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Living logs: Tree trait effects on decomposition and associated invertebrate diversity

Zuo, J.

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Chapter I

General introduction

Biodiversity, the great variety of life, is one of the most striking features of our planet. Species richness is distributed heterogeneously across the globe (Gaston 2000, Cardinale et al. 2006) governed by both abiotic and biotic factors that contribute to the heterogeneous distribution of species (e.g. Condamine et al. 2012, Hulshof et al. 2013). Species distributions also have consequences for ecosystems, as many species are involved in key ecosystem processes, such as primary production as well as the decay of this production after plant death (Paquette and Messier 2011, Handa et al. 2014). Determining how biodiversity dynamics, ecosystem processes, and abiotic factors interact is a major challenge in ecological science (Loreau et al. 2001). Forests are known for their high biodiversity, both above- and belowground. In terms of biodiversity, forests are very interesting ecosystems. Not only because global patterns of biodiversity are particularly emergent in forest ecosystems, but also because global changes are affecting forests very strongly (Achard et al. 2002, Perry et al. 2008, Millar and Stephenson 2015), putting large pressure on their biodiversity. Forests are also responsible for a large part of our global primary production, store significant amounts of chemical elements, especially carbon, nitrogen and phosphorus, and are strong regulators of local and regional climate conditions (Perry et al. 2008).

One profound characteristic of natural forest ecosystems is the large amount of dead trees on the soil, which is a key determinant of biodiversity and important ecosystem functions (Harmon et al. 1986, Wijdeven et al. 2010, Cornelissen et al. 2012). Also in forestry plantations, where parts of the trunks are removed, the remaining dead parts of the tree (branches, stubs and roots) are of great importance for biodiversity. The decomposition of dead tree material has a substantial influence on biogeochemical cycling (Cornwell et al. 2009, Brovkin et al. 2012, Freschet et al. 2012a), such as nitrogen and phosphorus cycling and availability, the release of carbon dioxide to the atmosphere (Brovkin et al. 2012, Jacob et al. 2013) and, on the opposite side of the carbon balance, soil organic matter formation and C sequestration (De Deyn et al. 2008). The decomposition rates of dead plant material including parts of trees are strongly determined by climate (Parton et al. 2007), community composition and activity of soil decomposer organisms (Lavelle et al. 2006, Bradford et al. 2014) and litter substrate quality ('species identity', a combination of physico-chemical characteristics) (Aerts 1997, Cornwell et al. 2009, Weedon et al. 2009, Freschet et al. 2011) and by interactions between these (Harmon et al. 1986, Cornelissen et al. 2012, Liu et al. 2015). But how the various abiotic and biotic factors of trees together drive variation in organic matter decomposition among tree species and their different organs is still far from resolved.

Dead trees not only join the biogeochemical cycle through decomposition, but also host a large number of organisms that need dead trees as a key resource, such as for food, shelter, or reproduction. Together, these organisms, from microbes and mosses to invertebrates and vertebrates are the actors in the process of decay. Although less conspicuous than herbivores living on trees, there is a fascinating diversity of life forms in decaying wood in forest with between 400,000 and 1 million wood-inhabiting species in the world (Stokland et al. 2012). Recent research has improved our understanding of habitat relationships for many species associated with dead wood. We now know that tree species differ in community composition of wood-inhabiting species (e.g. Ulyshen et al. 2011). However, one of the problems in generalizing the mechanisms behind tree-invertebrate community relationships is

