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Chapter VI

General discussion

The main aim of this thesis has been to investigate the decomposition of different organs of diverse logged tree species and the faunal communities associated with them in forest ecosystems. Trait-based approaches have been used to compare the dead plant matter quality across tree species and organs in order to understand the mechanisms of trait afterlife effects on associated fauna biodiversity and tree organ decomposition. As described in Chapter 1, this thesis has asked four main research questions: (1) How do multiple factors control tree decomposability in temperate forest? (2) What is the first filter for the colonizing faunal community in early-stage decomposing logs? (3) Is there facilitation within the faunal community on decaying logs? (4) What and how do multiple factors determine the logged wood fauna communities? From Chapters 2 through 5, some aspects of these questions were answered separately. In the following, I summarize and integrate the main results of this thesis connected to the research questions. This integration is done explicitly with a view to the future and will identify important research gaps, some of which emerging directly from this thesis, that requires further investigation.

6.1 Interacting drivers of tree decomposition and associated invertebrate diversity

Multiple factors are known to control tree decomposition rates (Cornwell et al. 2009, Cornelissen et al. 2012), including abiotic drivers (e.g. Harmon et al. 1986, Brovkin et al. 2012, Bradford et al. 2014), decomposer communities (e.g. Bradford et al. 2014, Liu et al. 2015) and the traits of different organs of different tree species (Weedon et al. 2009, Freschet et al. 2012a, Pietsch et al. 2014). The (a)biotic factors studied in this thesis were confirmed as having a significant influence on decomposition rates, as well as on invertebrate community composition. What is particularly new about this thesis is that it has explicitly addressed not only the single impact but also the combined effects of several (a)biotic drivers on litter decomposition and associated invertebrate communities (Figure 1). It has thereby quantified several important interactions between these drivers.

In Chapter 2 these interactions focused on litter decomposition *per se* highlighting the importance of considering the afterlife effects of functional traits of different organs of tree species in their local environmental context. Tree species was confirmed to be a strong determining factor for decomposition rate, which was explained by their traits related to litter quality. However, the species ranking of decomposition rate was only partly consistent between leaves, twigs and coarse branches and only partly consistent between contrasting forest environments. Interspecific variation in decomposition of leaves, twigs and branches were offset for different organs, i.e. generally leaves decomposed faster than twigs which in their turn decomposed faster than coarse branches. These contrasting decomposition rates between tree organs suggest dissimilar contribution to ecological processes such as dead organic matter accumulation and biogeochemistry. The findings partly supported the existence of a Tree Economics Spectrum (TES) of decomposability, reflecting an integrated tree canopy strategy that had important trait afterlife effects driving coordinated decomposability across the tree species. However, the cross-species coordination of organ decomposition was weaker than that reported for the Plant Economic Spectrum (PES) of litter decomposability (Freschet et al. 2012a), which included the whole range of growth forms from small herbs to trees. Moreover, the relative effects

of this TES of decomposability interacted with the local forest environment, which was presumably related to divergence in decomposer community composition and abiotic factors.

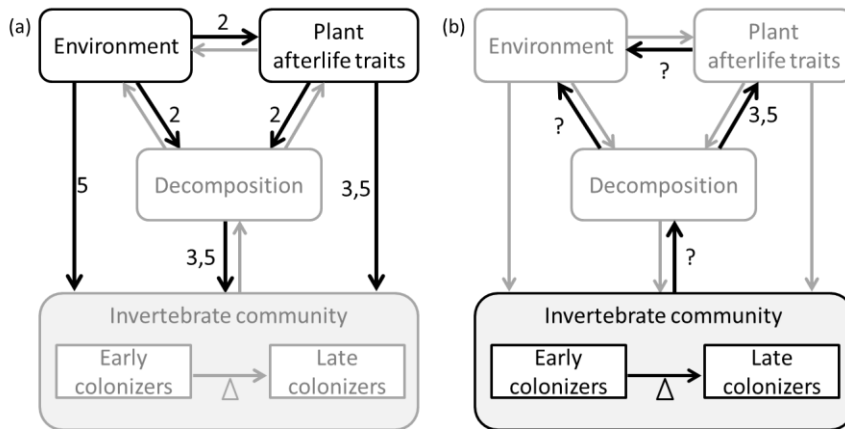


Figure 1. Direct and indirect relationships between abiotic and biotic factors that determine decomposition and invertebrate community composition of woody debris. Panel (a) refers to the drivers of decomposition and invertebrate communities, while panel (b) refers to the feedbacks of the invertebrates to decomposition and the forest environment. The numbers refer to the thesis chapters that have addressed these relationships (see also Figure 1 in the General Introduction). The triangle means interactions between early colonizers and later colonizers, e.g. facilitation (Chapter 4). The question marks refer to knowledge gaps.

