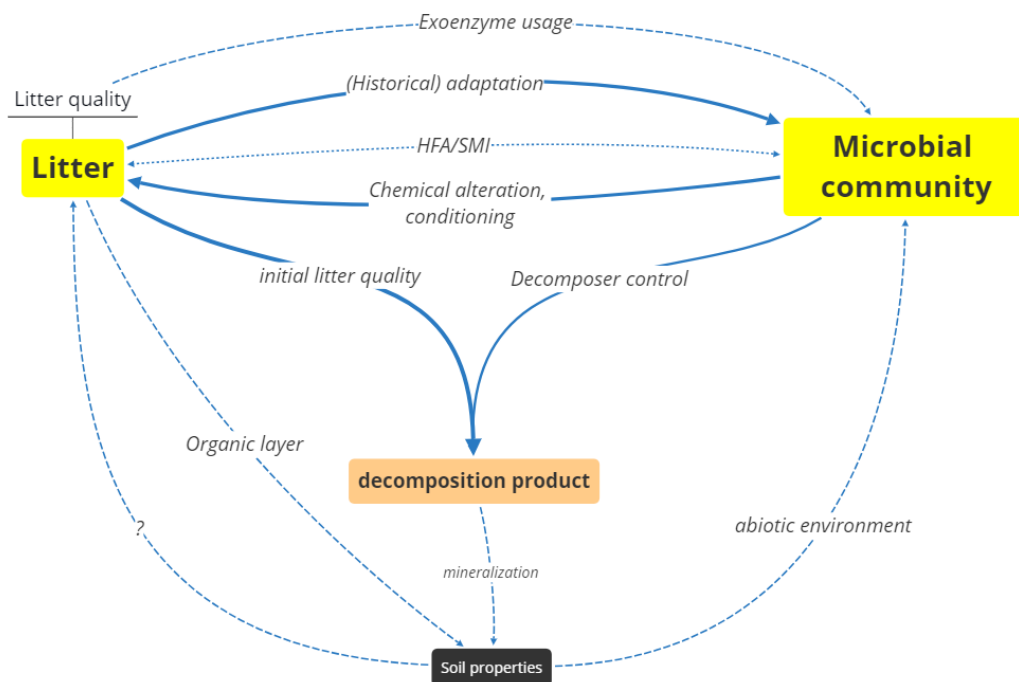


Figure 7: Current described relations between Litter and the microbial community, which can be linked to the soil properties.

4.2 Litter and detritivores

Effects of detritivores on litter

Detritivores can have multiple effects on litter. Not only does this consist out of direct alterations of the physical and chemical composition of litter, but they may also have an indirect effect on litter by altering the vegetation community.

When talking about the direct effect of detritivores, detritivores have shown to have significant impacts on the decomposition rate of litter (Vos, van Ruijven, Berg, Peeters, & Berendse, 2013; Dionne, Charles, & Nozais, 2014). This alters between detritivore species for significant amounts (Vos, van Ruijven, Berg, Peeters, & Berendse, 2010). The total effect detritivores have also increased with a higher detritivore functional diversity (Hedde, Bureau, Chauvat, & Decaëns, 2010). However, macrofauna only accounts for 5% of total soil respiration. Their major contribution to the decomposition process is the fragmentation of litter causing increased microbial activity (see section: *effects of detritivores on microbes*) (van Koppen, 1981, pp. 23; Chapin et al., 2011, pp 156-157; Schrama, van Boheemen, Olff, & Berg, 2015).

However, fragmentation is not the only alteration to the litter that macrofauna perform (Yang, Yang, Warren, & Chen, 2012). Yang et al (2012) performed an experiment where they tested the effects of

Collembola on normal litter and litter that was fragmented by hand. They showed that the presence of macrofauna is critical for the enhancement of decomposition rate. However, the exact mechanical reason is still debatable. They could either have a positive effect on the microbial activity (Mebes & Filser, 1998), or feed on the litter, making the litter chemically more available to degradation (Chahartaghi, Langel, Scheu, & Ruess, 2005). However, since the diet of macrofauna can diverge so much per species, the effect may be different per ecosystem, dependent on the functional diversity (Chahartaghi et al., 2005).

It also has been confirmed that macrofauna increase leaching of different forms of N and C (Huhta, Setälä, & Haimi, 1988; Fahey et al., 2011; Marhan, Auber, & Poll, 2015). During the shredding process, the litter being ingested by detritivores will get alkalized (Frouz, Špaldoňová, Lhotáková, & Cajthaml, 2015). The decomposition of excrement is therefore much slower (Frouz et al., 2015).

Overall, it is obvious that the decomposition rate increases with the presence of soil fauna. However, the impact of soil fauna differs per forest (Figure 12). Yang & Chen (2009) looked at the effect of soil fauna in different forest types, excluding or including them using different mesh sizes. While the density and richness of soil fauna was equal among sites, the effect of soil animals was much greater in a rainforest over other sites (Figure 12). Other studies also found that there was an increase in abundance and diversity in soil fauna based on tree diversity, finding the biggest correlation with tree species traits rather than overall species richness (Korboulewsky, Perez, & Chauvat, 2016).

Next to this, detritivores are known to be ecosystem engineers (Jones, Lawton, & Shachak, 1994; Chapin et al., 2011). They do this mostly in the form of bioturbation (Scheu & Wolters, 1991; Schrama, van Boheemen, Olff, & Berg, 2015; Howison, Olff, van de Koppel, & Smit, 2017). Bioturbation is caused by the movement and digging of soil fauna through the soil (Jones, Lawton, & Shachak, 1994). This alters the physical properties of the soil and the litter (Figure 13A) (Jones, Lawton, & Shachak, 1994; Chapin et al., 2011). As presented in section: *Effect of litter traits on microbial community*, the soil could have important impacts on the degradation of litter. The presence of bioturbators may cause the soil to have an effect earlier in the decomposition process. By altering physical properties of the environment, huge alterations in vegetation structure start to arise (Schrama et al., 2015; Howison et al., 2017). Howison et al (2017) describe how bioturbators stand in contrast with biocompactors (Figure 13B) (mostly large herbivores such as cows). They both have a significant effect on the vegetation structure, causing an autocatalytic loop between the two vegetation types. The difference in vegetation means a difference in plants, therefore a difference in litter.