that they may often be context dependent. From one forest to the next the regional species pool differs due to variability in local environmental conditions. Abiotic and biotic determinants of invertebrate community composition vary at the same spatial scales. Overall, we do not have much knowledge about how (1) abiotic factors, (2) available invertebrate species pools and (3) the wood and bark traits of tree trunks and branches of different species and decay stages, together drive variation in invertebrate fauna diversity (Figure 1). This PhD thesis will take on the challenge of filling part of this knowledge gap for temperate forests.
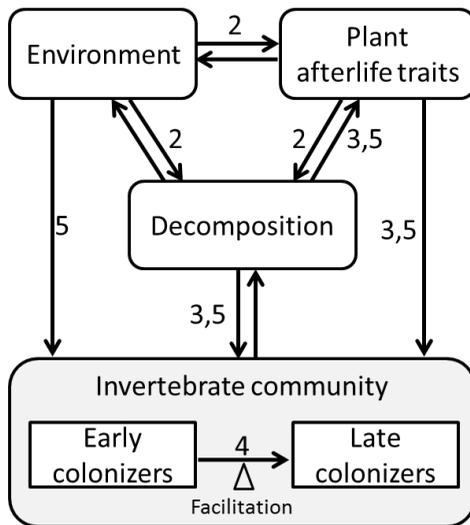
Figure 1. Schematic representation of the ecosystem components that determine decomposition process of dead trees and the associated invertebrate communities of dead tree organs. Differences in environmental factors, such as soil conditions, temperature and humidity influence decomposition rates and might also affect plant traits and plant afterlife traits that influence decomposition. Together these three factors determine the invertebrate communities associated with dead trees. Temperature and humidity, decomposition process (e.g. habitat volume variation) together with (among others) resource traits of plant influence species composition and their activity. Within the invertebrate community, species will interact with each other during community assembly. Among these, facilitation is an important positive interaction, e.g. early colonizers can facilitate the colonization of late colonizers by modification of the environment. The assembly of the wood-associated invertebrate community in return influences the process of decomposition. Numbers (2-5) indicate the respective chapters of this thesis that relate to each of the influences. Explanation of the content of each chapter is in the section "Aims and outline of this thesis".

Trait-based approach

It has been proposed that trait-based approaches in ecology may overcome context dependency (McGill et al. 2006). Trait-based approaches are a broadly used tool to better understand the mechanisms underlying ecological processes (Violle et al. 2007) and to provide more general patterns in community composition (McGill et al. 2006). Traits, i.e. "morphological, physiological or phenological features measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization" (Violle et al. 2007) are well-defined, quantifiable properties of organisms and used comparatively across species (McGill et al. 2006). A functional trait strongly influences organismal performance

(McGill et al. 2006), i.e. through an impact on the fitness of species via its effects on their growth, reproduction and survival (Violle et al. 2007). Numerous studies have focused on plant functional trait measurements and analyses across multiple species in order to find commonalities of plant function, of correspondence with environmental factors and of influence on ecosystem properties (Reich *et al.* 1997, Wright *et al.* 2004, Chave *et al.* 2009, Pérez-Harguindeguy et al. 2013). Functional traits are also important for understanding and predicting the response of macro-detritivores to stress (e.g. Dias et al. 2013). When trying to understand how environmental changes affect ecosystem processes, a trait-based approach allows scaling from individuals to ecosystems and directly links to patterns in communities (Cadotte et al. 2015) and ecosystem processes (Suding et al. 2008). Using trait-based approaches is the basis of numerous studies linking species to community and ecosystem properties.

Tree species differ in traits, both among their living and dead parts. All tree organs, from leaves to roots and from bark to wood, have 'afterlife effects', and trait-based approaches are also a key tool to understand afterlife effects of functional traits on important ecosystem processes, such as decomposition and associated C sequestration and nutrient cycling (Cornwell et al. 2008, De Deyn et al. 2008, Freschet et al. 2012a). In this thesis, a trait-based approach was used to study the influence of plant functional traits on decomposition of different tree organs and the associated biodiversity in woody debris (Figure 1).

Afterlife effects of plant traits on decomposition

Afterlife effects of functional traits of plants are a well-studied phenomenon, particularly in litter decomposition studies (Cornelissen et al. 2004). Plant species differ in afterlife effects due to inter-specific variation in the amount and quality of dead organic material, which are determined by species-specific differences in traits underlying litter quality. Variation in structural and chemical traits of living leaves, such as tissue toughness, dry matter content, pH, concentrations of lignin, defensive tannins and phenolic compounds and various mineral nutrients and cations, have strong effects on litter decomposition rates of different species (Cadisch and Giller 1997, Cornelissen and Thompson 1997, Cornelissen et al. 1999, Cornelissen et al. 2004, Santiago 2007, Cornwell et al. 2008, Makkonen et al. 2012), because they affect the composition and activity of decomposer communities. Also for wood, which is known to have great interspecific variation in functional trait values (Chave et al. 2009), afterlife effects occur, as differences in wood chemistry, anatomy and morphology influence the fate (Cornwell et al. 2009) and turnover rate (Weedon et al. 2009, Van Geffen et al. 2010, Freschet et al. 2012b, Pietsch et al. 2014) of dead wood. Although the role of the above-mentioned traits as drivers of decomposition is well established, little is known on the relative importance of variation in trait values in explaining relative differences in the decomposition rates of different plant organs across different plant species (but see Freschet et al. 2012a, Pietsch et al. 2014); or how these relative differences are influenced by environmental variation (Figure 1).