Besides by joining biogeochemical cycles through decomposition, logged trees also have significant ecosystem functions related to soil biodiversity. Recently logged trees are colonized by a vast array of invertebrates. Chapters 3, 4 and 5 have together demonstrated how invertebrate abundances and community composition associated with decaying logs and coarse branches depend on some of the same (a)biotic drivers, and their interactions, that affect decomposition. Moreover, invertebrates interacted with themselves and with bark traits adding further complexity to their community composition (Figure 1). Chapter 3 studied the colonizing of fauna in early-stage decomposing logs. Resource is sufficiently available within logs at this stage but is difficult to reach for most fauna due to the presence of outer bark that acts as a barrier. The results showed strong interspecific differences in bark traits and a suite of bark traits together had fundamental afterlife effects on invertebrate community assembly, and acted as an environmental assembly filter for the colonizing invertebrates (Figure 1; see also Figure 2 in General Introduction). A combination of bark traits, acting as a potential ‘bark economics spectrum’ (following the same rationale as in the plant economics spectrum; Freschet et al. 2010a), was a highly significant positive predictor of the abundance of each of the key invertebrate clades. Pairs of tree species supported more dissimilar faunal community composition and greater family richness when they differed more in bark traits overall. Thus bark trait dissimilarity among tree species in forest stands is likely a better indicator of early-phase dead trunk fauna diversity than tree species diversity *per se*. Forest floor invertebrates are themselves important as decomposers (Ulyshen

2014), thus bark trait afterlife effects on the community composition of invertebrates will feed back to logged tree decomposition rate and biogeochemical cycling (Figure 1b). Wood trait – invertebrate feedbacks have been quantified and found to be important in the context of dead wood consuming termites in South China (Liu et al. 2015), but are still a large knowledge gap, certainly in temperate forests.

The aim of chapter 4 was to study whether wood-boring species may facilitate the colonization of other components of the faunal community in decaying logs (Figure 1b). We demonstrated that the density of bark holes (but to some degree also surface area of their inner bark galleries) made by early-colonizing bark beetles facilitated the presence of invertebrates with a body width smaller than those of the bark beetles but without the ability to gnaw through bark. As discussed in Chapter 3, in the early decomposition stage bark is a crucial environmental assembly filter for associated fauna. Bark beetles can alter the accessibility of bark resource availability to other organisms, by modifying the structural properties of bark tissues, thereby speeding up the succession of logged tree communities. Including this facilitative interaction will eventually lead to a more accurate and inclusive understanding of logged tree community assembly, and may have important and tree species specific cascading effects on tree decomposition.

Chapter 5 answered the question whether and how multiple factors determine the log fauna communities (Figure 1a). Diversity of macro-detritivores in coarse branches was found to be influenced by tree species, tree growing site, decay stage, decomposition environment and interactions of those multiple factors. Logged trees provide shelter and resources to macro-detritivores. Afterlife effects of initial differences in resource quality of tree species such as bark morphology, wood density, nutrient content and secondary metabolites (e.g. terpenes, large-chain phenols) (Cornwell et al. 2009, Stokland et al. 2012) can be one explanation for differences in macro-detritivore community composition between trees. There was a curvilinear relationship between wood decay stage and abundance of macro-detritivores, by using wood density as a measure for the decay stage. Macro-detritivore community composition on different tree species converged during the decay process. Consequently, tree species are more important in the substrate selection of macro-detritivores at the beginning of their dead matter decomposition. Tree species, the growing environment of the trees and the decomposition environment of the logs strongly determined macro-detritivores community composition in dead wood, moreover these drivers interacted with each other and with the decay stage in complex ways.

Determining how ecosystem processes, biodiversity dynamics, and abiotic factors interact is a major challenge in ecological research. This thesis focused on the mechanisms controlling the decomposition of logged trees across organs and the diversity of the associated invertebrates in two temperate forests with a contrasting environment. To get a more comprehensive understanding of ecosystem processes, biodiversity dynamics, and abiotic factors interactions, the findings from this thesis, when held against the other available literature, have led to further research needs, challenges and opportunities, which will be discussed below in the context of the results.

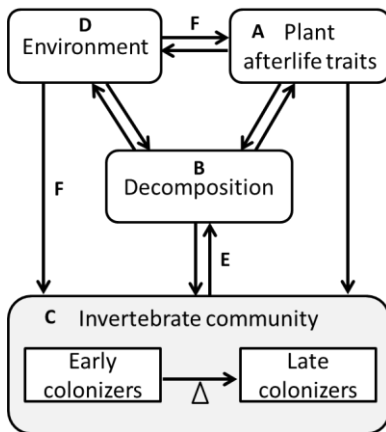


Figure 2. Knowledge gaps, emerging from this thesis, related to abiotic and biotic drivers of decomposition and invertebrate communities of woody debris. The letters refer to knowledge gaps and research opportunities discussed in the text.

6.2 A research agenda about logged tree biodiversity and decomposition

A. Research related to trait afterlife effects (Figure 2: A)

Evolutionary pattern: angiosperms versus gymnosperms

Angiosperms and gymnosperms represent the two major extant clades of woody species; these two evolutionary groups have striking differences in trait afterlife effects, e.g. on leaf (Cornwell et al. 2008) and wood decomposability (Weedon et al. 2009) and associated forest floor litter thickness (Augusto et al. 2015). In this thesis, even though the focus was not on the difference between these two groups, some interesting patterns were found in terms of decomposability and log-associated biodiversity. For instance, the decomposition rates of leaves and woody materials differed consistently between angiosperms and gymnosperms (Figures 1, 2, S2 and S4 in Chapter 2), confirming previous studies (Cornwell et al. 2008, Weedon et al. 2009, Pietsch et al. 2014). One explanation for the lower decomposability of gymnosperms can be that the studied species were all located on the nutrient conservative side of the tree economics spectrum (Figure 3 in Chapter 2). Gymnosperm wood decomposes more slowly than angiosperm wood within a common site, which correlates a higher carbon content in gymnosperm woody debris (Harmon et al. 2013).

