博士論文（要約）

Spatio-temporal variability of soil microbial communities and their identity for litter decomposition in cool-temperate montane forests

（冷温帯林の土壌微生物群集の時空間変動性と
落葉分解に対する固有性）

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Abstract

Chapter 1: General introduction

Microbial ecologists have long sought to understand what factors govern soil fungal and bacterial communities. Climate and soil conditions have been regarded as the main factors determining soil microbial communities. However, based on a number of observations that plant community structures also drive forest ecosystems, plant-soil linkages may affect soil fungal and bacterial communities. The interactions between plants and soil microbial communities show a direct pathway through plant roots and indirect pathway through soil food webs. Although the direct pathway has strong specificity, idiosyncratic relationships between soil microbial communities and plants are not fully clarified in the indirect pathway.

In forest ecosystems, one idiosyncratic relationship that is particularly relevant for litter decomposition has been identified as home-field advantage (HFA). Namely, soil microbial communities may become specialized in breaking down litter that they are associated with, resulting litter decomposing more rapidly in its ‘home’ environment than in an ‘away’ environment. Clarifying the mechanism of HFA can fully explain variations of litter decomposition and solve the problem of biogeochemical models. However, it is not clear how these idiosyncratic microbial communities are positioned in the whole community and how it responds to environmental changes.

This thesis aims to verify how soil microbial communities exhibit spatio-temporal variability and identity to litter decomposition. Chapter two clarifies the importance of relationships between plant communities and soil properties along elevational gradients. The following chapters also focus on two major spatio-temporal scales where aboveground

ecosystem components mainly influence soil microbial communities. The first is elevational change, which is covered in chapter three. The second is seasonal change, which is handled in chapter four. Chapter five deals with the relationships between HFA for litter decomposition and soil microbial identity. This thesis consists of the general introduction (Chapter 1), four chapters presenting the main research of the doctoral thesis (Chapters 2-5), and the general discussion of the key findings (Chapter 6).

Chapter 2: Relationships between understory plant diversity and soil properties along elevational gradients

Elevational diversity gradients (EDGs) of vegetation can be shaped by the evolutionary histories of plants as well as by ecological factors (Nogué et al. 2013; Merckx et al. 2015). However, few studies of EDGs have focused on the roles of phylogenetic constraints and the associations with complicated interactions among environmental factors (Schreeg et al. 2010; Ulrich et al. 2014). Chapter two examined the direct and indirect roles of environmental factors in forming EDGs of forest understory vegetation. In this research, taxonomic and phylogenetic diversities of tree seedlings increased monotonically with elevation, and the same pattern was found for the taxonomic diversity of herbs. Structural equation modeling indicated that both the taxonomic and phylogenetic diversity of tree seedlings were most associated with soil properties, although the phylogenetic diversity of herbs was related to light conditions. These results highlight the importance of environmental filtering by soil properties in shaping EDGs of tree seedlings. This research implies that phylogenetic constraints in adaptation to soil properties should be considered when predicting changes in EDGs under environmental fluctuations.

Chapter 3: Elevational diversity gradients of soil microbes

Elevational gradients represent model systems for understanding the relationships between soil microbial communities and environmental factors, but the multiple influences of plant-soil linkages and the climate on EDGs of soil microbes have never been explored. Chapter three examined how plant functional diversity, soil properties and soil temperature affect EDGs of soil bacteria and fungi at different soil depths. The diversity of bacteria decreased with elevation in surface soils but showed no relationship with elevation in deep soils. Structural equation modeling showed that soil bacterial diversity across elevational gradients was directly affected by plant functional diversity, especially where leaf C:N ratio diversity had stronger effects than soil properties. Chapter three found that EDGs of soil bacteria as a consequence of the total effect of elevation were determined by the degree of negative indirect effects of soil temperature, via plant functional diversity and soil properties, against a positive direct effect of soil temperature on bacterial diversity. These findings demonstrate that community assembly of soil microbes is causally linked with the climate, plant functional diversity and soil properties, which determine EDGs.

Chapter 4: Seasonal dynamics of soil microbial communities

Both aboveground and belowground properties operate over seasonal timescale in forest ecosystems at the mid-to-high latitude, but the seasonality of soil fungal and bacterial communities in this area has not been fully understood. Chapter four aimed to evaluate the importance of seasonality, elevation, and soil depth in determining soil fungal and bacterial communities, given the influence of climate conditions, soil properties, and plant traits. Seasonal diversity and abundance patterns did not match between fungi and bacteria, where the peak of fungal diversity and bacterial abundance was observed in April, but those of bacterial diversity occurred in January. Model-based clustering found taxonomic groups associating carbon and biogeographical cycles that were paralleled with seasonality, implying that they are indispensable taxa driving ecosystem processes in temperate forests. Furthermore, bacterial communities were profoundly explained by both spatial and seasonal changes in soil water contents, while many taxonomic groups of soil fungi were related to plant traits along elevational gradients. These findings suggest that the contribution of the seasonal variability of climate conditions, soil properties, and plant traits are equal to or greater than those of spatial changes for microbial communities in forest soils at mid-to-high latitudes.