Different plant organs have specific attributes, which may result in different trait values after death. For example, tree trunks tend to have thicker bark than branches, and branches have thicker bark than twigs because of a longer history of bark

accumulation (Rossell et al. 2015), while leaves do not have bark but protect their inner tissues with only an epidermis consisting of a single cell layer with a waxy cuticle on the outside, or with secondary metabolites. All these features largely persist during their senescence towards woody debris or leaf litter. Traits related to physical support functions, expressed in plant allometric relationships including organ sizes, may play important roles too; for instance, tree trunk diameter predicted variation in decomposition rates amongst 15 Bolivian tree species (Van Geffen et al. 2010). Any such differences in organ dimensions and function, as expressed in structural and physiological differences, might cause not only differences in overall decomposability between different organs due to different compositions and activity of decomposers, but also shifts in cross-species trait-decomposability relationships between organs (Freschet et al. 2012a). Plant organs have marked differences in function, morphology and microenvironment which implies a large variation in ecology and associated specific functional traits. Previous research found environmental factors to influence decomposition at a global scale (Makkonen et al. 2012, Pietsch et al. 2014) and in smaller regions across a wide range of plant taxa with different growth forms (Cornelissen 1996, Cornelissen et al. 1999). Different plant organs have their specific decomposability, but the variation among plant organs within the same growth form (i.e. trees) and whether it is environment depended is not fully known.

Afterlife effects of traits on inhabiting community assembly

Dead trees have also been identified as a crucial component of forest biodiversity with its beneficial role to microbial, plant and animal diversity (Freedman et al. 1996). High biodiversity is associated with differences in dead trees as a substrate, both in terms of habitat and nutritional resource of different tree species and in terms of decomposition stage within tree species. As explained above, differences in traits related to wood chemistry, anatomy and morphology influence the assembly of wood-detritivores. Wood-detritivores in turn affect the turnover rate of dead trees, thus influencing changes in trait composition of decomposing wood which result in alteration of the biodiversity associated with it (Figure 1). However, studies on afterlife effects of tree traits on wood decomposition have focused mainly on biogeochemical cycling, with a particular emphasis on wood turnover rates and accompanying carbon and nutrient dynamics. But despite the fact that a large variety of organisms live on and in dead trees, or even depend upon dead trees for their existence (Harmon et al. 1986), the biotic side of tree afterlife effects (the role of dead material quality for the assembly of deed wood organisms) has received far less attention to date (but see, among others, a review by Seibold et al. 2015).

The colonization and assembly of dead tree invertebrates at a site may be understood from assembly theory (Díaz et al. 1998, Weiher et al. 1998), which poses that the observed community at a site is determined by two assembly filters, i.e. an environmental filter and a limiting similarity (competitive exclusion) filter. A wealth of research has been carried out investigating vegetation assembly (Götzenberger et al. 2012) and other communities. In contrast, very little is known about the community assembly in detrital systems (but see Siepel 1996 for microarthropods), including the colonization and community assembly of invertebrates in logged trees in forests. A recently logged tree constitutes a new site for colonizing fauna, and as

tree species differ in functional traits of wood and bark, the environmental filter that restricts the range of viable strategies (Cornwell and Ackerly 2009) should be particularly strong at the early decomposition stage. The secondary phloem inside the outer bark is particularly important by providing resources and habitat to invertebrates. The afterlife effects of structural and chemical defence traits of bark of different tree species (Cornwell et al. 2009), which play a crucial role in protecting these nutrient-rich tissues against herbivores in living trees (Wainhouse et al. 1990, Paine et al. 2010, Rossell et al. 2014), may inhibit invertebrate access. The colonisation and assembly of invertebrates associated with logged trees of different species at a given site may therefore be understood from trait-based assembly theory (Figure 2). Whether or not species can 'pass' the environmental filter and (biotic) limiting similarity filter is determined by their trait composition, i.e. trait values that match dispersal and environmental challenges raised by the environmental filter, and trait values that limit competition between species that can survive under the given environmental conditions. Recently logged trees constitute a new habitat for colonizing fauna, but as a habitat and nutrient source put considerable constraints on the number of species that use this resource. This is due to the very high C/N ratio with significant stoichiometric imbalance compared to biota and because of the solid habitat that is very difficult to enter. Therefore, at the early (i.e., the first 1-2 years) decomposition stage, when the bark is still attached to the wood, bark traits may be a crucial part of the environmental filter for associated fauna assembly (see above and Wu et al. 2008). Strong environmental filtering is usually accompanied by trait under-dispersion or convergence (Weiher and Keddy 1995), as species have to be rather similar in tolerance traits to be able to survive in recently logged tree organs. However, there is little quantitative evidence on the ecological consequences of interspecific variation in bark traits for invertebrate community assembly and succession in decomposing dead trees.