The fauna communities in the logs of Norway spruce (*Picea abies*) were dominated by bark beetles that specialized on this gymnosperm species (Chapter 4). Bark beetles digging and feeding activity, facilitating other macro-detrivores, may represent a feedback by which the decomposition of the recalcitrant gymnosperm wood is accelerated to a certain degree (Figure 1b, Figure 2: E). Furthermore, the two tree species, silver birch (*Betula pendula*) and Norway spruce (*P. abies*), showed significant differences in associated macro-detrivore communities (Chapter 5). The difference in structure and content of lignins (Hammel and Cullen 2008) between the two tree groups might cause different ecological patterns of wood-decaying polypore

communities (Zhou and Dai 2012), which may also affect decomposition rates. Nevertheless, bark traits of the gymnosperm Black pine (*Pinus nigra*) were not particularly different from the angiosperm species and neither was the invertebrate community of this tree species compared to those in the angiosperms (Chapter 3). However, one year of decomposition was probably too short to compare these species for wood decomposability. Further research is needed for a more comprehensive understanding of the effect of gymnosperm vs angiosperm litter on biodiversity and ecosystem processes. In particular, it is still debated whether the lower decomposability of gymnosperm litter as compared to angiosperm litter translates into greater stable soil organic carbon content (Prescott and Vesterdal 2013).

Living versus naturally senesced tree joining woody debris

Trees lead a long life and shed litter throughout their lifetime. All leaves of most temperate species turn over and are shed on an annual basis (and evergreens after 1-3 years). Leaf litter is generally decomposed faster than woody debris (Freschet et al. 2013), so leaf litter represents the fast lane of the decomposition cycle. Many branches and stems in NW Europe are left after forestry management as well as after wind-throw, so the proportion of broken-off branches without nutrient resorption entering the decomposition subsystem can be rather high. Twigs are intermediate in this respect, with both living twigs (forestry, storms) and natural senesced twigs (with nutrient resorption and with intermediate shedding time compared to leaves and branches) entering the litter layer in significant proportions. Thus the litter layer is a mixture of recently alive and senesced material, representing different 'life' stages of tree material. Therefore, in Chapter 2, twigs cut from the tree in winter and collected from the ground in autumn were both included. There were differences between these two stages for a given tree species, e.g. decomposability was higher for fresh-cut twigs than for senesced twigs on the ground (Chapter 2, Figure S2), and is probably the result of nutrient resorption in the later, resulting in a lower substrate quality.

Tree materials of different 'life' stages differ ecologically. During leaf senescence, the coloration can change rapidly (Sanger 1971), and both interspecific (Cornelissen, 1996) and intraspecific variation (Cornelissen 2000) in leaf color can be predictors of decomposition of leaves. Green leaves have on average a faster decomposition than yellow, red or brown leaves (Cornelissen, 1996). The relationship between color and decomposability can be explained from the nutrient content and fungal composition in the tissues of the different colored leaves (Cornelissen 2000). Differences in nutrient content and fungal composition also exist in woody organs of different life stages. Nutrient resorption reduces the nitrogen and phosphorus pools during senescence (Aerts 1996, Freschet et al. 2010b), which is likely to decrease their decomposability. Tree materials of different life stages also influence other ecosystem functions, e.g. (1) biogeochemical cycling and chemical form of elements other than N and P, (2) associated biodiversity through resource availability and habitat heterogeneity (Seibold et al. 2016). As for the latter, in the LOGLIFE experiment we cut living trunks rather than using logs of naturally senesced trees for the reasons given above as well as to be able to standardize diameters and initial decay stage (i.e. zero) among species (Chapters 3, 4). This practice probably favored colonization by

bark beetles (Chapter 4), which tend to feed on resources in the fresh phloem. It is clear that more study is needed for the comprehensive understanding of the effects of living versus senesced woody organs on their decomposition rates and invertebrate biodiversity.

Other functional traits relevant to decomposition processes

To understand differences in decomposition rates among species and organs, a trait-approach was adopted. In Chapter 2, functional traits that represent the trade-off between acquisition and conservation of resources were measured for leaves, twigs and branches (see also Freschet et al. 2012a). These traits mostly correspond with those commonly measured as functional traits of living plants for tackling ecological and ecophysiological questions (Cornelissen 2003, Pérez-Harguindeguy et al. 2013). Interestingly, these traits included those commonly measured as predictors of decomposability: litter lignin content, C, N and P content, dry matter content and pH. This shows that some functional traits have afterlife effects in dead plant parts. In Chapter 3, bark traits that represent the micro-environment factor for invertebrates were measured. Although in a different context, bark thickness (Rosell et al. 2014), bark fissure index (MacFarlane and Luo 2009) and bark pH (e.g. Barkman 1958) have often been compared among tree species, while other bark traits (e.g. bark looseness, inner-to outer bark thickness ratio, water holding capacity, punching resistance; see Chapter 3) have so far been little if at all investigated in relation to the assembly and composition of logged tree invertebrate community composition. In Chapter 5, wood density and pH were analyzed as a measure for the decay stage of a given species.