Chapter 5: Soil microbial identity in home-field advantages for litter decomposition

Chapter five aimed to understand the relationships between HFA for litter decomposition and soil microbial communities. Given the "community-by-environment" interaction in microbial ecology, it is assumed that both soil and climate affinity strongly influenced litter decomposition, but this hypothesis was not supported. Rather, HFA effects of litter decomposition highly depended on the source soil via fungal and bacterial identity. Although a home-climate advantage for litter was significant in the early stage of decomposition, it was not a strong limiting factor as compared with a soil advantage. These suggest that litter decomposition in temperate forests was explained by microbial communities that are not functionally redundant, but these relationships may have the robustness to climate change. As mentioned in chapter one, HFA for litter decomposition plays an essential role in understanding overall decomposition processes that have implications for global climate and biogeochemical models. These findings contribute to an understanding of the impacts of global climate changes on belowground ecosystem processes and the role of microbial communities in biogeochemical cycles of forest ecosystems. Chapter five also implies that ignoring home-soil advantages for litter decomposition could lead to misinform biogeochemical models and potential cascading consequences for forest management.

Chapter 6: General discussion

Chapter six recaptures and discusses the results obtained in the main researches of the doctoral thesis (Chapters 2-5) and combines these findings. This thesis found that: (1) plant-soil linkages were significant along elevational gradients in cool-temperate montane forests; (2) Community assembly of soil fungi and bacteria was linked with the climate, plant traits, and soil properties, which determine elevational and seasonal diversity patterns; (3) Identity of soil microbial communities for litter decomposition has the robustness to climate change. The findings of the doctoral thesis highlight that soil microbial communities have spatio-temporal variability in response to environmental changes, but their identity for litter decomposition has the robustness to environmental perturbations, which explained by plant-soil linkages in forest ecosystems. The further elucidation of the linkages between microbial identity and forest ecosystem functionings may simplify an understanding of the manner how plant-soil linkages shape ecosystem processes.

Chapter 1:

General introduction

1-1. Introduction

With an estimated count of 3.4 trillion of trees (Crowther et al. 2015), forests cover about 30.6 % of the terrestrial portion of the earth and play a vital role in people's lives by providing many different goods and services (FAO 2015). Compared to the understanding of ecosystem functioning of aboveground components in forests, microbial decomposition processes in forest soils is not sufficiently investigated even though it is potentially essential equal to or greater than that of aboveground components. Forest soils contain a vast amount of organic carbon (Jobággy and Jackson 2000) which is more than the total carbon contained in aboveground vegetation (Lal 2005). In particular, the stocks of these soil carbon in temperate forests are dynamic over time (Melillo et al. 2002), with accumulation occurring through plant litter inputs, and losses via microbial decomposition of soil organic carbon (SOC) leading to the release of carbon dioxide (CO_2) into the atmosphere. Global climate changes are closely associated with belowground components as well as aboveground ones of forest ecosystems, as forest soils can accelerate the microbial degradation of SOC dramatically and increase the net emissions of CO_2 into the atmosphere (Magnani et al. 2007).

In forest ecosystems, the decomposition of plant litter is dependent on soil microorganisms, namely fungi and bacteria (van der Heijden et al. 2008; Baldrian 2017), as they are almost the only organisms that are capable to degrading lignin and cellulose (Wilhelm et al. 2018). According to a general framework for plant-soil linkages proposed by

Wardle et al. (2004), plant communities regulate the quality and quantity of available resources for soil microbial communities. In turn, those communities regulate plant growth and community structures directly through the activity of root-associated microbes, and indirectly through the action of microbial decomposer communities. In this way, these plant-soil linkages can play a central role in shaping unique microbial communities in soils because of acting as significant drivers of forest ecosystem processes. However, how these microbial communities change to environments is thoroughly unclear.

This introductory chapter aims to review the current understanding of soil microbial communities and their identity for litter decomposition. The second section starts by providing perspectives on plant-soil interactions in forest ecosystems, emphasizing the importance of exploring the relationships between plant communities and soil conditions (Section 1-2). The following two sections review the influence of abiotic and biotic factors on soil microbial communities in forests and explain how these influences can change across spatial (Section 1-3) and temporal scales (Section 1-4). Following these, the next section reviews factors controlling litter decomposition processes by focusing on the importance of idiosyncratic relationships between soil microbial communities and litter decomposition (Section 1-5). Lastly, four main studies presenting the main research of the doctoral thesis are introduced. The structure of the thesis is also outlined (Section 1-6).