The limiting similarity filter has been hypothesised, with some empirical support, to have a divergent effect on the trait composition within the community (Figure 2). Species that are too similar in the way they exploit the resources provided by dead wood will compete strongly, resulting in the exclusion of one or more species (Weiher and Keddy 1999; Van der Plas 2013). However, in the dead tree invertebrate community, during the colonization process the species composition may also be influenced by positive interspecific interactions. A frequently overlooked, but essential, interaction is facilitation due to the presence of ecosystem engineers (*sensu* Jones et al. 1994). Facilitation is the direct or indirect positive impact that one species can have on another species without itself being negatively affected by the other species (Bruno et al., 2003, Brooker et al. 2008). One of the most occurring facilitative interactions is the creation, directly or indirectly, of a more favourable environment by an individual or group of individuals (Jones, et al. 1994, Bruno et al. 2003). For instance, leaf-rollers can act as diversity amplifiers with indirect facilitation of arthropod communities at different temporal and spatial scales, because they provide shelter to secondary users (Vieira and Romero 2013). Facilitation may have significant effects on colonization and community composition because it feeds back to the environmental assembly filter (Figure 2). However, to our knowledge, very little is known about this phenomenon in detrital systems, including the colonization and community assembly of invertebrates in dead tree in forest during decomposition.
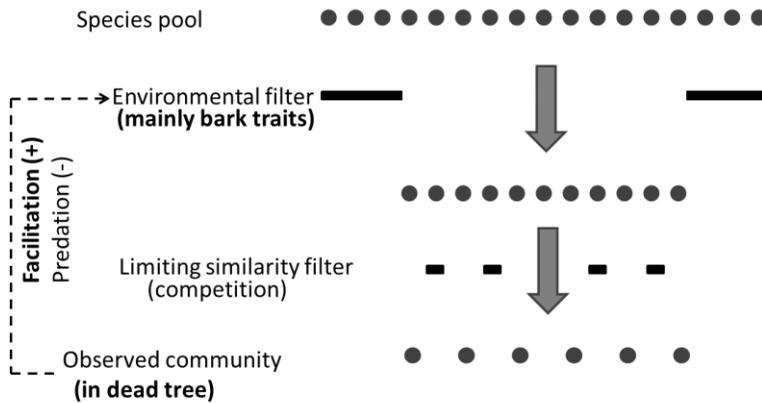
Figure 2. Community assembly in dead trees via two assembly filters. Recently logged trees constitute a new habitat for fauna from the local species pool. The afterlife effects of bark traits are a strong environmental filter for colonizing fauna during early-stage decomposition. A strong environmental filter results in trait under-dispersion or convergence in community trait composition. The limiting similarity filter results in over-dispersion or a divergent community trait composition due to competitive exclusion of species that are too similar in trait values. During the colonization process, the species composition may also be influenced by positive interspecific interactions (e.g. facilitation) and negative interspecific interactions (e.g. predation), that feedback to the the environmental filter, and changes its strength. The diagram was adapted from the conceptual ideas of community assembly by Diaz et al. (1998) and Weiher et al. (1998).