The selected traits were fairly representative of the quality and decomposability of the organs of different tree species, even though not exhaustive. To get a more comprehensive understanding of variability in decomposition rates among species and organs, other important traits need consideration. For instance, the ratio between heartwood and sapwood varies greatly among species, ranging from a large ratio in oak (*Quercus robur*) to zero in beech (*Fagus sylvatica*); heartwood generally gets impregnated with secondary compounds, making it very recalcitrant to decomposition (Cornelissen et al. 2012), while sapwood tends to be more decomposable. Anatomical traits are potentially important too, for instance vessel densities, distributions and diameters may influence water retention and penetration by microbes and invertebrates (Cornwell et al. 2009). Diameter of woody organs has a similar potential effect on decomposability via accessibility and may explain part of the greater decomposability of twigs than branches (Chapter 2). In our study woody organ diameters were standardized, while in other studies it is often accounted for as a covariate rather than a species trait. However, in a tropical study diameter explained a great proportion of the decomposability of logs among species (Van Geffen et al. 2010), making this a valuable trait to understand variability in decay rates of species.

In this study, plant functional traits present in logged tree organs showed afterlife effects on invertebrate diversity. For further study, functional traits that relate to the habitat characteristics of wood and bark of those invertebrates might also be interesting in efforts to explain their response to the woody environment. In this sense it is interesting that invertebrate body diameter was highly relevant to the

facilitative effect of bark beetles on invertebrate access and abundance in Norway spruce (*P. abies*) in Chapter 4.

Interspecific and intraspecific variations

In this thesis relationships between logged tree traits, decomposition and community assembly were based on average species values, assuming that interspecific trait variability is higher than intraspecific variability. In chapter 2 the focus was on interspecific variation of litter decomposition rate for each of the tree organs. In Chapter 3 a large interspecific variation of bark traits was found, and it determined the dissimilarity of invertebrate communities that colonized the logged trunk. In Chapter 5, different macro-detritivore communities were found in two tree species across a range of decay stages. Although we were able to explain interactions based on interspecific differences in means, intraspecific trait differences may also be of importance.

There is currently great interest in partitioning the relative contributions of interspecific and intraspecific trait variation, as both can be important to plant functions (Albert et al. 2010, Albert et al. 2011, Violle et al. 2012). However, besides interspecific variation, the trees in this thesis also exhibited important intraspecific variation. For Instance, in Chapter 2, such variation was found to be significant for the initial traits and decomposition rates of leaves, twigs and branches of Norway spruce (*P. abies*) and Oak (*Q. robur*) collected from contrasting forest growing environments for the same species. In Chapter 4, a fully reciprocal experiment was carried out with logs of Norway spruce (*P. abies*) that had been collected from two sites with contrasting environments and had also been incubated in those two sites. There was an effect of incubation site on bark beetle abundance. In Chapter 5, the effect of collection sites of Birch (*Betula pendula*) and Norway spruce (*P. abies*) on macro-detritivore abundances and composition was highly significant but dependent on tree species and wood density (i.e. decomposition stage). All in all, this thesis revealed differences within the same tree species between the two sites of origin of the tree sampled, in terms of functional traits (Chapter 2), decomposability (Chapter 2) and supported fauna community (Chapter 4, 5). In the experiment, the trees were selected based on diameter. For the same diameter, the growth rate and age might vary between two sites of the same tree species, with consequences for wood quality. It is therefore important to determine the age of the trees that are collected from different sites with similar diameter. The collection environment had an influence on the age (N. van der Velden, unpublished MSc thesis) and wood characteristics (e.g. lignin content) of Oak (*Q. robur*) and Norway spruce (*P. abies*) (Vincent Crétin, unpublished MSc thesis). Thus the intraspecific variations due to differences in the growing environment have afterlife effects on decomposition of woody debris and biodiversity of invertebrates inhabiting it.

Other organs not studied

Large variation exists among plant species in above versus below ground biomass allocation (Cairns et al. 1997, Poorter et al. 2012), which is likely to drive highly contrasting patterns of litter production (Freschet et al. 2013). Differences in organic

matter quality between the above and below ground litter, such as dead roots, might lead to different, parallel food webs, with consequences for soil organic matter stabilization and biogeochemistry (Schmidt et al. 2011, Freschet et al. 2013). In this thesis, only above ground tree organs were studied with their influence on soil fauna. Course and fine roots constitute a very important knowledge gap for further study on decomposability and associated fauna. Roots produce large amounts of litter in the soil with generally slower decomposition rate than leaves (Freschet et al. 2013). The root system is of great important as a below ground organ that acts as an important conduit of carbon input to soils, which in turn stores more carbon than vegetation and the atmosphere combined (Norby and Jackson 2000, de Graaff et al. 2013). Further study on the effects of interspecific variation in root traits on root decomposition, and its influence on the soil fauna community (Figure 2: E), is needed for better understanding the processes leading to soil carbon storage.

