

**Dissertationes Forestales 226**

Effects of climate, wood quality and fungal diversity  
on coarse wood decomposition of Scots pine

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Academic dissertation

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## ABSTRACT

In this thesis, I investigated the independent and interactive effects of abiotic factors viz. temperature, humidity and biotic factors viz. fungal diversity (species richness and assemblage composition) and substrate quality on fungal wood decomposition. In the first phase, the phenolic composition of six types of Scots pine (*Pinus sylvestris* L.) substrates were assessed using high-performance liquid chromatography. The wood types were living mature trees with no fungal sporocarps, living mature trees with *Phellinus pini* sporocarps, fallen non-kelo trees, soon-to-be kelo trees (standing), standing kelo trees, and fallen kelo trees. In the second phase, I tested the effect of drivers on wood decomposition using two temperature (16 and 21 °C) and humidity (70 and 90%) levels on three wood types (fast-grown and slow-grown wood from managed forests and kelo from old-growth forest) with four different wood-decaying fungi (*Antrodia xantha*, *Dichomitus squalens*, *Fomitopsis pinicola* and *Gloeophyllum protractum*) in one, two and four species assemblage compositions in a 9-month experiment in the laboratory.

The main findings of the thesis were as follows:

- 1) Substrate quality (based on heartwood (HW) phenolic composition) varied widely even within one tree species. This showed that the chemical quality of the dead wood also varied remarkably and that it could potentially be as important as quantity in fulfilling its role as a key component of the forests. Evidently, external factors, such as fungal decomposition and fire injury were related to the HW phenolic composition of Scots pine. However, it remained unclear to what extent the differences in phenolic composition are caused by fungal infection and fungal decomposition.
- 2) The phenolic composition of the fallen rare Fennoscandian substrate 'kelo' was significantly different from standing and fallen Scots pine; the difference was more pronounced with increasing decay thereby indicating variations in their respective decay patterns. The centuries old 'kelo' pine trees from natural forests decayed more slowly than the pine wood from the managed forests even under changing climate conditions, which suggested that kelo is a more stable substrate for the fungal decomposers. This necessitates further consideration when dead wood restoration activities are planned and when the role of coarse wood debris (CWD) as a carbon (C) store is estimated.
- 3) Fungal wood decomposition was affected by temperature, humidity, substrate quality and fungal diversity. However, wood quality and fungal assemblage composition modified the influence of climatic factors on fungal decomposition rates. When the drivers act simultaneously, the interactions between temperature, humidity and wood quality were more prominent than their independent effects.

- 4) The decay response to changes in climatic variables and wood type was highly specific to fungal species. Higher temperature (21 °C) did not always result in an increase in the fungal wood decay rate.
- 5) The decay rate varied with species richness, although no definite trends were observed. In fact, the fungal assemblage composition was found to be more important than fungal species richness in mixed cultures, which indicated that species-specific fungal traits are essential in driving decomposition.
- 6) An averaging effect in the decomposition rates of the CWD substrate was found during possible interactions of diverse fungal species with the simultaneous changes in climate variables. This indicated the importance of identifying the key species that make the largest contribution to ecosystem processes and are also most affected by environmental variables.

To increase the reliability of the present climate-carbon prediction models and to assess the resilience of forests for the adaptation and mitigation of climate change, it is essential to study the interactions between the various drivers of fungal wood decomposition. The results presented in this thesis emphasize that it is critical to understand the different and complex mechanisms that affect wood decomposition. It is also of utmost importance to understand the differences in the functionality of the different fungal decomposers and wood types as they have a disproportionate influence on ecosystem processes, which needs to be accounted for predictive models containing wood-decay species (and wood-based C). From an ecosystem restoration and biodiversity conservation view point, further studies are warranted to discern the properties of rare substrates such as kelo, a highly specific substrate for several decomposer species. This will increase the possibility of restoring dead wood with similar properties to kelo for fungal biodiversity conservation.

**Keywords:** climate change; dead wood; dead wood-associated fungi; fungal interaction; kelo; substrate quality

## ACKNOWLEDGEMENTS

My journey as a doctoral student had been a long and arduous one and it would have been impossible to reach this stage without the devoted support and love of a great many people. I owe my heartfelt gratitude and love to all those people who helped me during my graduate experience and made it into something I will cherish forever.

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Joensuu, May 2016  
Parvathy Venugopal

## LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following listed papers referred to in the text by the Roman numerals I-III. Article III is the authors' version of the submitted manuscript. Articles I-III are reproduced with the kind permission of the publishers:

- I** Venugopal P., Julkunen-Tiitto R., Junninen K., Kouki J. (2016). Phenolic compounds in Scots pine heartwood: are kelo trees unique woody substrate? *Canadian Journal of Forest Research* 46:225-233.  
<http://dx.doi.org/10.1139/cjfr-2014-0498>
- II** Venugopal P., Junninen K., Linnakoski R., Edman M., Kouki J. (2016). Climate and wood quality have decayer-specific effects on fungal wood decomposition. *Forest Ecology and Management* 360: 341-351.  
<http://dx.doi.org/10.1016/j.foreco.2015.10.023>
- III** Venugopal P., Junninen K., Edman M., Kouki J. Wood-decayer assemblage composition has major influence on how climate and wood quality modify fungal wood decomposition. Manuscript.

### Contributions of the authors to the articles and to the manuscript

	<b>I</b>	<b>II</b>	<b>III</b>
<b>Original idea</b>	PV; KJ; JK	JK	JK
<b>Study design</b>	PV; KJ; RJT	PV; JK	PV; JK
<b>Data collection</b>	PV; KJ	PV	PV
<b>Laboratory work</b>	PV; RJT	PV; RL	PV
<b>Data analysis</b>	PV	PV	PV
<b>Manuscript preparation</b>	PV; JK; RJT; KJ	PV; JK; KJ; ME; RL	PV; JK; KJ; ME

JK: Jari Kouki; KJ: Kaisa Junninen; RJT: Riitta Julkunen-Tiitto; ME: Mattias Edman;  
RL: Riikka Linnakoski

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## ABBREVIATIONS

Ax	<i>Antrodia xantha</i>
BEF	Biodiversity-Ecosystem functioning
C	Carbon
CWD	Coarse Woody Debris
dbh	Diameter at Breast Height
DL	Diversity level
DS	<i>Dichomitus squalens</i>
Fp	<i>Fomitopsis pinicola</i>
Gp	<i>Gloeophyllum protractum</i>
HPLC	High Performance Liquid Chromatography
HW	Heartwood
NPP	Net Primary Productivity
Pg	Petagram
PS	Pinosylvin
PSM	Pinosylvin Monomethyl Ether
RH	Relative humidity
St	Strain
°C	degree Centigrade
%	percent



## 1. INTRODUCTION

Boreal forests are one of the most important global carbon (C) pools<sup>1</sup> (Lindroth et al. 1998; Myneni et al. 2001; Bradshaw et al. 2009; Pan et al. 2011) making them a key driver of the global C budget. Boreal forests are one of the largest forest ecosystems in the world, covering approximately 11% of the earth's terrestrial surface (Esseen et al. 1997), and store approximately ~300 Pg of C (equivalent to ~50% of the total atmospheric C) in their vegetation and soil.