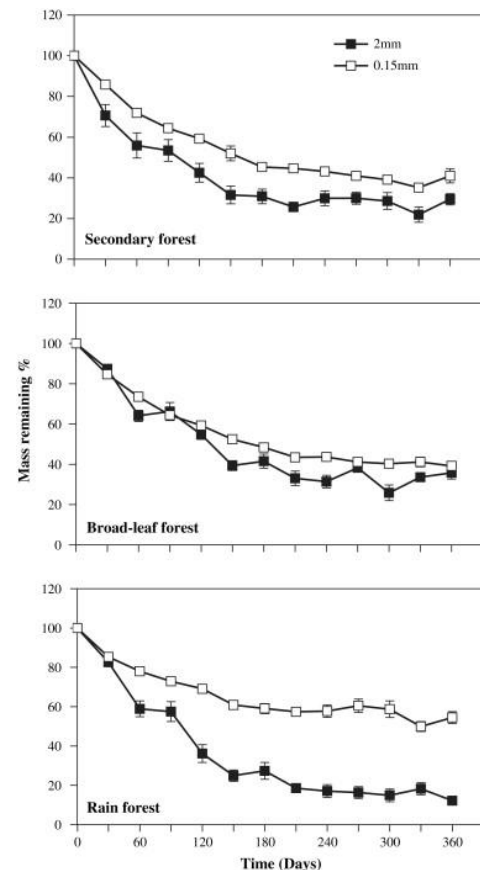


Figure 8: Effect of soil fauna in different forest types. Difference between decomposition rate with and without soil fauna in secondary forest: $19.5\% \pm 1.7\%$; In broad-leaf forest $8.7\% \pm 2.6\%$; In rain forest: $41.6\% \pm 1.3\%$. (From Yang & Chen, 2009)



Figure 9: A: Bioturbation by soil fauna causing a loose soil. B: Biocompaction causing a compact soil. (From: Howison et al., 2017. Original fotos by Han Olff)

Effects of litter on detritivores

Since there is a high diversity in feeding habits among saprophagous macrofauna, it is hard to classify all of them. However, there are some things to say about food preference, food conversion, influence on the physical- and life history traits of detritivores and influences on the soil fauna community. It should be kept in mind that the soil fauna community does not only include detritivores but also other species that have different feeding patterns.

The community is mostly determined by the (a)biotic components of the environment. The accumulation of plant litter has a big effect on the chemical composition of the O-horizon in the soil (Chapin et al., 2011). This change in abiotic components will cause a shift in the selection of species. Reich et al. (2005) found that litter with high calcium content causes an increase in earthworm abundance (figure 14). This is caused by the alterations in abiotic factors the calcium causes, such as higher soil pH. However, different litter types have little to no effect on the soil fauna abundance or richness (Yang & Chen, 2009). Species diversity and evenness are the major differences in soil fauna communities between different forests (Yang & Chen, 2009). Furthermore, litter output and increasing plant cover have a positive effect on soil biota density (Frouz et al., 2008).

There is plenty of research that shows that detritivores prefer litter of higher quality (Zidar, Kaschl, Drobne, Božič, & Štrus, 2003; Ashwini & Sridhar, 2005; Quadros et al., 2014). When looking at the physiological side of the effects, this preference seems quite logical. The litter quality seems to have a significant effect on the physiology of detritivores. The nutritional content in detritus seems to have a positive effect on life history traits, such as growth and survival rates in Amphipoda (Danger, Arce Funck, Devin, Heberle, & Felten, 2013; Cothran, Stoler, & Relyea, 2014), while also causing a development of larger sexual traits (Cothran et al., 2014). The effect on life history traits was also found in Isopoda, linking it to phenotypic plasticity (Hassall, Helden, & Benton, 2003). The phenotypic plasticity is quite obvious, since there are major differences between a generation and the next. Though as presented in section: *Effect of litter traits on microbial community*, a high litter quality also promotes microbial activity and abundance. This should be considered when looking at the effects on detritivores.

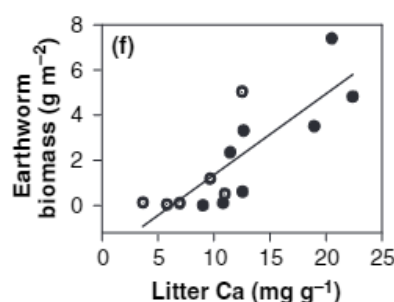


Figure 10: An increase in litter calcium causes an increase in total earthworm biomass. (From: Reich et al., 2005).

Food preference is different for every species depending on the niche they fill in the ecosystem. However, species may have the same fundamental and realised niches when looking at their diets (Dias & Hassall, 2005). Therefore, there might be some general patterns to describe. Ashwini & Sridhar (2005) did research on the feeding preferences of a tropical pill millipede, *Arthrosphaera magna*. They found that the millipedes did not only prefer higher quality of plant litter, they also preferred older litter that is conditioned by microbes over fresh litter. This was also found in Amphipoda (Bärlocher & Kendrick, 1975; Foucreau et al., 2013) and Isopoda (Zidar et al., 2003; Zimmer, Kautz, & Topp, 2003; Ihnen & Zimmer, 2008). The way litter is influenced by microbes also has an effect on feeding preferences. As readable in section: *Effect of microbes on litter decomposition rates and products*, lignin is degraded in several ways. It seems that woody structures degraded by white-rot have a higher nutritional value than if they were degraded by brown-rot (Harrop-Archibald, Didham, Standish, Tibbett, & Hobbs, 2016). Thus, this might encourage detritivores to eat easier digestible food. However, there are multiple theories around this phenomenon. Ihnen & Zimmer (2008) summarise the three hypotheses. The first hypothesis (H1) describes that microbes process the litter and facilitate digestive utilization before feeding and during gut passage. The second hypothesis (H2) describes that they do not eat the litter but detritivores feed on the microbial biomass on the litter. The last hypothesis (H3) describes that the microbes maintain a healthy gut flora of detritivores.