Plant litter also consists of other plant organs than leaves, twigs, branches and wood; besides roots, reproductive organs have also received little attention in terms of decomposition, but some plants can produce large amount of litter derived from reproductive organs. Angiosperms and gymnosperms have different reproductive organs, i.e. fruits and cones, respectively. Within gymnosperms, woodiness of reproductive organ follows the order: *Pinus* > *Pseudotsuga*, *Picea*, *Abies* > *Larix*. For angiosperms, fruit woodiness follows the order: *Fagus* > *Quercus*, *Alnus*, *Castanea* > other species. Fruit and cone fall varies greatly among species and years (Graber and Leak, 1992; Ostfeld and Keesing 2000); trees produce large amount of fruits, cones and seeds in mast years. The annual production of reproductive organs differing in traits likely has an important influence on the litter layer quality and decomposition, as well as on the biodiversity living with it.

Shrubs: similar structures as tree canopy but without the trunk

Bushes/shrubs have a similar structure as a tree canopy but without the trunk. Thus when studying the leaf and fine stem decomposition and its contribution to biodiversity, bushes are another important woody group to look at.

Recent increases in shrub biomass, cover and abundance, “shrubification”(Myers-Smith et al. 2011), have been observed in some ecosystems, especially in tundra’s subjected to climate warming (Myers-Smith et al. 2011, Naito and Cairns 2011, Elmendorf et al. 2012). Shrub species may alter decomposition rates by altering litter quality and by altering the environmental conditions below the plants. Temperate shrubs generally grow faster than trees (Cornelissen et al. 1996). However, the patterns and causes of decomposition of dead shrub material of different species is little known (but see De Marco et al. 2011, Maisto et al. 2011). The study of the fates and rates of different dead organs of different shrub species is important for a better understanding of carbon and nutrient cycling in several biomes of the world, especially tundra and drylands.

B. Decaying tree changes through decomposition process

Decomposition is a dynamic process, both in terms of woody debris quality and associated biodiversity. Little is known about the species trait effect on the long term

dynamics of tree decomposition, which is because of the low decay rates of wood and, until recently, the lack of methods assessing tree species effects on long term decomposition in field conditions. Freschet et al. (2012b) presented a method relying on the sampling and short term incubation of dead wood from several decay stages covering the entire decay process, applying a model to derive long-term decay curves of different tree species based on these incubations. The results revealed not only overall differences in wood decomposition rates, but also changing decay dynamics among wood species and types. Thus, also based on our findings from Chapter 2, the changes in decay processes through time are species and organ specific and in-depth studies are needed for a more comprehensive understanding of long term decomposition.

For the invertebrate community diversity in fallen trees, this thesis focused on the early stage of decomposition (Figure 2, B). Bark traits act as an environmental assembly filter, which strength changes with decay and interacts with the invertebrates. The findings of Chapter 3 also yield an emerging hypothesis that warrants in-depth study, extending the relationship conceptually by broadening the decay trajectory. It will be interesting to follow the next decomposition phase (currently underway in the LOGLIFE experiment, or in related studies elsewhere), when, for instance, cerambycid beetles will invade the logs and will bore relatively large diameter holes into the xylem. Whether, in which tree species and to which extent they will also facilitate other invertebrate taxa, especially larger macro-detritivores that could provide possible positive feedback to further decomposition (Figure 2: E), will also contribute to the (w)hole story of facilitation in dead wood, and thus fauna community assembly in dead trees.

After passing through the environmental filter at the early decay stage, with the progression of decay, invertebrates will interact more strongly with each other, making community assembly in dead wood less predictable. During decay the initial difference in bark traits will become smaller and the resource pool (inner bark) will diminish, which will probably result in fewer available niches and increased competition among bark-inhabiting species. Also, bark traits may affect the species composition indirectly by changing the composition and abundance of the competing species and the prey species to predators. At later decomposition stages variation in wood traits will become more important, partly because much of the bark will have fallen off, but especially because wood-specialized decomposers, such as wood-boring beetles will colonize the wood. The initial high faunal community dissimilarity may decrease as the bark cover diminishes and bark is decomposed further, followed by another loop driven by wood traits. In the early stage of wood colonization by wood-boring arthropods the combined effect of still attached bark, and their traits, as well as wood traits, will quickly increase the dissimilarity in wood community composition (Figure 3). As for bark, with the progression of decay of wood by microbes, wood-inhabiting arthropod communities may become more similar in species composition over time due to a decrease in wood trait dissimilarity. However, the timing and duration of this phase of decreasing wood trait dissimilarity and increasing arthropod composition similarity with decomposition will be different from bark due to the lower decomposability of wood compared to bark. This hypothesis is obviously in need of empirical data to test it.