In an extensive study in *Nature* in which over 500 boreal and temperate old-growth forests aged between 15 and 800 years were analyzed, it was seen that although C uptake<sup>2</sup> gets slower as forests grow older, the net sequestration<sup>2</sup> of biomass and C stocks<sup>3</sup> remains positive (Luyssaert et al. 2007; Luyssaert et al. 2008). This positive net ecosystem productivity and biomass change could be partly due to old-growth forests housing dead wood of all types (decay stages, sizes) leading to an increase in structural heterogeneity (Jonsson 2000). Consequently, old natural forests are not C neutral as was previously believed but instead are net C sinks<sup>4</sup>. However, it was also seen that C uptake and net primary productivity (NPP) gets slower as these forests grow older. This could be partly attributed to the fact that these centuries-old old-growth forests with high above ground biomass are more prone to sporadic disturbances, for example, fires, insect outbreaks and wind-throw (Luyssaert et al. 2008).

Conversely, climate change models have predicted that warming effects will be greatest in the boreal realm (IPCC 2007), particularly Fennoscandia (Kirschbaum and Fischlin 1996; Christensen et al. 2007). When taken in combination; the large extent of the boreal forest biome, the enormous amount of C stored in boreal ecosystems, their sensitivity to climatic changes and the predicted climatic warming, could result in a switch from a net C sink into a potential C source<sup>5</sup>, causing positive feedbacks in the global C cycle. However, it is not known how current environmental changes will influence C accumulation in boreal forests, or what are the principal ecological mechanisms related to these phenomena (Ruckstuhl et al. 2008; Bradshaw et al. 2009; Cornelissen et al. 2012). Assessing how vulnerable this source/sink strength may be to climate change is essential to understand the role that forests may have in the mitigation and adaptation to climate change, and to correctly incorporate this information into global C models.

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<sup>1</sup> “A reservoir. A system that has the capacity to accumulate or release carbon. Examples of carbon pools are forest biomass, wood products, soils, and atmosphere. The units are mass”.

<sup>2</sup> “The process of increasing the carbon content of a carbon pool other than the atmosphere.”

<sup>3</sup> “The absolute quantity of carbon held within a pool at a specified time (measured in terms of mass).”

<sup>4</sup> “Any process or mechanism which removes a greenhouse gas, an aerosol or a precursor of a greenhouse gas from the atmosphere. A given pool can be a sink for atmospheric carbon if, during a given time interval, more carbon is flowing into it than is flowing out.”

<sup>5</sup> “Opposite of sink. A carbon pool (reservoir) can be a source of carbon to the atmosphere if less carbon is flowing into it than is flowing out of it.” IPCC. (2000). Land use, land-use change and forestry. Summary for policy makers. In: Nakicenovic, N., Swart, R. (Eds.). Intergovernmental panel on Climate Change (IPCC), Geneva, Switzerland: p. 570.

## 1.1 Biodiversity, ecosystem functioning and climate change

Biodiversity-ecosystem functioning (BEF) studies have taken the high ground in ecological research in the past few years (Aerts et al. 2008). The issues of climate change and biodiversity are closely interconnected through climate change effects on biodiversity and feedbacks, when changes in biodiversity lead to climate change (Hooper et al. 2005; UNEP 2009). The effects of biodiversity loss and changes in community composition on BEF have provided compelling evidence over the past decade and have highlighted the urgency of this issue (Loreau et al. 2002). In the realm of global climate change, it is critical to understand the various aspects of biodiversity in BEF to successfully incorporate it into forest restoration projects (Aerts and Honnay 2011). The concept of ‘*biodiversity*’ generally encompasses numbers of entities (e.g. genotypes, species, or ecosystems), the evenness of their distribution and differences in their functional traits along with their interactions (Gaston and Spicer 2004). Species richness (number of species present) has often been used as a synonym for biodiversity, however the effects of the other components of biodiversity, such as relative abundance, composition, presence/absence of key species, on ecosystem properties are also important (Hooper et al. 2005). In my study, I focused on the two key aspects of biodiversity; ‘species richness’ and ‘composition’ and investigated how they modify the effects of abiotic factors, such as temperature, humidity and wood quality, as well as their interactive effects on wood decomposition. With increasing concern over biodiversity loss, there is a clear need to assess the effect of biodiversity on ecosystem functioning processes (Chapin III et al. 2000; O’Connor and Crowe 2005).

There have been several contradictory theories in regard to the effect of BEF; a consequence of limited empirical evidence that would show the consistency of species richness and rates of ecological processes. Some of the previous disparate theories or models regarding biodiversity effects were termed as redundant, rivet, and idiosyncratic models (Lawton and Brown 1994). Species diversity using facilitative interactions and complementary resource use / partitioning have been considered to be a major determinant of ecosystem processes, such as decomposition and nutrient dynamics (Gessner et al. 2010).

## 1.2 Boreal forests and coarse woody debris

Forest C is stored in several ecosystem components (Pregitzer and Euskirchen 2004). The two most prominent C pools in the forest ecosystem can be listed as live biomass (such as trees, ground vegetation etc.) and dead biomass (Liski et al. 2003) (such as standing dead logs/snags, decaying recumbent wood including fine woody debris (FWD; diameter 5-9 cm) and coarse woody debris (CWD; diameter  $\geq 10$  cm) (Kruys and Jonsson 1999; Siitonen 2001; Iwashita et al. 2013), stumps, dead roots etc.) (Allard and Park 2013). However the dead wood CWD component is often overlooked in estimating the forest carbon pool leading to gross underestimation of the ecosystem C storage (Gough et al. 2007). Hence in this study, I will concentrate on the relevance of dead woody biomass<sup>6</sup>, also known as CWD on the ecosystem functioning. The CWD greatly

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<sup>6</sup>“The mass of the woody parts (wood, bark, branches, twigs, stumps and roots) of trees, living and dead shrubs and bushes, measured to a minimum diameter of 0 mm.” Liski J., Korotkov A. V., Prins C. F. L., Karjalainen

contributes to the structure and microhabitat diversity as well as acting as a long-term nutrient source (Harmon et al. 1986; Siitonen 2001; Laiho and Prescott 2004). Many saproxylic species, particularly fungi, are highly dependent on dead wood (Kuuluvainen 2002). For example, Siitonen (2001) estimated that about 20–25% of the forest saproxylic species in Finland (4000-5000 species) are dependent on dead wood. However, it is also estimated that the CWD in managed forests has been extremely low (for example, the average CWD content is 2-10 m<sup>3</sup>/ha in managed forests compared to 60-90 m<sup>3</sup>/ha in natural forests in southern Finland) leading to high risks of biodiversity loss among saproxylic species under managed forest regimes (Rassi et al. 2010; Valentin et al. 2014).