Foucreau et al. (2013) found that microbes alter the physical structure of leaf litter. Leaf toughness decreases with microbial facilitation (Figure 15), while it is also known that isopod palatability decreases with increasing leaf toughness (Quadros et al., 2014). This is a strong argument for H1, but there are other aspects that Quadros et al. (2014) describe that influence palatability, such as an increase with high nitrogen and calcium and a decrease with a high C:N ratio and leaf thickness. Foucreau et al. (2013) found that thickness barely altered when litter was conditioned and found an increase in ergosterol, other traits were not measured. The total abundance of elements as Ca, C and N in the litter and microbes should not be decreased unless leaching is a factor. However, the allocation and forms of these elements may differ due to microbial conditioning. This could mean an alteration in availability to detritivores.

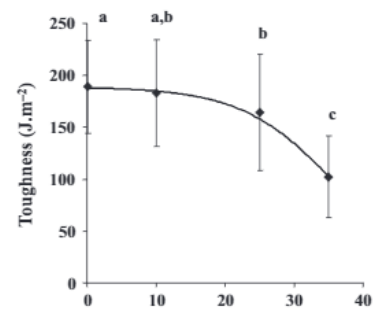


Figure 11: leaf toughness decreases over time in *Alnus glutinosa* when conditioned by microbes. (From Foucreau et al., 2013).

Ihnen & Zimmer (2008) found that *Porcellio Scaber* prefer feeding on litter colonized by actinomycetes (Gram-positive bacteria). If this behaviour is consistent when feeding on other Gram-positive bacteria, across other detritivores species, it would make a strong argument for the second hypothesis (Ihnen & Zimmer, 2008). For more information on H2 and H3 see section: *Effect of microbes on detritivores*.

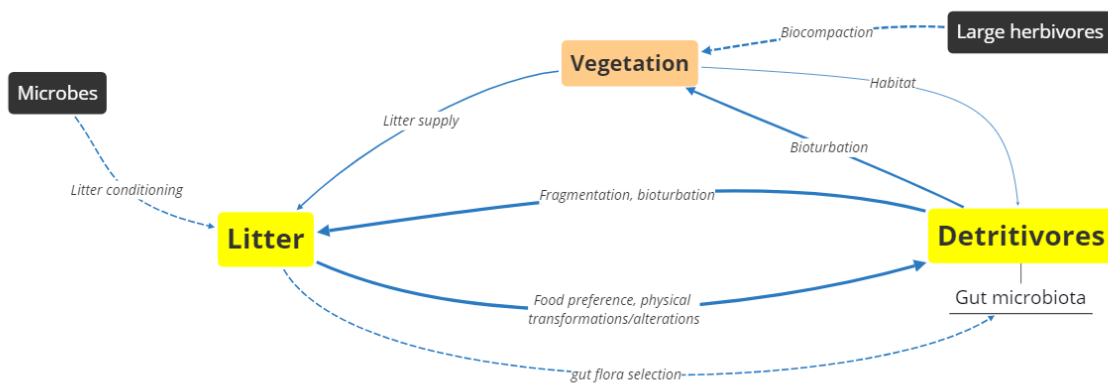


Figure 12: Currently described relations between litter and detritivores, linked with vegetation as a minor factor.

4.3 Detritivores and microbes

Effects of detritivores on microbes

Since microbial communities are very vulnerable, there are many ways how detritivores alter the functioning of microbes. These could be either positive or negative (David, 2014). Detritivores may also have an impact on the community composition and abundance. The ecosystem engineers may also alter the habitat of the microbes.

When looking at positive effects that detritivores have, they have a positive effect on microbial decomposition rates of nitrogen, microbial biomass, metabolic activity, N mineralisation and C mineralisation (Lopez, Levinton, & Slobodkin, 1977; van Koppen, 1981, pp. 23-24; David, 2014; Schrama et al., 2015). Van Koppen (1981, pp. 24) describes four possible reasons for this in amphipoda, though there may be more when looking at all detritivores. Reason 1: Microbial colonisation of the faeces (R1). Reason 2: Improved mixing of sediment and litter, inducing better availability to microbes (R2). Reason 3: Excreted ammonia is a rich source of nitrogen (R3). Reason 4: Detritivores influence growth and food uptake of microbial populations directly (R4).

Looking at the microbial colonisation of the faeces (R1), the most important part is the chemical structure change litter undergoes when being transformed to faeces (Joly, Coulis, Gérard, Fromin, & Hättenschwiler, 2015). Joly et al (2015) found that after litter was transformed into faeces, microbial activity (measured in substrate induced respiration (SIR)) was homogenized. This means that the respiration rate on the faeces was equal in all litter species. They measured initial litter SIR and compared it to SIR when the litter was transformed into faeces. They found that when the initial litter quality was low, the difference of SIR between litter and faeces was greater than when the initial quality was high. Therefore, the consequence of the effect of the transformation is dependent on the initial litter quality, the effect being greater in lower quality initial litter (Figure 17) (Joy et al., 2015).