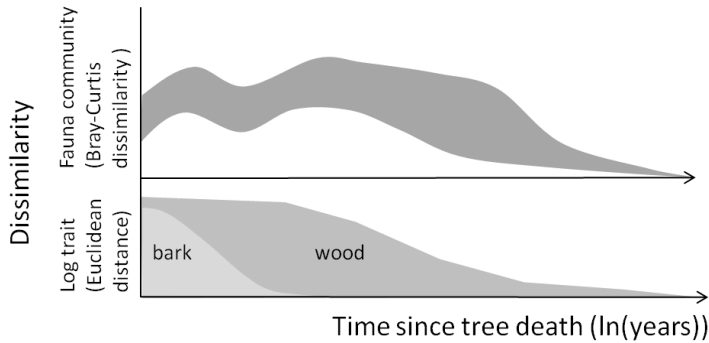


Figure 3. Hypothetical model of dissimilarity in log traits (lower panel) and their invertebrate community composition (upper panel) between pairs of tree species through the log decomposition trajectory. During early decay, the fauna community dissimilarity (upper dark grey area) is high due to a strong effect of bark trait filtering (bottom grey area), while wood has not been colonized yet. The dissimilarity in fauna community composition will first increase due to colonization of the bark and then decrease with a diminishing bark cover and with an increase in bark trait similarity between species due to decomposition. As decay proceeds, wood colonization by specialist wood-boring arthropods will commence. Wood traits (bottom grey area) will strongly filter the community composition leading to an increase in community dissimilarity, because of a colonization event. A long phase of continuous species turnover takes place, in which the competitive exclusion filter might gain strength. The broad range in community dissimilarity is because tree species will not only vary in wood traits at given decay stage, but will also differ in decay stage owing to differences in decomposition rate, which adds to trait dissimilarity even if trees have the same initial traits. Towards very advanced wood decay stages, wood traits will converge and the dissimilarity in invertebrate composition will decrease accordingly.

C. Species interactions within detrital communities

Invertebrates interact with each other within the detrital communities. The facilitation effects we observed between bark beetles and macro-detritivores are also found in other studies, for groups of fauna that were not included in this thesis, e.g. for the diversity of cavity-nesting bees (Sydenham et al. 2016). This suggests that facilitation might be a common phenomenon in community assembly of wood-inhabiting species. The priority effects of early successional insects in dead wood can also influence late successional organisms other than invertebrates, e.g. fungi (Jacobsen et al. 2015). Beside the facilitation effect studied in this thesis (Chapter 4), there are other important species interactions. Negative species interactions, such as competition and predation, and positive interactions, i.e. mutualism, commensalism, and ecosystem engineering, are also important community-level processes (Figure 2: C). These types of interactions deserve more attention in the framework of wood traits, decomposition, and wood-inhabiting fauna.

Finally, vertebrates may become more important to the biodiversity associated with dead trees at more advanced decay stage; and contribute to decay themselves (Figure 2: E). For instance, woodpeckers often forage for invertebrates in strongly decayed wood. In search for prey they remove bark and significantly damage the wood. Moreover, they use tree trunks for nesting. These behaviors might influence the decay process of logs strongly through modification of the substrate, and facilitation of certain species.

D. Research related to environmental factors

Interaction with local environment, SMI hypothesis (Figure 2: F)

In this study, we compared the decomposability and fauna composition of tree species in two environmentally contrasting forests. A strong influence of and interaction with forest environment were found for decomposition rate (Chapter 2) and associated biodiversity (Chapters 4, 5).

Our study provides some anecdotal evidence of a “home-field advantage” (HFA) effect, which means that decomposition occurs more rapidly when litter is placed in its “home” environment (beneath the plant species from which it has been derived) than away from its plant species beneath a different plant species (Ayres et al. 2009, Veen et al. 2015). In Chapter 2, poplar (*Populus x canadensis*) twigs decomposed faster in the LOGLIFE experiment poplar stand, while larch (*Larix kaempferi*) twigs decomposed somewhat faster in the larch stand when compared with the overall twig decomposition pattern in both sites. The existence of HFA is somewhat controversial (Veen et al. 2015) and is spatial scale dependent. Freschet et al. (2012c) defined an alternative substrate quality-matrix quality interaction (SMI) hypothesis, expecting a continuum from positive to negative interactions between specific litters and decomposer communities as specific litters and the ecosystem litter layer 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. Although the effect sizes of SMI appear to be smaller than overall effects of dead wood species and decomposition environment, when trying to understand and predict future patterns of decomposability and associated biodiversity of tree species under regimes of changing land-use and climate, these interactions with environment should be taken into account.

Expand local environment to global scale

Biodiversity associated with dead wood contributes to the global biodiversity. But dead-wood experimental studies are geographically biased towards temperate and boreal forests of Europe and North America, as well as Australia (Seibold et al. 2015). In general, taxonomic diversity decreases from the equator towards the poles (Gaston 2000). Plant and invertebrate diversities, and their interactions may explain partly of the latitudinal trends. More research is needed in other areas, such as tropical and subtropical forests for a more comprehensive understanding of dead tree decomposition and associated biodiversity.

6.3 Conclusion

Environmental factors, trait afterlife effects and their interactions have a strong influence on the decomposition of different aboveground parts of trees of temperate species. Together they also determine the invertebrate communities associated with these decomposing trees. Within logged wood inhabiting communities, invertebrates interact with each other during the community assembly, in which early colonizing

specialist beetles facilitate the colonization of more generalist species. This thesis has provided some insight into these processes. However, further research on the remaining knowledge gaps, some of which have been highlighted above, is needed to enlarge our understanding of how biodiversity dynamics during wood decay, soil ecosystem processes and (a)biotic factors that drive them interact in forests.