The functional significance of woody biomass depends not only on the quantity but also on other key features such as the size distribution, degree of decay, species, position (snags vs. logs), and spatial arrangement (Harmon et al. 1986; Renvall 1995). Hence, an understanding of CWD dynamics is of major importance in determining the impacts of current management practices on the relationship between CWD and biodiversity, stand health, and ecosystem productivity (Lee et al. 1997; Jonsson 2000; Pedlar et al. 2002).

### 1.3 Wood decomposition and fungal decomposers in boreal regions

The amount of dead woody biomass is mostly affected by the activities of decomposer fungi (Boddy 2001; Boddy and Heilmann-Clausen 2008; Stenlid et al. 2008). Hence any changes in decomposer fungi assemblages may considerably affect the functioning of boreal forests, although the responses of the fungal decomposer to environmental changes are unclear.

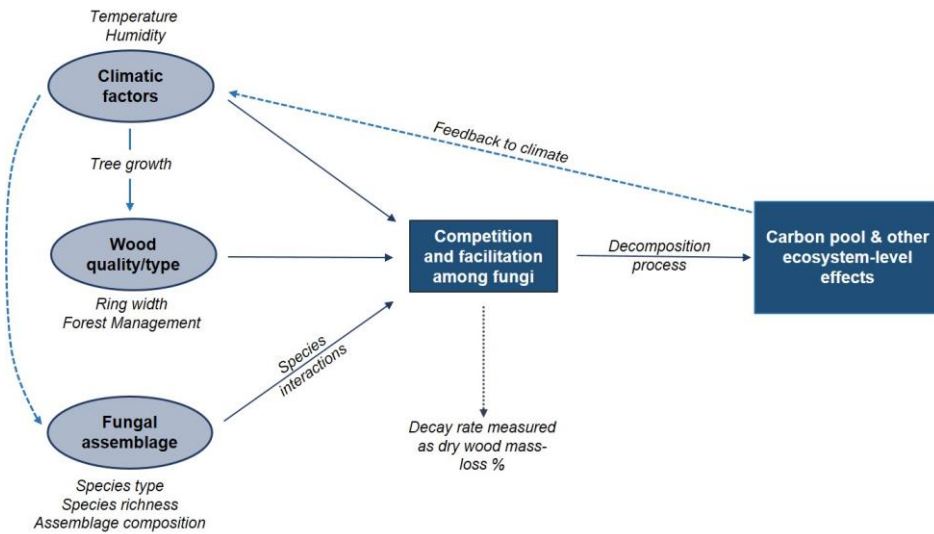
Fungi are known to be quite sensitive to climatic conditions (Gange et al. 2007), and the changing climate may considerably affect the decomposer assemblages and decomposition process. Additionally, habitat changes and forest management currently affect species richness of the fungal decomposer communities (Tikkanen et al. 2006; Junninen and Komonen 2011) that may influence decomposition. Thus, the current environmental changes are likely to influence the structure of the wood decomposer communities.

The climatic changes and the changes in the decomposer community structure may have a major direct influence on decomposition rates. For example, different moisture and temperature conditions, the long autumn season or the lack of snow cover in winter may directly affect the rate of annual decomposition and sporocarp production rates (Gange et al. 2007; Piao et al. 2008). Additionally climate affects the growth of trees and wood properties and thus modifies the resources of the decomposers indirectly (Edman et al. 2006).

Finally, the fungal decomposer communities that occur on dead wood are highly interactive. Different species are known to have both competitive (pre-emptive interspecific competition, combat) as well as mutualistic (facilitative succession where definite species follow each other) relationships (Niemelä et al. 1995; Renvall 1995). If these relationships are altered in response to changes in species diversity and climate, this may have a substantial effect on the community structure and possibly also on

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T., Victor D. G., Kauppi P. E. (2003). Increased carbon sink in temperate and boreal forests. *Climatic Change* 61: 89-99.



**Figure 1.** Conceptual relationship between the abiotic and biotic factors in this study illustrating their effect on carbon pools via fungal wood decomposition and related feedbacks

decomposition process. However, there is a severe dearth of information in regard to CWD decay rates in boreal forests and on the factors that control this process (Harmon and Hua 1991).

Some fungal species in Fennoscandian forests are currently under serious threat of endangerment and extinction, principally due to a lack of dead wood in the forest landscape due to intensive forest management (Siitonen 2001). The consequences of reduced fungal diversity on decomposition and C storage are still mostly unexplored. Furthermore, this could also dramatically affect the stability and functioning of forest ecosystems and their ability to adapt to rapid environmental changes (Stenlid et al. 2008).

Overall, three factors seem to be overwhelmingly important in woody biomass decomposition: climate, the properties of the wood, and the decomposer communities. My thesis has investigated the independent and interactive effects of these three main drivers in CWD decomposition.

#### 1.4 Premises, aims and hypotheses

The study is built upon five premises, schematically represented in Figure 1, coined on the basis of previous empirical research:

1. Boreal forests are a major global C pool (Gower et al. 2001) and act as net C sink (Keeling et al. 1996; Liski et al. 2003). In particular, the old growth forests, earlier considered as C neutral or redundant in the global C cycle, have positive net ecosystem productivity and are significant C sinks (Harmon and Hua 1991; Luysaert et al. 2008).
2. CWD is an important detrital C pool (Siitonen 2001; Pregitzer and Euskirchen 2004) and hence CWD decomposition has the potential to create large feedbacks in the

global C cycle (Woodall and Liknes 2008). However, the decomposition of CWD and its subsequent impact on the terrestrial C balance is sensitive to climate changes and wood trait variation (Weedon et al. 2009).