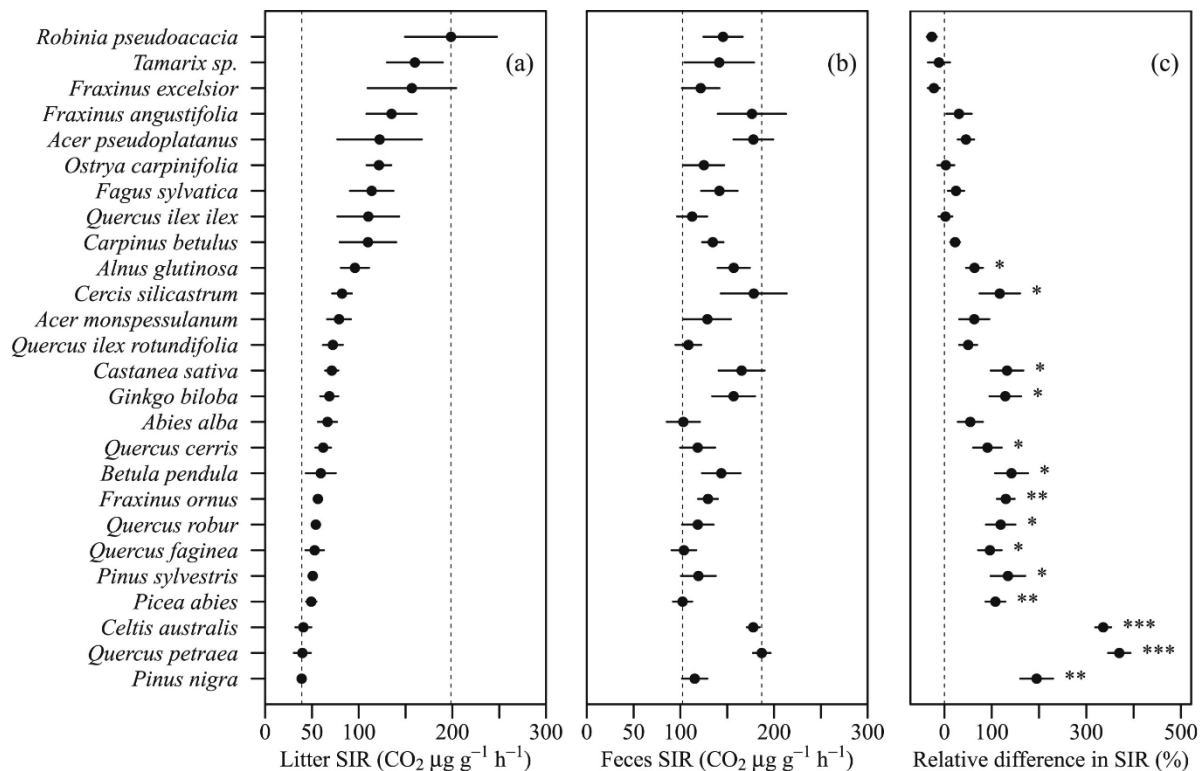


Figure 13: Substrate induced respiration (SIR) Litter (a) and Faeces (b). Litter SIR ranging from 50 $\text{CO}_2 \mu\text{g g}^{-1} \text{h}^{-1}$ to 200 $\text{CO}_2 \mu\text{g g}^{-1} \text{h}^{-1}$. Faeces SIR ranging from 100 $\text{CO}_2 \mu\text{g g}^{-1} \text{h}^{-1}$ to 200 $\text{CO}_2 \mu\text{g g}^{-1} \text{h}^{-1}$ seemingly independent of initial litter SIR. In (c) the relative difference (%) in SIR can be seen, showing an inverse correlation to the initial SIR. (Edited figure from Joy et al., 2015).

Not only is colonisation of the faeces a reason for an increase in microbial activity, during gut passage the microbial abundance also increases, especially caused by rapid growth in the hindgut (Diplopoda) (Anderson & Bignell, 1980).

The mixing of litter and soil (R2) is done by bioturbators. These do not necessarily have to be detritivores, but in many systems, this is a large role that detritivores fill (Meysman, Middelburg, & Heip, 2006). However, this is more of an interaction between bioturbators and the physical properties of litter as seen in section: *Effects of detritivores on litter*. The mixing of litter and soil is mostly an indirect effect on the microbial communities. There is also proof of detritivore bioturbation having a direct impact on the soil microbe community boosting diversity, abundance and mostly activity, enhancing N and C mineralisation (Fonte, Kong, van Kessel, Hendrix, & Six, 2007; Noguez et al., 2008; Fujimaki, Sato, Okai, & Kaneko, 2010).

Litter being transformed into frass (faecal pellets) is known to enhance ammonia extraction and N availability (R3) by Diplopoda, this is however still influenced by the digested plant material (Cárcamo, Abe, Prescott, Holl, & Chanway, 2000). Reason 1 and reason 3 are therefore very closely related. For R4, it is highly likely that detritivores help the colonisation of fresh litter by transferring it with movement or faeces, this affects the microbial decomposition rate (Schrama et al., 2015). Other than that, there is little confirmation for R4.

Detritivores also have the capability to feed on microbes, but the significance of the impact is still unknown. M. Berg et al. (2001) presented a food web of a scots pine forest soil. While it does not specifically show macrofauna, the only macrofauna group described are *Collembola*. They are seen as mostly fungivorous, but their direct relation to detritus is still unknown. It is known that detritivores prefer feeding on litter inhabited by microbes (Ihnen & Zimmer, 2008). However, there is little

knowledge on feeding having either a direct or an indirect effect on microbial communities (see sections: *Effects of litter on detritivores* & *Effects of microbes on detritivores*). The negative effect of potential predation next to the positive influence of the presence of detritivores on the functioning/composition of microbial communities is yet unknown. Not all detritivores mainly feed on microbes and actually promote microbial density with nutrient enrichment, caused by detritus processing (Hoekman, Winston, & Mitchell, 2009). Pure microbe predators, that do not have a secondary function promoting microbial growth, have a negative effect on microbes. However, these are not considered detritivores (Hoekman et al., 2009).

Many different studies have found different results in microbe reactions to detritivores. They seem to have different effects on the microbial community depending on the species. Earthworms show a reduction in fungal and bacterial species density, diversity and richness (McLean, Migge-Kleian, & Parkinson, 2006; Gómez-Brandón et al., 2010). This is possibly caused by the disruption of hyphae (McLean et al., 2006). However, when a system is adapted to the earthworm presence, they perform better with a higher microbial activity (McLean et al., 2006). While Amphipoda seem to have a positive impact on the microbial richness and diversity in the litter (Lopez, Levinton, & Slobodkin, 1977; Mengoni, Focardi, Bacci, & Ugolini, 2013). In Isopoda it was found that *Porcellio scaber* had a negative effect on the microbial density, while *Oniscus asellus* had a positive influence on the microbial density (M. Zimmer & Topp, 1999). Both species still had a positive impact on the soil respiration and the cellulolytic activity (M. Zimmer & Topp, 1999). However, isopods are known to have significantly different diets between species (Abd El-Wakeil, 2015). Thus, the niche differential and effect on decomposition between isopod species could be very diverse.