Influence of decomposers on decomposition

Besides substrate quality, the process of decomposition is also determined by decomposers (Figure 1). They are the two sides of the same coin: wood traits determine biota assembly, biota presence (via assembly) determines wood decomposition, wood decomposition determines alterations in wood traits over time, which in turn determine changes in biota composition over time (and so on and so forth). Decomposition of plant material is directly driven by a vast diversity of organisms. This biological diversity exists at multiple trophic levels and includes plants that produce litter mixtures, microbial decomposers and invertebrate consumers (Gessner et al. 2010, Reiss et al. 2009, Handa et al. 2014). Decomposition is ultimately directly driven by microbial activity and community composition but invertebrates also play a significant role (Verhoef and Brussaard 1990) and the cumulative effect of the entire invertebrate community is generally to accelerate wood decomposition (Ulyshen 2014). Primary mechanisms include enzymatic digestion, substrate alteration, litter fragmentation and surface increase, biotic interactions and nitrogen fertilization (Ulyshen 2014). Litter species richness and soil fauna interactively determine rates of decomposition in a temperate forest, suggesting a combination of bottom-up and top-down controls of litter diversity effects on ecosystem C and nutrient cycling (Hättenschwiler and Gasser 2005). In ecosystems supporting well developed soil macrofauna communities, animal activity plays a fundamental role in altering decomposition in response to changing litter diversity, which in turn has important implications for biogeochemical cycles and the long-term functioning of ecosystems with ongoing biodiversity loss (Hättenschwiler and Gasser 2005, Handa et al. 2014).

The decay of dead plant material is performed by a vast number of species, among which invertebrates and fungi play particularly important roles (Ulyshen 2014). Microbial diversity can have positive effects resulting from functional niche complementarity, while antagonistic interactions among fungi competing for similar resources can also slow decomposition (Hättenschwiler et al. 2005). Heemsbergen et al. (2004) and Ulyshen (2014) also stated that the effects of individual invertebrate taxa or functional groups can be accelerative or inhibitory, but the cumulative effect of the entire community is generally accelerative, at least during the early stages of the process. Soil fauna diversity, indicating the number of trophic levels, species identity, and the presence of key-stone species, have a strong impact on decomposition (Heemsbergen et al. 2004, Hättenschwiler et al. 2005). Therefore, a reduction of biodiversity associated with dead trees may also affect its decomposition rate (Jonsson et al. 2005, Ulyshen 2014). Thus, studying this feedback will also contribute to the ongoing "hot" debate in the literature about the impact of biodiversity on ecosystem functions (Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2006, Lefcheck et al. 2015). Indeed, much remains unknown about the role of invertebrate in detrital systems, especially in dead wood.

Environmental interaction with tree afterlife traits

Environment and its interactive effects with afterlife traits on decomposition

Climate is traditionally thought to be the predominant control on decomposition, but climatic factors are particularly important at regional to global scales (Swift et al. 1979, Berg et al. 1993, Bradford et al. 2014). Within biomes at the scale of landscapes, local environmental drivers and species' litter quality are the predominant controls on decomposition (Cornwell et al. 2008, Freschet et al. 2012c), by controlling the identities, abundances and activity of the decomposer organisms (especially fungi, bacteria and invertebrates) that carry out the actual decomposition. Important local environmental drivers that determine decomposition in forest include topography and soil texture (both determining soil moisture regimes), soil chemistry (e.g. N, P and cation availability, pH, organic acids), and canopy cover (associated with soil temperature and humidity). Litter quality has two important aspects. First, as discussed before, the (afterlife) traits of the individual litter species are important controls on their decomposition rates. High N, low lignin and large-chain phenolics tend to enhance litter decomposition (Freschet et al. 2012a). Second, the litter species interact within the litter layer matrix (Wardle et al. 2003, Quested et al. 2005, Hoorens et al. 2010, Makkonen et al. 2012), leading to different decomposition rates of the same species depending on the traits of their neighbors in the litter matrix. Freschet et al. (2012c) defined a substrate quality-matrix quality interaction (SMI) hypothesis, which expects a continuum from positive to negative interactions between specific litter species and the decomposer community as specific litter species become increasingly dissimilar in quality. The studies addressing these hypotheses all indicated that the same plant material might decompose differently when put in different environments, and that those differences were the result of interactions between environment and litter afterlife traits. However, how different environments are affecting the interaction between wood traits and invertebrate community composition, and how this affects wood decomposition, is less clear.