3. Decomposer fungi (saprotrophic basidiomycetes) are the main agents affecting CWD decomposition and the subsequent net C balance (Boddy 2001; Boddy and Heilmann-Clausen 2008).
4. Both resource quality (characteristics of dead wood) and species interactions have a major influence on fungal diversity and on the decomposition processes (Renvall 1995; Edman et al. 2006; Tikkanen et al. 2006)
5. Decomposer fungal communities, sensitive to changes in climate and substrate quality (Gange et al. 2007; Lonsdale et al. 2008), are currently facing increased risks of extinction (Rassi et al. 2010; Valentín et al. 2014), particularly in managed Fennoscandian forests (Siitonen 2001).

Based on these premises, the study focused on the following four questions:

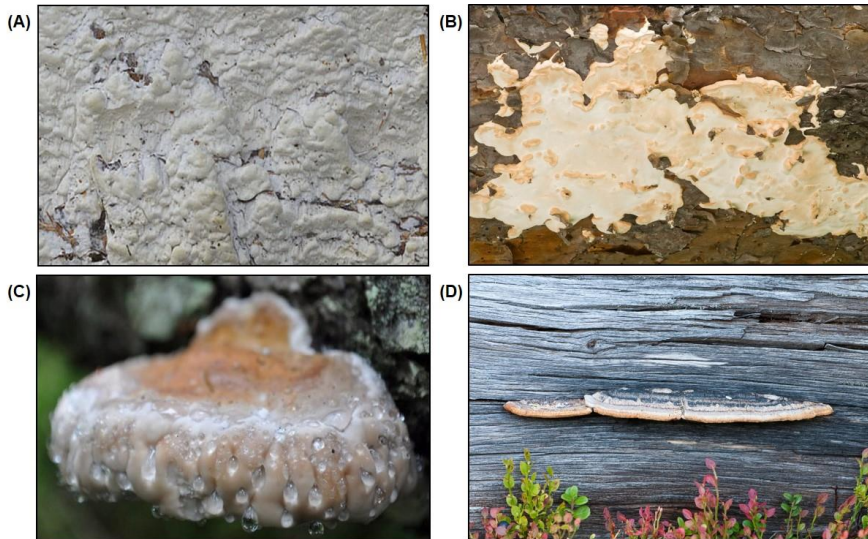
- i. Does CWD quality vary between different Scots pine substrates from managed and old growth forests?
- ii. What are the effects of climate, wood quality and fungal diversity on CWD decomposition in boreal forests?
- iii. How does the influence of species composition change in multi-species assemblages with changes in fungal species, climate and wood quality?
- iv. Will decomposer communities that consist of fewer species behave functionally similar to communities with more diverse communities with simultaneous changes in climate and wood quality?

From these questions, the following hypotheses were formulated and tested in my study:

1. The chemical quality of dead wood (within one tree species) varies depending on degree of decay, position (standing vs. fallen trees) and biotic and abiotic factors.
2. Climatic conditions, wood quality and the idiosyncrasies of fungal species affect the decomposition process.
3. When climate or wood quality changes, the effects of this change vary between communities that consist of a single or a few fungal species when compared to communities with a higher number of fungal species.
4. When species co-occur on a shared substrate, the influence of species composition modifies the effect of climate, wood quality and decomposer species.

## **2. MATERIALS AND METHODS**

The study was conducted in laboratory environments, using naturally grown wood and a group of ecologically-representative decomposer fungi species.



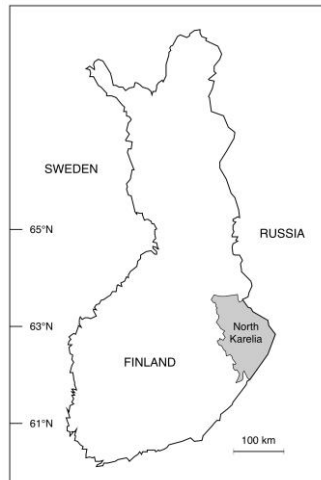
**Figure 2.** Fungal species used in the study, (A) *Antrodia xantha* (Brown rot); (B) *Dichomitus squalens* (White rot); (C) *Fomitopsis pinicola* (Brown rot), and (D) *Gloeophyllum protractum* (Brown rot) (Picture courtesy for B, D: Mattias Edman)

## 2.1 Substrates, species and assemblages

All the studies focused on ecological patterns and decomposer assemblages on Scots pine (*Pinus sylvestris* L.), the most common tree species in Finland. The decomposer species in this study are saprotrophic polypore fungi (Basidiomycota). This group is a typical and common decomposer group in boreal forests. Their general biology is quite well known, and the recent population trends of this group in Fennoscandia are well documented. Four species of basidiomycetes that vary in their natural commonness-rarity and ecological specialization were selected. All species were chosen as (a) they occur exclusively or mainly on Scots pine and (b) on the basis of pre-experimental laboratory work where the suitability of the species for laboratory cultures and their growth patterns were verified. The chosen species were *Antrodia xantha* (generalist on pine), *Dichomitus squalens* (a rare generalist on conifers, mainly pine), *Fomitopsis pinicola* (a very common generalist on conifers and broadleaf trees) and *Gloeophyllum protractum* (a rare generalist on conifers, mainly pine) (Figure 2).

This thesis focused on the climatic factors, wood samples and fungal species recorded in Fennoscandian boreal forests in North Karelia, eastern Finland (Figure 3).





**Figure 3.** North Karelia in Eastern Finland where the wood samples were collected

The study primarily included four types of Scots pine trees:

- partial and full kelo<sup>7</sup> trees in the old growth forest in Patvinsuo National Park in Lieksa and Ilomantsi
- mature Scots pine trees in Patvinsuo National Park in Lieksa and Ilomantsi
- final felled trees in managed boreal forests
- fallen kelo tree logs stored by the Metsähallitus forestry enterprise

## 2.2 Experimental designs

The experimental designs were built to test the four hypotheses stated earlier. The study design with the hypotheses and related experiments with increasing level of complexity (at each level) are outlined in Figure 4. Estimates of fungal growth, wood biomass and C storage will be used as response variables in each experiment.

Hypothesis I: *Quality of dead wood (within species itself) varies depending on the degree of decay, position and biotic and abiotic factors* (Figure 5).