Effects of microbes on detritivores

The three hypotheses presented in section: *Effects of litter on detritivores*, present if detritivores feed on microbes or litter, or if microbes have an indirect effect on the litter digestibility. To recap the hypotheses, the first hypothesis (H1) describes that microbes process the litter and facilitate digestive utilization before feeding and during gut passage. The second hypothesis (H2) describes that they do not eat the litter but detritivores feed on the microbial biomass on the litter. The last hypothesis (H3) describes that the microbes maintain a healthy gut flora of detritivores (Ihnen & Zimmer, 2008). If H1 is true, it would mean the only effect microbes have on detritivores is indirect, basing it on how well they can facilitate litter. If H2 is true, it would have a direct impact, basing it on the nutritional value of the microbes. If H3 is true, the nutritional value of the litter or the microbes should not matter, but the optimization of the gut flora would be the most important aspect. For more information on H1 see section: *Effects of litter on detritivores*.

Looking at H2, in research conducted by Hodgson, Bréchon, & Thompson (2018), they found that *Orchestia Gammarellus* (Amphipoda) can shred plastics into microplastics. They used three different types of plastic, but the plastic type did not make any difference in the amount of shredding while the presence of biofilm did. This could mean that the quality of litter matters very little for *Orchestia* and that they mainly feed on the microbiota. This is again a good argument for the second hypotheses (H2). However, this only confirms they are able to feed on microbiota. This does not mean it is their preferred feeding type, since the experiment was done with plastic and not litter, which is nutritionally of much lower quality. This means it does not necessarily disprove the first hypothesis since the effect of microbes on the plastic was non-existent.

The third hypothesis (H3) is relatively less researched. To research this, both the microbial gut fauna and the microbial community on the litter have to be documented. Since many detritivores do not

produce enzymes to break down ingested food on their own, they rely almost completely on their gut microbiota to extract nutrition. It is confirmed that the microbiota of saltmarsh detritivores (Amphipoda & Diplopoda) alters dependent on the composition of the litter (Dittmer, Lesobre, Raimond, Zimmer, & Bouchon, 2012). For example, the gut flora of amphipod species reflects the microhabitat and feeding habitat of their host, since the ingested food has significant effects on the gut flora of amphipods (Abdelrhman, Bacci, Nistri, Mengoni, & Ugolini, 2017). Depending on how specialized a species is, it could cause more shifts in the gut flora (Abdelrhman, Bacci, Nistri, et al., 2017). This is probably caused by the low intraspecific diversity in the gut flora (Personal source: Matty P. Berg). This means that there is a strong selection on the gut flora dependent on the litter composition. However, in these experiments, the impact of microbial communities on the litter was not analysed, which is why it is not known what the effect of the microbes is. This means it does not confirm nor deny hypothesis 3 (H3).

In Isopods, Zimmer & Topp (1998) determined that different locations in the gut contain different microbial gut communities. They found that cellulose was digested at the beginning of the hindgut. This was done by cellulases produced by bacteria that are naturally present in the isopod. Ingested microbes also get digested in the hindgut. Zimmer & Topp (1998) hypothesised that this may be an important food resource. However, in later research Zimmer & Bartholmé (2003) found that Isopods and Amphipods have different mechanisms of the use of endosymbiotic bacteria versus ingesting external microbes. While Isopods seem to rely mostly on endosymbiotic bacteria, Amphipods rely for a significant amount on the ingestion of external microbes, complementary to their gut microbes for cellulase activity, though there may be other sources of cellulase in Isopods, such as cellulases from ingested microbes (Kostanjšek, Milatovič, & Štrus, 2010). However, microbes do have the capability to stay resident in isopod guts for longer periods (Kostanjšek, Štrus, & Avguštin, 2002). In other species it was also found that some habitat microbiota stay resident in the gut and others are just transient, while also confirming that it differs per species (Harris, Seiderer, & Lucas, 1991). This indicates that, depending on detritivore species, the third hypothesis (H3) may be true or not. The true source of cellulase is still under heavy discussion among scientists (Kostanjšek, Milatovič, & Štrus, 2010).

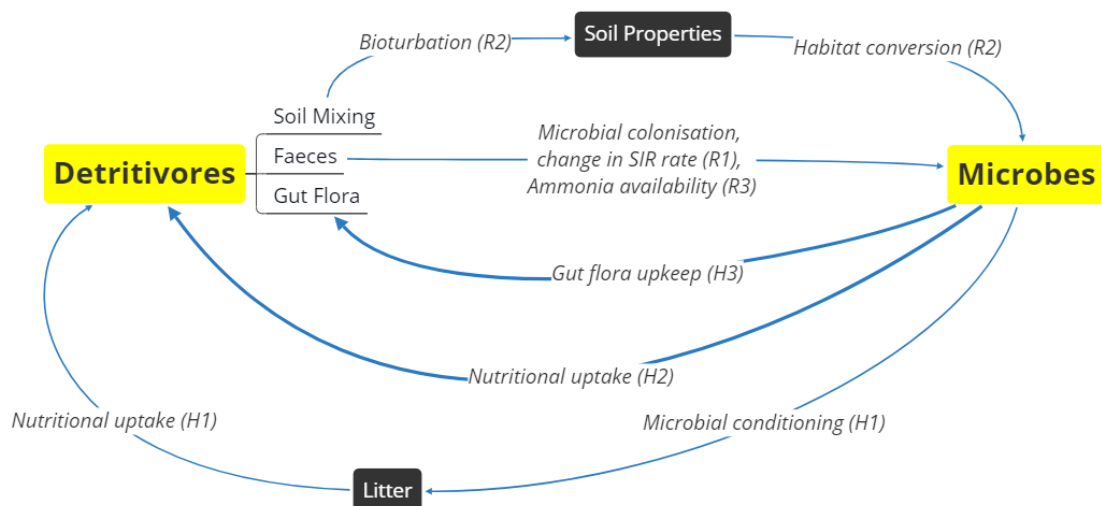


Figure 14: Current described relations between detritivores and microbes.