References

- Addison, J., Trofymow, J. and Marshall, V. (2003) Abundance, species diversity, and community structure of Collembola in successional coastal temperate forests on Vancouver Island, Canada. *Applied Soil Ecology*, 24, 233-246.
- Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, 84, 597-608.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. and Lavorel, S. (2010) A multi-trait approach reveals the structure and the relative importance of intra- versus interspecific variability. *Functional Ecology*, 24, 1192-1201.
- Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. and Violle, C. (2011) When and how should intraspecific variability be considered in traitbased plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, 13, 217-225.
- Barkman, J.J. (1958). Phytosociology and ecology of cryptogamic epiphytes. Assen, the Netherlands: van Gorcum and Comp. N.V.
- Berg, M.P., Soesbergen, M., Tempelman, D., Wijnhoven, H. (2008) Verspreidingsatlas Nederlandse landpissebedden, duizendpoten en miljoenpoten (Isopoda, Chilopoda, Diplopoda). EIS-Nederland, Leiden and Vrije Universiteit-Afdeling Dierecologie, Amsterdam.
- Brovkin, V., van Bodegom, P.M., Kleinen, T., Wirth, C., Cornwell, W.K., Cornelissen, J.H.C. and Kattge, J. (2012) Plant-driven variation in decomposition rates improves projections of global litter stock distribution. *Biogeosciences*, 9, 565-576.
- Cairns, M.A., Brown, S., Helmer, E.H. and Baumgardner, G.A. (1997) Root biomass allocation in the world's upland forests. *Oecologia*, 111, 1-11.
- Chapin III, F.S., McFarland, J., McGuire, A.D., Euskirchen, E.S., Ruess, R.W. and Kielland, K. (2009) The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. *Journal of Ecology*, 97, 840-850.
- Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, 84, 573-582.
- Cornelissen, J.H.C., Castro-Díez, P. and Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84: 755-765.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335-380.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V. and Westoby, M. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11, 1065-1071.
- Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F., Weedon, J. T., Wirth, C., and Zanne, A. E. (2009) Plant traits and wood fates across the globe: rotted, burned, or consumed? *Global change biology*, 15, 2431-2449.
- David, J.F., Handa, I.T. (2010) The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biological Reviews*, 85, 881-895.
- De Graaff, M.-A., Jastrow, J.D., Six, J., Wulschleger, S.D. (2013) Variation in root architecture among switchgrass cultivars impacts root decomposition rates. *Soil Biology and Biochemistry*, 58, 198-206.
- De Marco, A., Meola, A., Maisto, G., Giordano, M., Virzo De Santo, A. (2011) Nonadditive effects of litter mixtures on decomposition of leaf litters in a Mediterranean maquis. *Plant and Soil*, 344, 305-317.
- Diamond, J.M. (1975) Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jonsdottir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Levesque, E., Magnusson, B., May, J.L., Mercado-Diaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Martin Schmidt, N., Shaver, G.R., Spasojevic, M.J., Porhallsdottir, P.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2, 453-457

- Ferrenberg, S. and Mitton, J.B. (2014) Smooth bark surfaces can defend trees against insect attack: resurrecting a 'slippery' hypothesis. *Functional Ecology*, 28, 837–845.
- Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P. and Aerts, R. (2010a) Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, 98, 362–373.
- Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. and Aerts, R. (2010b) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist*, 186, 879–889.
- Freschet, G.T., Aerts, R. and Cornelissen, J.H.C. (2012a) A plant economics spectrum of litter decomposability. *Functional Ecology*, 26, 56–65.
- Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R. and Cornelissen, J.H.C. (2012b) Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *Journal of Ecology*, 100, 161–170.
- Freschet, G.T., Aerts, R. and Cornelissen, J.H.C. (2012c) Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology*, 100, 619–630.
- Freschet, G.T., Cornwell, W.K., Wardle, D.A., Elumeeva, T.G., Liu, W., Jackson, B.G., Onipchenko, V.G., Soudzilovskaia, N.A., Tao, J.P. and Cornelissen, J.H.C. (2013) Linking litter decomposition of above and belowground organs to plant-soil feedbacks worldwide. *Journal of Ecology*, 101, 943–952.
- Graber, R.E., Leak, W.B. (1992) Seed fall in an old-growth northern hardwood forest. Radnor, Pa.: USDA, Research paper NE-663, 11 pp.
- Hammel, K.E., Cullen, D. (2008) Role of fungal peroxidases in biological ligninolysis. *Current Opinion in Plant Biology*, 11, 349–355.
- Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S., et al. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133–302.
- Harmon, M.E., Fasth, B., Woodall, C.W., Sexton, J. (2013) Carbon concentration of standing and downed woody detritus: effects of tree taxa, decay class, position, and tissue type. *Forest Ecology and Management*, 291, 259–267.
- Hättenschwiler, S., Bretscher, D. (2001) Isopod effects on decomposition of litter produced under elevated CO₂, N deposition and different soil types. *Global Change Biology*, 7, 565–579.
- Hendriksen, N.B. (1990) Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils*, 10, 17–21.
- Jackson, B.G., Peltzer, D.A. and Wardle, D.A. (2013) Are functional traits and litter decomposability coordinated across leaves, twigs, and wood? A test using temperate rainforest tree species. *Oikos*, 122, 1131–1142.
- Jacobsen, R.M., Birkemoe, T., Sverdrup-Thygesen, A. (2015) Priority effects of early successional insects influence late successional fungi in dead wood. *Ecology and Evolution*, 5, 4896–4905.
- Jones, C.G., Lawton, J.H., Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.
- Liu, G., Cornwell, W.K., Cao, K., Hu, Y., Van Logtestijn, R.S.P., Yang, S., Xie, X., Zhang, Y., Ye, D., Pan, X., Ye, X., Huang, Z., Dong, M., Cornelissen, J.H.C. (2015) Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. *Journal of Ecology*, 103, 1214–1223.
- MacFarlane, D.W. and Luo, A. (2009) Quantifying tree and forest bark structure with a bark-fissure index. *Canadian Journal of Forest Research*, 39, 1859–1870.
- Maisto, G., De Marco, A., Meola, A., Sessa, L., Virzo De Santo, A. (2011) Nutrient dynamics in litter mixtures of four Mediterranean maquis species decomposing in situ. *Soil Biology and Biochemistry*, 43, 520–530
- Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M. et al. (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters*, 15, 1033–1041.
- McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185.
- Myers-Smith, I.H., Forbes, B.C., Wilkening, M. et al. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6, 045509
- Naito, A.T. and Cairns, D.M. (2011) Patterns and processes of global shrub expansion. *Progress in Physical Geography*, 35, 423–442.
- Norby, R.J., Jackson, R.B. (2000) Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist*, 147, 3–12.
- Ostfeld, R.S. and Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution*, 15, 232–237.