In paper I, the heartwood (HW) phenolic composition of six Scots pine substrates: ‘living mature trees with no fungal sporocarps’, ‘living mature trees with *Phellinus pini* sporocarps’, ‘fallen non-kelo trees’, ‘soon-to-be kelo (standing)’, ‘standing kelo’, and

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<sup>7</sup>Kelos are the Finnish term for old, large and dead pine trees (*Pinus sylvestris* L.), typical in natural old-growth pine forests in boreal Europe, which has died gradually while still standing. The whole process from a growing tree to a dead tree takes several centuries. During this process, the sapwood gets colonized by blue-stain fungi, giving these decorticated trees a silvery grey color on the debarked surface. The usage of the term, although in Finnish, has been extended to English to describe similar type of trees. Niemelä T., Wallenius T., Kotiranta H. (2002). The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Botanical Journal 47: 91-101.

‘fallen kelo’ were tested. The HW samples extracted with an increment corer were analyzed with high performance liquid chromatography (HPLC). It has been hypothesized that kelos, a specialized substrate from old growth forests (Niemelä et al. 2002), are likely to be rich in some secondary phenolics that are otherwise not normally present in live or recently killed pines due to the lengthy death process of the kelos. It was also postulated that a trend could be observed in HW phenolic composition during the transition of the tree from living to fungal infected to dead and from a partially dead kelo to fully dead kelo. This was tested with a two-way ANOVA. In addition, multivariate ordination was applied using non-metric multidimensional scaling (NMDS) to analyze the possibility of distinct chemical groups in the six tree substrate categories.

*Hypothesis II: Climatic conditions, wood quality and fungal species idiosyncrasies affect the decomposition process (Figure 6).*

This was tested using a simple but effective 2 x 2 factorial ANOVA experiment where the main factors were climate (humidity and temperature) and wood quality. Climate ‘change’ was represented using current and predicted climate values. For the wood quality factor, kelo from old growth forests, and slow and fast-grown wood from managed forests were used. Decomposition was carried out by four different decomposers; *A. xantha*, *D. squalens*, *F. pinicola* and *G. protractum*. A species-specific response on the decomposer activity to abiotic factors such as temperature and humidity, and substrate quality for the pure fungal monocultures was hypothesized (II, III). ‘Climate’ was based on simultaneous consideration of temperature and humidity, both of which are likely to be most important for the decomposition process. For the sake of simplicity and to retain statistical power at higher levels, combined-climate categories were preferred rather than the application of more complex types of hierarchical designs.

*Hypothesis III: When climate or wood quality changes, the effects of change varies between communities that consist of a single or fewer fungal species when compared to communities with a higher number of fungal species (Figure 6).*

The wood decay rates on HW samples from old growth and managed forests by four different decomposer species at species richness level one (S1), two (S2) and four (S4) were compared. The nature and direction of the relationship between diversity and function, and the relative importance of the underlying factors causing this, such as species diversity or the species-specific properties of the individuals in the community, are much discussed topics among ecologists (Setälä and McLean 2004; Gessner et al. 2010; Cardinale et al. 2011). Higher species richness in saprotrophic fungi have generally been assumed to enhance the decomposition process (when compared to monocultures) caused by increased facilitative interactions among decomposer species. Earlier Setälä and McLean (2004) has found the functional efficiency of the fungal communities to increase with the number of fungal taxa. Similar findings where higher microbial diversity increases litter decomposition rate through facilitative interaction or resource-partitioning were reported by Gessner et al. (2010). Hence, it was hypothesized that higher decomposer species richness levels could result in increased overall decay rates (III). This was tested using general linear model univariate ANOVA where the main factors were fungal decomposers (species richness and assemblage composition), climate (humidity and temperature) and wood quality.

Hypothesis IV: *When species co-occur on a shared substrate, the outcome of their interaction (facilitation or competition) depends on climate, wood quality and decomposer species* (Figure 6).

The effect of abiotic factors such as temperature and humidity, and substrate quality on decomposer activity is species-specific in pure fungal monocultures (II). Hence, it was postulated that the species interaction at various species richness levels is modified by biotic factors such as assemblage composition and by abiotic factors such as humidity, temperature and substrate quality. Higher species richness in decomposer species may also enhance the decomposition process (when compared to monocultures) owing to possible synergistic activities of the constituting decomposers. Hence, an increased overall decay rate at higher decomposer species richness levels was expected (Hypothesis III). This was tested using general linear model univariate ANOVA where the main factors were fungal species richness (S), fungal assemblage composition, climate (humidity and temperature) and wood quality.

### 3. MAIN RESULTS AND DISCUSSION

#### 3.1 Decay process of CWD varies with fungal decomposers, degree of decay, position (snags or fallen), and biotic and abiotic factors.

In the first study (I), the chemical differences between heartwood samples of different Scots pine CWD types were explored. The role of CWD in C storage is still mostly unexplored and questions related to the formation of CWD, rates of decay and the major factors that control decay remain open (Harmon and Hua 1991). The mature living trees (without any visible fungal infection) differed considerably in their phenolic composition from the fungal-infected living trees and fallen kelos. The fungal-infected living trees and fallen kelos were found to have more similarities to each other than to the living and fallen trees and the standing kelos. The difference was found to become more pronounced with increasing degree of decay in fungal infected living trees and fallen kelos. The similarities between the fungal-infected living trees and the fallen kelos was notable illustrating a possible correlation between fungal infection and the HW phenolic composition of Scots pine. A previously undocumented correlation between the phenolic groups and trees with fire scars on the trunks was also observed. Article I confirms the earlier findings (Harmon et al. 1986; Niemelä et al. 1995; Renvall 1995) that wood quality matters as much as quantity in regard to the functional significance of CWD. The decay process of the CWD is indeed influenced by degree of decay, position (fallen or standing) and biotic (fungi) and abiotic (fire) factors. Many minor phenolics, such as vanillic acid derivative and ferulic acid derivative were more correlated with the differences between the tree types than the better known pinosylvin (PS) and pinosylvin monomethyl ether (PSM) derivatives. The difference in the spectral chromatograms between the different tree types also suggests differences in the chemical decomposition patterns and resultant by-products. Old-growth forests accommodate several substrates with unique characteristics which cannot be replaced or reclaimed by human interference or by “just letting the trees grow old” (Niemelä et al. 2002).

The results signify the need for maintenance of heterogeneous CWD of diverse qualities produced through natural mortality patterns (Jonsson 2000). Wood quality had a pronounced effect on wood decomposition (**II**, **III**) and conformed to earlier reports where the difference in decay rates was caused by management and rate of tree growth (Niemelä et al. 2002; Bouriaud et al. 2004; Edman et al. 2006). The CWD decay also differed depending on climatic variables. The difference was more pronounced between wood from old-growth and the wood from managed forests than between slow-grown and fast-grown wood from the managed forests. Under warming conditions, wood from old-growth forest decayed more slowly. This emphasizes the need to account for the differential decay sensitivity of different wood types of same tree species by fungal species in boreal climate change models.