<https://www.sciencedirect.com/science/article/pii/S0022098114000458> : isopoda microbial community

Orchestia gammarellus

Because there are many different ecosystems, species and other variables in decomposition, one species of detritivore will be explained in further detail to show an example and a model of the relations described. It is also used to show what relations are yet undiscovered, specifically within this species, but may also apply to other detritivore species. First of all, a brief description of *Orchestia Gammarellus* (Pallas, 1766) (Figure 19), the model species, and the salt marshes it occurs in will be given. After this the effects it has on the vegetation and thus litter will be shown. And lastly the effects it has on the microbial community will be presented.



Figure 15: *Orchestia Gammarellus*. Picture: Dick Belgers, Terschelling 2018. Dutch Species Register

Orchestia gammarellus (Amphipoda) is a macrofauna species that plays a major role in decomposition of litter in north-western Europe saltmarsh vegetations. Just like many detritivores, *O. Gammarellus* is a bioturbator. The bioturbation of *O. Gammarellus* causes it to be an important ecosystem engineer in saltmarsh vegetations (Andresen, Bakker, Brongers, Heydemann, & Irmiler, 1990; Howison et al., 2017). The bioturbation from *O. Gammarellus* and biocompaction from large grazers causes an autocatalytic loop between the two vegetations. The *Orchestia* mainly populates the high vegetation for it provides a better habitat, while the cows barely graze in the high vegetation and mainly graze on the short vegetation because of the cow feeding habits (Howison, Olff, Steever, & Smit, 2015).

The two vegetation types caused by bioturbation and biocompaction are not the only influences when looking specifically at salt marshes. The tidal floods are also of importance. Frequent floods, causing a more aquatic environment, causes an increase in litter mass loss and microbial respiration (Pfauder & Zimmer, 2005). However, a low frequency of flooding causes a bigger increase in mass loss and respiration than an intermediate frequency of floods (Pfauder & Zimmer, 2005). This means there is a gradient along the intertidal zone of salt marshes, with differing chemistries in microhabitats (Personal source M. P. Berg; Pfauder & Zimmer, 2005). This difference in chemistry on a small geographic scale is interesting because many other factors, like flora and fauna species, are reasonably constant on this gradient. Not only does the flooding have direct effects on the decomposition rate, it also has an indirect effect through *O. Gammarellus* (Pfauder & Zimmer, 2005). An intermediate flooding frequency increases the influence of *O. Gammarellus* on mass loss and microbial respiration. In the initial stages of decomposition *O. Gammarellus* does not have any effect on microbial abundancy, but after 12 weeks it has a negative effect on microbe abundancy while still having a positive effect on overall microbe activity (Pfauder & Zimmer, 2005).

As presented in sections: *Effects of litter on detritivores* and *Effects of microbes on detritivores*, different detritivores have different feeding habits. In *O. Gammarellus*, it is currently unclear what their main food source is. They have shown that they prefer items colonised by microbes, even when the item itself has no nutritional value such as plastic (Hodgson et al., 2018). However, this only

shows they are capable of feeding on microbes. This does not exclude other feeding sources nor confirm their regular diet. *O. Gammarellus* seems to be very generalist and adaptable when it comes to food availability, maintaining a high feeding rate on many different resources (Dias & Hassall, 2005). Dias & Hassall (2005) analysed the gut content of *O. Gammarellus* in Portugal, showing a high preference for *Zostera* sources. However, when comparing it to other detritivores in the same habitat, it was the only species containing *Spartina* in their gut. This confirms a preference for certain food items, which may alter depending on the geographical location. For the *O. Gammarellus* on Schiermonnikoog, the latest confirmed preference was found by van Koppen (1981), showing an increased preference for Algae and for litter that has been conditioned for four weeks especially, *Halimione*. However, no further research on the combination of microbes and litter in feeding behaviour and digestion has been carried out.

5. Discussion

The method used should have given a proper representation of the current knowledge of these decomposition drivers. By asking several experts for the most relevant articles gives proper guidance to staple articles that are necessary to understand these relations. However, only two researchers from the same university were asked to give insight. While Matty P. Berg has expertise in soil fauna and James T. Weedon has extensive knowledge of general decomposition, litter quality and microbial interactions, there is no way to exclude that some bias is included in this thesis. Other researchers may have considered other factors in decomposition more important than those described. However, there has to be a limit in the description of drivers. While this thesis mostly describes biotic interactions, there are many other factors in decomposition that are of importance.

When looking at decomposition, there is a broad understanding on surface level of the individual factors as shown in the introduction. When looking at details of drivers in decomposition, a lot of interactions are described as a direct effect. However, when considering that many of the drivers interacting with each other have indirect effects, some current assumptions should be reconsidered. The main problem with describing the decomposition progress seems to be that different ecosystems and environments have such a large divergence in circumstances. For example, detritivores are a large group of species that by definition eats detritus. However, there may be some species that primarily feed on litter and other species that focus on eating microbes on the litter. Thus, a difference in litter quality might not have a direct effect on microbe-eating species, it could have an indirect effect by influencing the microbial community on the litter. The same phenomenon could occur vice-versa. In scientific experiments these indirect effects could also have impact on for example decomposition experiments and feeding experiments. In a hypothetical experiment relative quality between two types of litter could diverge over time due to faster or slower microbial conditioning.

Thus, many other factors should be considered before drawing a conclusion when measuring certain effects of single drivers on decomposition. As seen in section: *Orchestia gammarellus*, a lot of different (a)biotic drivers influence the decomposition, even when excluding the original three drivers. Vegetation, soil type, water circumstances etc. all have effect on the drivers and thus have an indirect effect on the decomposition. For nature management and forestry organisations this thesis shows that decomposition drivers are all of importance in ecosystem nutrient cycling. Even if high litter quality is present in an ecosystem, the other drivers should not be ignored. For example, different detritivore species can have differences in litter breakdown activity (M. Hedde, Bureau, Akpa-Vinceslas, Aubert, & Decaëns, 2007). When applying the presented information into practice, forest management is an important sector since forests have a high litter production and economic interests.