Environmental effects on biodiversity associated with decaying trees of different species

Together with dead plant material, environmental factors strongly influence the microclimate habitat conditions for the associated organisms. The most important abiotic environmental factors determining biodiversity in dead wood are temperature, moisture and oxygen pressure (Stokland et al. 2012). Organisms have limits to the range over which they tolerate these abiotic factors. Soil organism are particularly sensitive towards changes in substrate moisture conditions. The moisture content of dead wood is regulated primarily by soil water content and the amount of shading, but also by the decay process itself (Stokland et al. 2012). A minimum level of water is needed for decay to occur, and above a certain level, excessive water might limit access to oxygen. Barker (2008) showed that high moisture levels restrict decomposition of coarse woody debris, and what constitutes a high moisture level depends on the decomposition stage and tree species. Besides, the chemical content of dead material also changes during decomposition and the rate of such changes may differ significantly among sites varying in environmental factors (McTiernan et al. 2003). All these factors provide variation in the dead wood microenvironments available to the associated organisms.

The local environment also determines the species pool available for colonization of dead trees. Soil fauna community composition is strongly determined by soil type (Berg et al. 2008), and environmental heterogeneity at hierarchical spatial scales is an important component of soil biodiversity (Berg 2012). For example, Stašiov et al. (2012) found a significant influence of soil properties on millipede (Diplopoda) communities in an arboretum. Also, Topp et al. (2006) found species assemblages of woodlice (Isopoda) and millipedes (Diplopoda) living on the forest floor of four primeval forests were strongly influenced by forest type. Invertebrates may also interact with each other within dead wood and the outcome of these interactions may also be environment dependent. For instance, Lawrence and Wise (2004) found that the net effect of predators on forest litter decomposition can either be positive or negative depending on how environmental conditions affect predator-prey interactions. However, the interactions within an invertebrate dead wood community, and how these interactions depend on environment, are generally poorly known. An in-depth study is evidently needed for a better understanding of the mechanisms underlying decomposition of dead trees and the fauna communities associated with them.

Aims and outline of this thesis

The main aim of this thesis is to investigate the decomposition of different organs of diverse recently logged tree species and the faunal communities associated with them during early decomposition in temperate forest ecosystems. Trait-based approaches have been used to compare the dead plant matter quality across tree species and organs to understand the mechanisms of trait afterlife effects on decomposition and associated fauna biodiversity. This thesis asks the following specific research questions and the chapters addressing these questions are indicated below and in Figure 1.

How do multiple factors control tree decomposability in temperate forest?

Different tree organs have specific traits resulting in different afterlife effects on decomposition of these organs. **Chapter 2** compares decomposability of different plant organs of 10 tree species in two contrasting forest sites. As determined by inter-specific variation in leaf, twig, wood and bark traits, it is hypothesized that (1) leaf litter has a higher decomposability than twigs and twigs higher than coarse branches and that there is a correlation of decomposability rankings between these organs across species. In other words, does the 'plant economics spectrum of decomposability' reported across wide-ranging plant growth forms (Freschet et al. 2012a) also manifest itself among species of the same growth form only? Also, if such a 'tree economics spectrum of decomposability' exists, how robust is it to environmental variation, for instance between two sites varying strongly in nutrient availability and other factors?

Which bark traits determine the environmental filter for the colonizing faunal community in early-stage decomposing logs?

Bark acts as the first barrier for invertebrates to colonize the log. **Chapter 3** studies afterlife effects of bark traits of 11 different tree species on the assembly of invertebrate community composition in early decay stage logs. Specifically, it is hypothesized that (1) bark traits of different tree species are a major driver of the abundance of key invertebrate taxa inhabiting early-decomposing dead trunks; (2) at the community level, the more dissimilar bark traits are between tree species, the more the invertebrate faunal community composition will differ and the more invertebrate faunal richness can be supported by those tree species. This is because, if tree species differ more in bark traits, they should also differ in the environmental conditions (i.e., microclimate, shelter, food) that invertebrates are adapted to.

Is there facilitation within the faunal community on decaying logs?

There are negative and positive interactions within fauna communities associated with dead plant matter, e.g. negative between predator-prey or competing species or positive where particular species can facilitate the occurrence of other species by habitat modification. Although the focus so far has mainly been on negative interactions, positive feedbacks can strongly affect colonization and succession. **Chapter 4** investigates the hypothesized positive interaction, i.e. facilitation, of bark beetles (Scolytinae) on the other faunal groups in the early-stage decomposing logs. Bark beetles are among the first invertebrates to colonize freshly fallen trunks; they are well-known to invade and feed on weakened, dying, or dead trees, enter the wood by gnawing small holes in the bark and subsequently engraving both bark and wood with their galleries (Rose et al. 1994). Based on incidental field observations of earthworms and millipedes going into bark beetle holes in Norway spruce (*Picea abies*), this chapter tests the hypothesis that (1) the holes and galleries that bark beetles make in the inner bark might act as a facilitative agent of dead wood colonization by other invertebrate taxa of the second successional stage. While facilitation among bark beetles themselves has been reported (Smith et al. 2011), there has, to the best of our knowledge, been no research on interspecific facilitation

between evolutionarily distant invertebrates during plant dead matter decomposition.