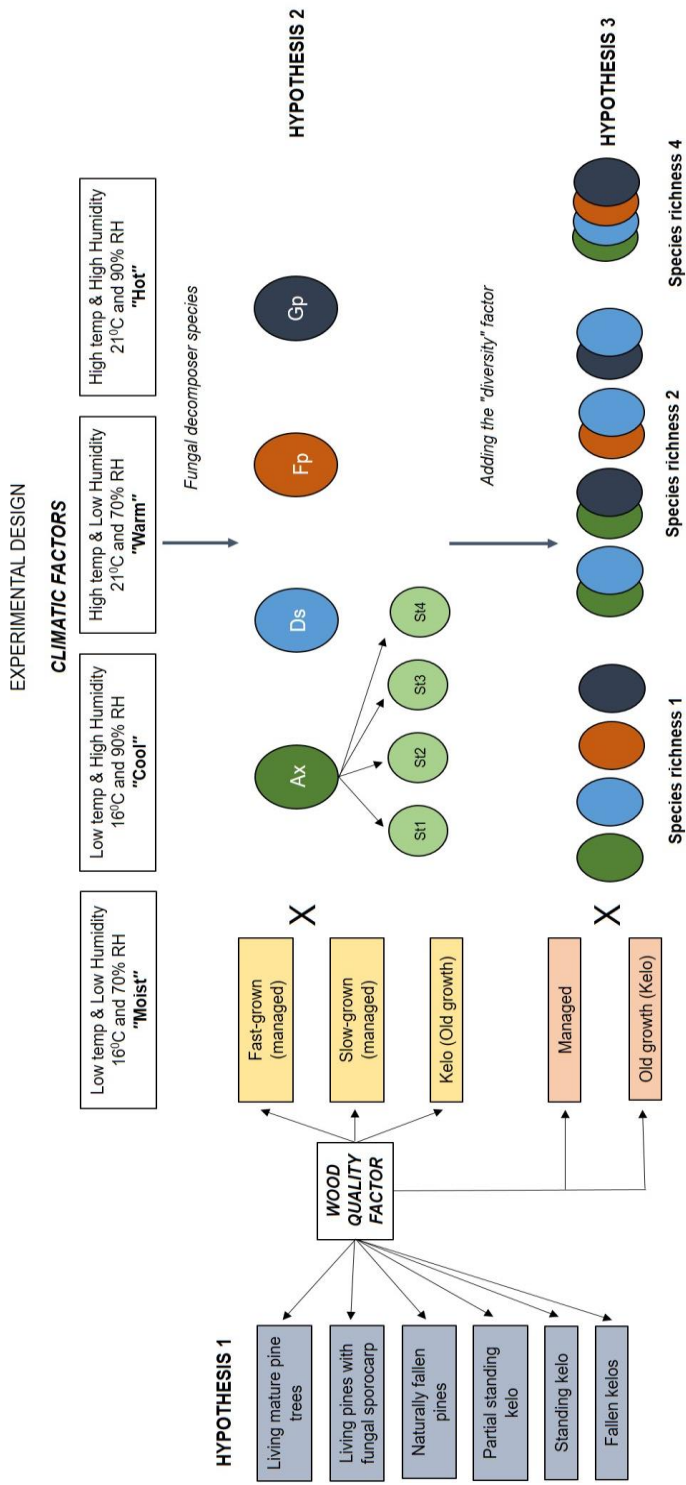
### **3.2. Wood quality has a more pronounced impact than climatic conditions in the decomposition process**

Wood quality had a more pronounced impact on fungal decomposition than climatic variables. Many of the studied fungal species responded only to wood quality and wood quality  $\times$  climate interactions rather than to the independent effects of climate variables (**II**, **III**).

Climate is traditionally assumed to be the predominant control on decomposition rates at global and regional scales, with biotic factors such as decomposers and substrate quality controlling local rates only (Meentemeyer 1978; Berg et al. 1993). This was based on the assumption that climate is the predominant control on decomposition (Bradford et al. 2014). However, the findings (including **II**, **III**) have suggested that substrate quality may be more important than climate variables in controlling wood decomposition. Similar findings were earlier reported for litter quality in litter decomposition (Zhang et al. 2008; Currie et al. 2010). We also found that the decay responses to the independent effects of climate and wood quality variables were different to that of the interaction between the variables. Hence, it is critical to understand the complex mechanisms that affect decomposition between climate variables, fungal decomposers and wood quality and, consequently, C storage in forests, in order to increase the reliability of the climate-C prediction models.

### **3.3 Climate and wood quality effects on decomposition are decomposer species-specific**

Although climate change is estimated to accelerate soil microbial processes (Allison and Treseder 2011; Karhu et al. 2014), many climate-C prediction models incorporate this relationship as a generic effect rather than taking into account the specificity or the functionality of the decomposer species. Until recently, the main drivers of fungal wood decomposition and its underlying mechanisms have not been comprehensively evaluated (Cornelissen et al. 2012). One of the studied species exhibited declining decay rates with increased warming unlike the other three species (**II**), which raises the question as to whether increased temperature could inhibit some saproxylics (Donnelly and Boddy 1997) in a warming regime.