However, this does not mean that the drivers need to be balanced equally. For example, in European commercial forestry, the Douglas fir (*Pseudotsuga menziesii*) is a popular tree for the fast growth and high wood value. However, this exotic tree has a few differences compared to native trees. Such as showing a decreased fungal diversity and arthropod abundance (Schmid, Pautasso, & Holdenrieder, 2013). The litter decomposition rate however, is still comparable with native conifer species like Norway spruce (*Picea abies*). There are some differences between a Douglas fir forest and a Norway spruce forest: soil fauna is of a general larger size in Douglas fir forests and the overall litter quality is also higher in Douglas fir forests. Considering the larger soil fauna and higher litter quality bundled with the lower fungal diversity and arthropod abundance, the decomposition drivers may be in a different balance but the functionality of the ecosystems in terms of decomposition rate stays somewhat the same.

For forestry management to be sustainable it is important that the three drivers as described in the results can sustain the nutrients in the soil. When using a tree species with low litter quality but high economic value, it is still possible to be sustainable by compensating with a prosperous soil fauna and microbial community. However, since tree harvesting is very damaging to the microbial community and the soil fauna, it is hard to maintain a similar decomposition rate after harvesting (Siira-Pietikäinen & Haimi, 2009; Cardenas et al., 2015). To prevent this, different harvest methods might be able to prevent the loss of microbial community quality and quantity. Clear felling, of all harvesting methods, has the biggest effects on the soil fauna (Siira-Pietikäinen & Haimi, 2009). The best possible harvesting method is a selection felling where a maximum of 30% of the present stand volume is removed does not show large effects on the decomposer community in a boreal spruce forest (Siira-Pietikäinen, Pietikäinen, Fritze, & Haimi, 2001). However, this may also fluctuate over time and in different ecosystems, for short term effects may differ from long term effects. Furthermore, the selection felling has economic and convenience downsides.

Next to the microbial community damage, forestry causes nutrient depletion in soils. Especially in pine forests, the high litter layer accumulation, combined with the removal of nutrients by logging, causes a large deficit in total nitrogen in the soil (Wiesmeier et al., 2009; Himes et al., 2014). The introduction of alder trees in pine forests could contest the nitrogen depletion. Alder trees are nitrogen fixating, introducing nitrogen into the ecosystem that may have been removed by logging. Nitrogen leaching into the soil in mixed alder-conifer stands can be ten times more compared to pure conifer stands (Binkley, Sollins, Bell, Sachs, & Myrold, 1992). Furthermore, alder trees have a high litter quality and thus a fast decomposition rate decreasing the litter accumulation (Fyles & Fyles, 1993; Edmonds & Tuttle, 2010). The increase in litter diversity also has effects on the detritivore community. A high diversity in litter increases the diversity of the microclimates and thus contributes to an increase in detritivore diversity compared to monocultures (Hättenschwiler, Tiunov, & Scheu, 2005; Gessner et al., 2010). While detritivore diversity does not have large effects on decomposition rates (within mixed litter ecosystems) (Martin Zimmer, Kautz, & Topp, 2005), it does increase the ecosystem resilience and stability. Since functional diversity does influence leaf litter mass loss and soil respiration (Heemsbergen, 2004), the loss of one microclimate and thus a specific species would not mean loss in functional diversity within the ecosystem. Lastly, the introduction of alder trees in pine forests has a positive effect on microbial properties, showing higher microbial biomass, basal respiration rate, N mineralisation rate, urease activity and functional diversity up to three to four meters near an alder row in a pine forest (Sroka, Chodak, Klimek, & Pietrzykowski, 2018). However, this could be caused by the improved water holding capability in the soil and nitrogen accumulation near alder trees (Demoling, Figueroa, & Bååth, 2007; Sroka et al., 2018). This is merely one example in how the decomposition drivers could be influenced to alter ecosystem functioning. While alder trees are an example of influencing all three drivers in a positive manner, other measures might have a positive effect on one driver while having a negative effect on the other.

6. Conclusion

The goal of this research was to describe the decomposition drivers of litter, microbes, detritivores and the interactions between them. To answer the main question: What is known about the interactions between the drivers of litter decomposition and where are the gaps in our knowledge? The sub questions were answered to describe the direct relations between the drivers.

The most important relationship between litter and microbes is the ability of the microbes to alter the chemical composition of litter (even condition litter for detritivores). The litter also has effect on the microbial community, for a microbial community is adapted to the litter that they have been given historically. More detailed interactions between the specific relations between these two drivers can be seen in figure 7 (litter and microbes).

The most important relationship between litter and detritivores, is the shredding of litter by detritivores. This increases the surface area and decomposition rate. However, it is still up for debate if detritivores feed on the litter or the microbes on the litter. This may also differ between species of detritivore. It is known that detritivores still prefer higher litter quality overall. More detailed interactions between the specific relations between these two drivers can be seen in figure 12 (litter and detritivores).

The most important relationship between detritivores and microbes, is the influence of bioturbation and faeces on the microbial community. It increases microbial activity (especially in systems with low quality litter). Microbes may be of nutritional importance to detritivores, but this is not confirmed. They also influence the gut microbes of detritivores, which define the organism functioning in the ecosystem. More detailed interactions between the specific relations between these two drivers can be seen in figure 14 (detritivores and microbes).

While there is a lot known about the effects of litter on both the microbial community and detritivores and vice versa, there are still some gaps in our knowledge about the other relations between the decomposition drivers. Especially the effect of microbes on the microbial gut community of detritivores is still unclear. While some patterns are described, there are differences between detritivore species. A large problem in a lot of studies is that not all the three drivers were considered while they possibly could have impact on the results. Thus, while there is a broad knowledge of surface level, looking at very specific interactions there is a lot of unknown relations. Such as if detritivores mainly feed on microbes or litter itself. These added together could have an impact on the entire decomposition process. The most important relations and interactions can be seen in figure 20.