- Paoletti, M.G., Hassall, M. (1999) Woodlice (Isopoda: Oniscidea): their potential for assessing sustainability and use as bioindicators. *Agriculture, Ecosystems and Environment*, 74, 157-165.
- Pérez-Harguindeguy, N., Cornelissen, J.H.C., Gwynn-Jones, D., Diaz, S., Callaghan, T.V., Aerts, R. (2000) Autumn leaf colours as indicators of decomposition rate in sycamore (*Acer pseudoplatanus* L.). *Plant Soil*, 225, 33-38.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167-234.
- Pietsch, K.A., Ogle, K., Cornelissen, J.H.C., Cornwell, W.K., Bonisch, G., Craine, J.M., Jackson, B.G., Kattge, J., Peltzer, D.A., Penuelas, J., Reich, P.B., Wardle, D.A., Weedon, J.T., Wright, I.J., Zanne, A.E., Wirth, C. (2014) Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs. *Global Ecology and Biogeography*, 23, 1046-1057.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. and Mommer, L. (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist*, 193, 30-50.
- Prescot, C., Vesterdal, L. (2013) Tree species effects on soils in temperate and boreal forests: emerging themes and research needs. *Forest Ecology and Management*, 309, 1-3.
- Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M. et al. (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecology Letters*, 8, 811-818.
- Rosell, J.A., Gleason, S., Mendez-Alonzo, R., Chang, Y., Westoby, M. (2014) Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist*, 201, 486-497.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J. and Manning, D.A.C. (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, 478, 49-56.
- Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J. (2015) Experimental studies of dead-wood biodiversity - a review identifying global gaps in knowledge. *Biological Conservation*, 191, 139-149.
- Seibold, S., Bässler, C., et al. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, DOI: 10.1111/1365-2664.12607
- Sommer, B., Harrison, P.L., Beger, M. and Pandolfi, J.M. (2014) Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology*, 95, 1000-1009.
- Stokland, J.N., Siitonen, J., Jonsson, B.G. (2012) Biodiversity in Dead Wood. Cambridge University Press, Cambridge.
- Sydenham, M.A.K., Häusler, L.D., Moe, S.R., Eldegard, K. (2016) Inter-assembly facilitation: the functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees. *Ecology and Evolution*, 6, 412-425.
- Ulyshen, M.D. (2014) Wood decomposition as influenced by invertebrates. *Biological Reviews*. doi: 10.1111/brv.12158.
- van Geffen, K.G., Poorter, L., Sass-Klaassen, U., van Logtestijn, R. and Cornelissen, J.H.C. (2010) The trait contribution to wood decomposition rates of 15 neotropical tree species. *Ecology*, 91, 3686-3697.
- Van Geffen, K.G., Berg, M.P., Aerts, R. (2011) Potential macro-detritivore range expansion into the subarctic stimulates litter decomposition: a new positive feedback mechanism to climate change? *Oecologia*, 167, 1163-1175.
- Veen, G.F., Freschet, G.T., Ordóñez, A. and Wardle, D.A. (2015) Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos*, 124, 187-195.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. and Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*, 27, 244-252.
- Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C. and Coomes, D.A. (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters*, 12, 45-56.
- Weihner, E. and Keddy, P.A. (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159-164.
- Wu, J., Yu, X.D., Zhou, H.Z. (2008) The saproxylic beetle assemblage associated with different host trees in Southwest China. *Insect Science*, 15, 251-261.
- Zhou, L.W., Dai, Y.C. (2012) Recognizing ecological patterns of wood-decaying polypores on gymnosperm and angiosperm trees in northeast China. *Fungal Ecology*, 5, 230-235.