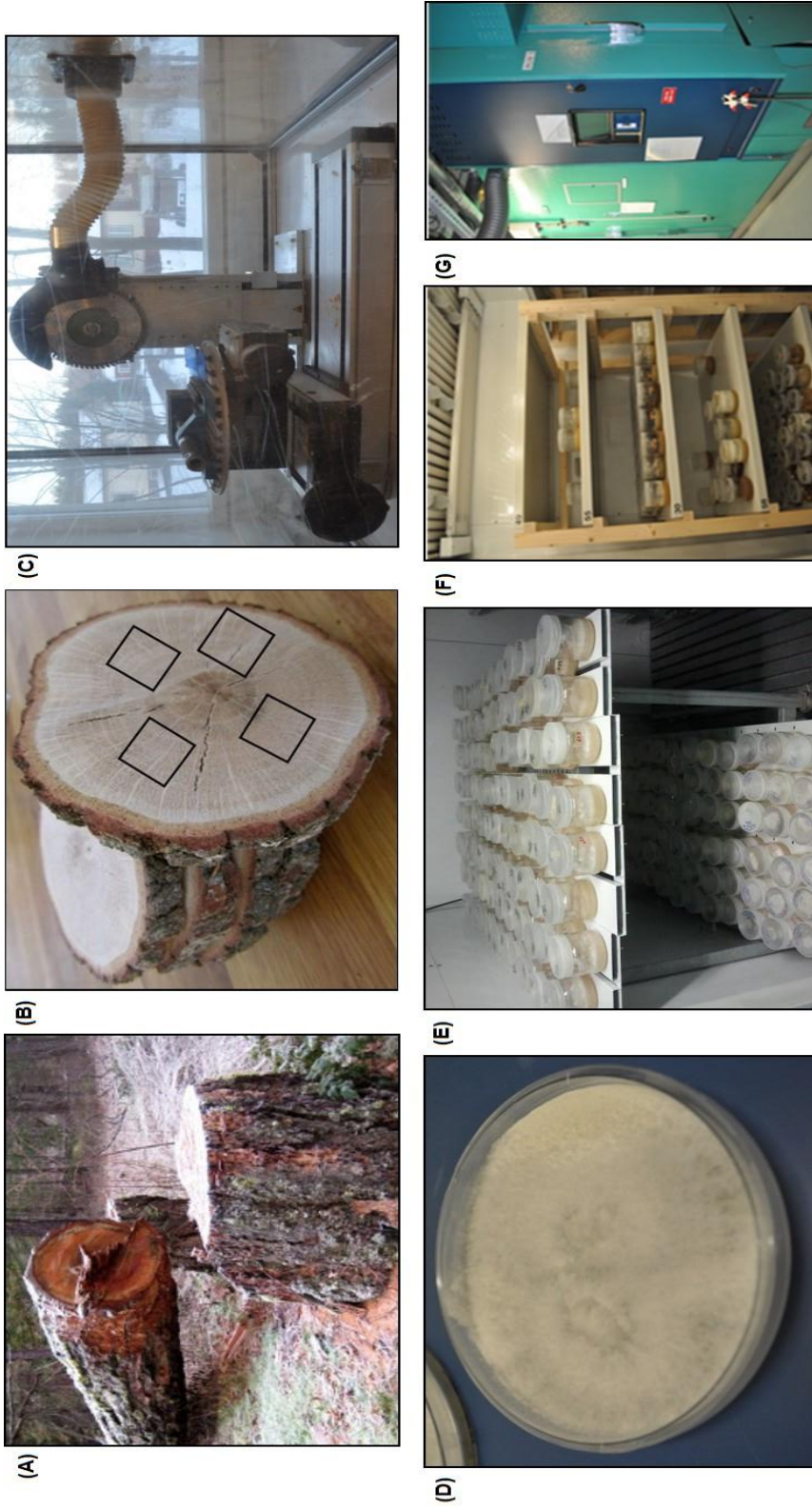


**Fig. 4.** Schematic outline of the experimental setup of the study with all the hypotheses and the tested variables. The different fungi are displayed in different colors with Ax (green); *A. xantha*; Ds (blue); *D. squaletus*; Fp (Orange); *F. pinicola*; Gp (black); *G. protractum*. St(1-4) indicates the different geographical strains used as replicates for each fungal species.



**Figure 5** (A) Standing kelo; (B) living Scots pine with *Phellinus pini* sporocarp on the trunk; (C) standing kelo with extensive fire scars (Picture courtesy: Philippe Fayt); (D) measuring the diameter at breast height (DBH) of a partial kelo, and (E) extraction of a heartwood (HW) sample using increment corer.

This unexpected observation implies that in addition to the increased risk of accelerated decomposition and C loss, warming would also initiate biodiversity loss due to increased sensitivity of certain species to climatic change. Although every organism contributes to ecosystem functioning and processes, they can vary dramatically in their relative contributions. Hence, an understanding of the dynamics of different fungal compositions and specific properties of the fungal species in a community may be equally important (Naeem et al. 1999). This was further demonstrated in **III** where I observed that all species levels (S1, S2 and S4) can have similar decay rates despite the overall decay rate differing at higher species richness (DL4). The significant interaction between assemblage composition and abiotic factors such as temperature and wood quality (**III**) also emphasizes the differential sensitivity based on composition. The fact that different species might have a disproportionate effect and response to environmental variables could be a serious challenge to the validation and reliability of the current biodiversity ecosystem functioning-C models.



**Fig. 6.** (A) Disc extracted from newly harvested stump; (B) Disc with the sample extraction points marked; (C) Wood sample preparation for decomposition studies; (D) principal fungal culture; (*F. pinicola*) prepared in petridish for fungal plug extraction; (E) Fungal plug inoculated in the glass jar and maintained in the climate chambers; (F) Glass jars with wood samples inoculated on fungal culture in the climate chambers; and (G) Climate chambers

### **3.4 Assemblage composition is more important than the species richness effect in fungal wood decomposition**

Species richness has been considered as a major determinant of ecosystem processes such as decomposition and nutrient dynamics (Gessner et al. 2010), owing to factors such as facilitative interactions and resource partitioning. However, the positive relationship of microbial species richness with decomposition and nutrient cycling via additive or synergistic activities of fungal species is a popular yet much debated concept in biodiversity-ecosystem functioning studies (Loreau et al. 2001). It was shown using soil fungal species that although complementarity effects increase the decomposition rates in communities with low levels of species (up to 10), the relationship generally saturates at higher species-richness (Setälä and McLean 2004; Gessner et al. 2010). Many ecosystem functioning experimental studies (Jonsson and Malmqvist 2003; Dang et al. 2005) have observed a saturation of litter decomposition rates at a low level of species richness.

Although species richness was significant in decomposition, there was no direct relationship between richness and decay rate (**III**). Competitive (inter- and intraspecific) interactions predominated synergistic interactions between wood-decay species at all stages of wood decomposition, thereby markedly affecting wood decay (Woodward and Boddy 2008). An averaging or “jack-of-all-trades” effect previously observed by van der Plas et al. (2016) was also observed in the results (**III**) when the ecosystem-function levels in species-rich diverse communities were intermediate and never as extremely low or high as in the corresponding monocultures.

### **3.5 Wood quality, functionality of decomposer species and assemblage composition modifies the decay response to climate variables.**

The identity and functionality of the species in the fungal assemblage composition modified the decay response to wood type and climatic variables (**II**, **III**). The differential response of the fungal species and assemblage composition to climate change highlights the disproportionate influence on ecosystem processes. *A. xantha* exhibited a decreased decay rate with increase in temperature (from 16 to 21 °C) (**II**). This declining decay rate associated with increased temperature was unexpected, as all other species exhibited an increase in their decay rates with warming. Different effects of warming on decay rates depending on fungal species was earlier noted by Donnelly and Boddy (1997). Furthermore, if the sensitive species exhibiting such a trait are common decomposers in boreal environments, such as *A. xantha* (Kotiranta et al. 2009) in this case, the differential temperature-decay responses could alter the direction of decomposition under a warming regime. It was also observed that pine wood from managed forests decayed more rapidly than kelo wood from natural forests (**II**, **III**) indicating that the wood-decay processes in fast-grown managed forests would be more sensitive to climatic changes than the processes in natural forests.