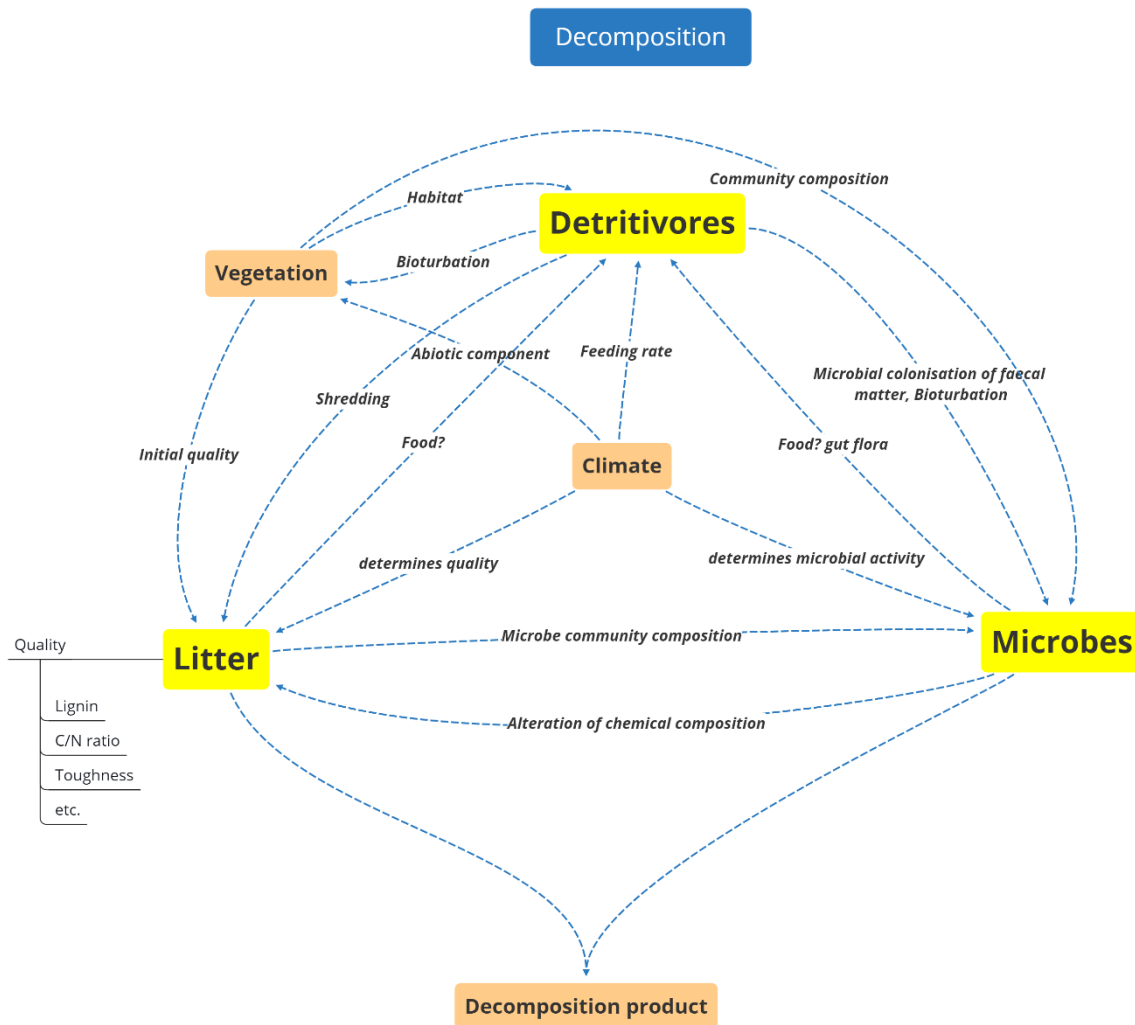


Figure 20: surface level interactions between the large decomposition drivers; litter, microbes and detritivores. Climate being a state factor, controls all other drivers. Vegetation is the base of litter and has a large influence on detritivores and microbes.

Recommendations

The decomposition drivers do not need to be in perfect balance to maintain a similar decomposition rate, the drivers can compensate and even stimulate each other. When relating this to practical problems, this could mean that making slight adjustments to forestry management could increase sustainability. However, finding a balance between economic success and sustainability is a challenge that forestry management may struggle with for years to come. Therefore, it is of importance to perform research to harvest methods in ecosystems with large acreages of forestry. However, not only decomposition should be considered when choosing a harvest method. Conservation of biodiversity, ecosystem functioning and the recreational aspects (when applicable) are also of importance in forest management. A method of making commercial coniferous forests more sustainable on a longer time scale is the introduction of alder trees, which has a positive impact on all three decomposition drivers. However, other methods might be required depending on the target situation of a certain ecosystem.

Possible interventions for a commercial coniferous forest to make it more sustainable are:

- Planting of alder trees in between the coniferous forest
- At one alder tree per 4 m² would give an enormous boost to biodiversity, microbial biomass and litter quality.
- At one alder tree per 36 m² will still give somewhat higher, microbial biomass and litter quality.
- Less than one alder tree per 36 m² would still boost biodiversity within the area of the alder but barely any significant effects out of that area. The area within the 36 m² could still serve as a buffer area for these species.

This will increase decomposition rate and N₂ fixation giving the specific area a higher sustainability. Other trees than alder with high litter quality may increase biodiversity and microbial biomass. The N₂ fixating ability of alder trees will cause them to be the best option for sustainability improvement.

Appendix

Appendix I: search terms

Microbe – litter

Microbial community composition, litter microbial communities, microbe soil depth, organic horizon microbial community, microbial decomposition litter, plant litter, soft rot lignin, microbial abundance litter, microbial function litter, soil fauna home field advantage.

Litter- detritivores

Soil fauna community, Orchestia saltmarsh, bioturbation, biocompaction, litter fragmentation, litter leaching microbe, litter leaching earthworm, macrofauna chemical conversion litter, macrofauna litter diet, leaf conditioning, macrofauna litter diet microbe conditioning, life history traits detritivores, life history traits isopoda, soil fauna litter quality, leaf toughness litter detritivore, Orchestia decomposition, Orchestia food preferences.

Microbe – detritivore

Orchestia decomposition, Orchestia saltmarsh, amphipod gut microbiota, detritivore microbe predation, microbial colonization detritivore faeces, earthworm microbe, detritivore microbial community, amphipoda microbial community, isopoda microbial community, millipede microbial community.

Orchestia gammarellus

Martin Zimmer Orchestia, salt marsh cow grazing, salt marsh gradient Orchestia. Orchestia gammarellus feeding. Orchestia gut microbes.

Appendix II: provided literature

This is all literature provided by Matty P. Berg and James T. Weedon.

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