*What and how do multiple factors determine the dead wood fauna communities?*

Faunal diversity in dead wood is determined by multiple factors which may also interact. **Chapter 5** studies the overall effects and interactions of tree species, decay stage and environment on macro-detritivore communities in dead wood, to test the hypotheses that (1) different tree species, through variation in dead wood and bark traits, will host different faunal communities, (2) faunal abundance will increase and species composition will become more similar in composition in dead wood with the progression of its decomposition, as indicated by a decline in wood density (Harmon et al. 1986; Freschet et al. 2012b). Their abundance will increase as more decayed, softer wood with a high microbial activity becomes accessible to the animals. This wood also has higher moisture content and more available resources (nutrients, carbon and microbes). But as wood decay progresses, different tree species will become more similar in community composition, because structural and chemical components that inhibit access to wood will breakdown during decomposition, leading to convergence of dead wood quality among species; also, microbes that are an important additional food source will increase in abundance. (3) The environment in which dead wood decays will interact with the factors decay stage and tree species as trees and logs of different species may influence site conditions, such as temperature, moisture and nutrient availability, with consequences for the macro-detritivore species pool and feedback to log moisture, nutrition status and decomposition rate.

In the closing **Chapter 6** of this thesis, I synthesize the most important results of previous chapters in answer to the specific research questions introduced above, which together also yield an emerging hypothesis that warrants in-depth study. After confirming that faunal community composition dissimilarity is positively related to interspecific bark trait dissimilarity at the early stage of decay, I expand the relationship conceptually by extending the decay trajectory and project invertebrate community assembly in relation to environmental and biotic filters at play.

Temperate forest as the study system

The research to test the hypotheses introduced above was carried out in two temperate forests in the central part of the Netherlands. Two sites were selected to represent two predominant and highly contrasting forest types: (1) the Hollandse Hout forest plantation in Flevoland, called Flevopolder (F) (52.46 N, 5.42 E) and (2) a forest estate in the Veluwe region, called Schovenhorst (S) (52.25 N, 5.63 E) (Figure 3). With only around 30 km between them, both are in the same climatic zone. Site F was reclaimed from the former Zuiderzee in the 1960s. This relatively young soil consists of marine clay and is calcareous, moist and fertile, with a pH$_{H2O}$ close to neutrality. This forest site mainly consists of monospecific tree plantations used for commercial forestry. In contrast site S is much older (from late-Pleistocene sand deposits that were probably displaced by wind during the Holocene), has a sandy and

podzolic soil that is well-drained. The soil is strongly acidic and has a low fertility. More site details are given in Cornelissen et al. (2012).
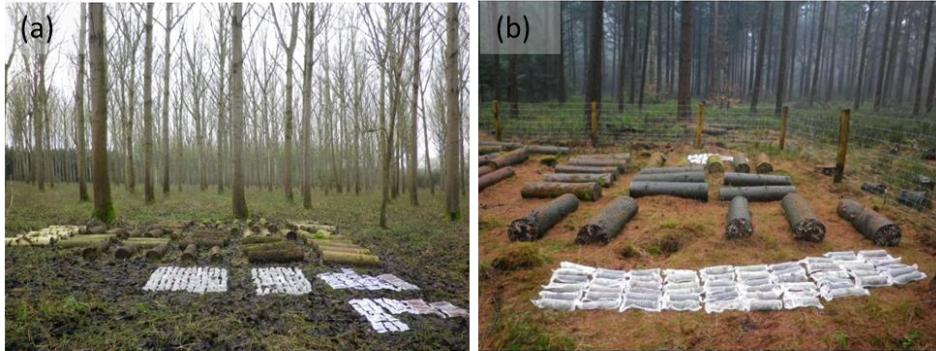
Figure 3. Part of one subplot (block) in two temperate forests, (a) the poplar stand in Flevoland (b) the larch stand at Schovenhorst (Veluwe) site. Photos by J. Zuo on 20th and 18th December 2012 respectively.

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