## 4. CONCLUDING REMARKS

The results of my study demonstrate that CWD decomposition, a key factor in global C cycling, is simultaneously affected by climate, wood quality and fungal decomposer assemblages. The results have several implications for our current understanding of wood decay and related processes, as well as for future research.

### 4.1 Climate change and boreal C storage - sink to source?

Ecosystem studies have demonstrated that the storage of C is highly dependent on stable and resilient forests (Thompson et al. 2009; Aerts and Honnay 2011). Boreal forests as the second largest biome on earth (FAO 2001) are on “the hot seat” of predicted warming (Bernstein et al. 2007; IPCC 2007). Given the enormous C stock contained in boreal vegetation, there is an increasing chance that forests in the boreal zone could shift from being a massive C sink to C source with a warming climate (Ruckstuhl et al. 2008).

Old-growth forests act as an effective global C sink, sequestering C in live woody tissues. Rare woody substrates such as kelo, which stand for several centuries, are specific to the old-growth forests and almost absent in managed forests. Kalliola (1966) stated that kelos can be considered as one of the most conspicuous characteristics of untouched forests. The Finnish National Forest Inventories between 1936 and 1963 show a clear decrease in the number of kelo trees (of dbh > 20 cm) from the natural forests. The decrease of the more than five kelo-trees per hectare plots is particularly noticeable in the east and north parts of the country such as Karelia as well as in the provinces of Oulu and Lapland (Kalliola 1966). This warrants the need for conservation of Kelos, and also emphasizes the need to better understand the role that these long-lasting woody substrates may have in overall carbon storage and dynamics in boreal pine-forests.

This present study shows that decomposition of CWD, an important component of boreal forests, particularly old-growth forests, is also affected by climatic changes (III). The decomposition of the persistent kelo from the old growth forest increased in response to a rise in temperature and humidity levels, although the impact was much less than fast-grown wood from the managed forest (II, III). This is particularly alarming since almost 75 % of the boreal forest biome is managed (Ruckstuhl et al. 2008). Hence, there is an urgent need for more robust forest management practices for the adaptation and mitigation of climate change effects, and to consider the sensitivity and vulnerability of managed forests producing fast-grown wood.

Conversely, my results also demonstrated that climate, which was considered to be the predominant control on decomposition (Berg et al. 1993), is overshadowed by the effects of fungal decomposers and wood quality (II, III). The study recognizes the importance of the independent and interactive effects of the main drivers such as climate factors and wood quality traits as well as the differential functionality and sensitivity of the fungal decomposers (II, III) on environmental variables. Inclusion of these factors in current forest management strategies and predictive ecosystem models could increase our understanding of the boreal BEF, as well as improving forest management strategies involving C dynamics of decomposing wood.

## 4.2 Fungal decomposers and wood quality in C cycling

There is compelling evidence suggesting a strong correlation between biodiversity, ecological processes and forest C (Aerts and Honnay 2011). However the dynamics underlying the relationships that occur between biodiversity, dead woody biomass, and C dynamics are still mostly unexplored. It was also shown in my study that even in cases where the fungal decomposition was unaffected by climatic changes, wood quality took a pivotal role (II). The results of this thesis emphasize the need to include substrate quality as well as fungal decomposer diversity aspects in wood-based C-ecosystem models. However, the nature and magnitude of the contribution of different decomposers to the ecosystem processes (in this case decomposition) vary considerably (III). Most ecosystem processes are driven by the combined activities of diverse groups of species, and the role that different species may have in these processes awaits further and more detailed exploration.

## 4.3. Wood quality

Decomposers are important elements in the restoration of ecosystems, although it is not generally known what specific substrate types will be most effective for the reintroduction of these species in the current realm of increasing biodiversity losses. Decomposers have specific substrate requirements and not all can be maintained under intensive forest management (Jonsson 2000), particularly the fungal decayers from old-growth forests (Niemelä et al. 2002). The quality of dead wood may be equally important a factor as quantity in determining the success of any decomposer species. The current study points out the importance of rare substrates such as kelo from the old growth natural forests, and that these could form a more resilient and constant substrate for fungal decomposers, compared to wood from managed forests, in the realm of climate change (II, III).

Analyses of the formation and dynamics of rare substrate types such as kelos are likely to provide novel insights into wood quality characteristics and decomposition. The results warrant further studies for the identification and extraction of the natural phenolics or other extractives (particularly the minor phenolics) from the more resistant and rare substrate types (I), and to increase our understanding of their key decay resistant properties. It is also critical to understand the role of external processes such as fungal infection and fire injury in modifying the characteristics of the substrate (I) and how best to manipulate them for effective dead wood formation.

Unraveling the exact relationship between climate change, C storage and biodiversity, and their implications in BEF are some of the major fundamental challenges currently faced by ecologists. I started the thesis under the strong presumption that climate would be the most prominent driver for CWD decomposition and would modify the effects of several other drivers. Although my study included only a few decomposers and substrate types under limited climate variations under controlled conditions, I would like to conclude at this stage that CWD decomposition is driven by the idiosyncrasies of the fungal decomposers as well as the substrate type that modifies the effects of changes in climatic variables. I observed a disconnection between climatic variables and decomposition in II, where wood quality and fungal decomposers played the greater role. Not undermining the fact that climate change is still one of the biggest global factors that

is likely to affect BEF and C cycling, I would like to emphasize here that the impact of the changes in environmental variables is not uniform. Hence, a major challenge for ecologists is to determine the more sensitive decomposers and substrate types, particularly in managed forest systems, which appear to undergo major human-induced changes in their biodiversity, in addition to a globally changing climate. I wish to further comment that the results of this study should be complemented by further studies employing more fungal decomposers at higher diversity levels under more climatic variation combinations. The direct effects of the drivers of CWD decomposition are increasingly understood, but more focus should also be given to their interaction effects. Considering the increasing focus on dead wood restoration activities and the importance of dead wood on forest biodiversity in general, the current results suggest that an examination of the HW chemistry of the artificially created dead woods, in addition to other qualitative variations, is highly recommended, and that these results should be compared with the properties of natural dead woods.

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