1-2. Importance of plant-soil linkages in forest ecosystem processes

As has long been documented elsewhere, soil abiotic and biotic conditions influence plant growth and community structures, and the activities of plants also contribute to soil aggregate formation and fertility, shaping plant-soil interactions (Schlesinger and Pilmanis 1998; Wardle et al. 2004). In forest ecosystems, these relationships have been recognized since the pioneering pedological studies of the Danish forester P.E. Müller. In his seminal work, plant communities are strong determinants of the types of soils that develop under them, showing that the type of soil layer to be dependent not only on climate but also vegetation type (Müller 1889; Romell and Heiberg 1931). However, such influences on soil abiotic and biotic conditions result in positive or negative feedback effects, which influence plant performance and community structures (Bever 1994; Bezemer et al. 2006). For example, litter decomposition can be part of positive feedback in forest ecosystems (e.g., McClaugherty et al. 1985; Reich et al. 1997) because soil microbial communities can further enhance nitrogen availability and productivity of inherently fertile soils (Aponte et al. 2013). Although these positive feedback effects have often been reported, negative feedbacks are also possible when the plant improves belowground conditions that then promote competition between plant species (Ehrenfeld 2003). The well-known negative plant-soil feedback in forest ecosystems is a consequence of autotoxicity, enhanced by the activity of pathogenic soil microbes (Janzen 1970). This process can maintain biodiversity by preventing a small number of species from dominating a forest tree community (Bever 1994; Klironomos 2002). Most importantly, these indicate that specific soil microbial communities can drive forest ecosystem processes through either positive or negative feedback.

The influence of plants on soil microbial communities is assumed to be direct and indirect; the direct pathway involves the characteristics of plant roots determining the accessibility of root-associated microbial communities to resources produced by roots, whereas the indirect pathway involves plants influencing microbes in a soil food web by determining the quantity and quality of plant litter (Wardle et al. 2004). The direct pathway often results in species-specific effects of plants on soil microbial communities (Costa et al. 2006; Leff et al. 2018), but the indirect effects of plants on soil microbial communities are context dependent (Ayres et al. 2009). An increase in plant primary productivity is one of the main factors that directly and indirectly affect soil microbial communities because it increases the amount of litter and root exudates. In the glasshouse experiments of nine plant species, Wardle and Peltzer (2003) found that the abundance of soil microbes tends to be highest in productive plant species. It has been reported that the relative effect of each plant species on ecosystem processes should be proportional to its relative contribution to the total biomass of the ecosystem (Urbanová et al. 2015; *sensu* mass ratio hypothesis by Grime 1998).

1-3. Microbial community ecology in forest soils

Environmental factors affecting soil microbial communities

Soil temperature

As temperature affects the physiological activities of all living organisms, it drives microbial community structures directly and indirectly. A considerable part of bacterial community patterns in aquatic environments can be primarily explained by temperature (Fuhrman et al. 2008), whereas soil bacterial communities show various patterns (Fierer and Jackson 2006; Zhou et al. 2016). For soil fungal communities, community composition generally changes but diversity shows various patterns with changes in soil temperature. For example, Allison and Treseder (2008) found that warming with closed-top greenhouses in boreal forests led to an increase in fungal diversity with increasing soil ammonium and nitrate availability. Here, the relative abundance of a dominant Thelephoroid fungus decreased with increasing soil temperature, while the relative abundance of Ascomycetes and Zygomycetes increased with soil temperature (Allison and Treseder 2008). On the other hand, DeAngelis et al. (2015) also conducted warming experiments in temperate forest soils and found that fungal diversity tended to decrease with increasing soil temperature. Although there is a doubt as to whether the results of warming experiments can be applied in natural ecosystems (Sundqvist et al. 2013), field experiment studies such as reciprocal translocation experiments are expected to improve understanding the relationships between soil microbial communities and soil temperature. In addition, soil temperature can change not only directly but also indirectly soil microbial communities through plant communities. Climate warming can cause plant diversity loss or gain in future, but the relative importance of direct effects of soil temperature and indirect effects through abiotic factors has not been fully elucidated.

Soil pH

Soil pH is often mentioned as one of the significant factors determining soil bacterial diversity and community structures (Rousk et al. 2010a; Fierer et al. 2017). Generally, the relationship between bacterial diversity and soil pH shows hump-shaped patterns with peaks at pH 7 (Fierer and Johnson 2006), which is assumed to be the similar mechanism with plant communities. Fungal diversity often does not correlate with soil pH, or even if that is the case, the correlation is weaker than bacterial diversity (Lauber et al. 2008; Rousk et al. 2010a). This difference in tendency seems to be due to the fact that the range of the optimum pH for growth is different between bacteria and fungi, where bacteria have a narrow pH range of optimum activity (Bååth 1996; Rousek et al. 2010b) although fungi shows wide optimum pH range (Wheeler et al. 1991; Rousek et al. 2010b).

Soil moisture

The soil moisture also has considerable influence on microbial activity, shaping soil microbial communities. Although the relationship between soil microbial diversity and soil moisture content has been discussed concerning the soil pore size (Carson et al. 2010), the results are different between soil fungi and bacteria. As a general trend, the diversity of soil bacteria increases with soil water contents although soil fungal diversity shows various trends (Toberman et al. 2008). Soils with high clay and silt content have low water potential and pore connectivity, resulting in increasing opportunities for spatial isolation of competitively inferior bacteria (Carson et al. 2010). On the other hand, fungi are modular organisms that consist of multicellular networks, and then this feature may create different diversity patterns between fungi and bacteria.

Soil organic matter

In general, the concentration of soil organic matter can be a significant factor in determining the soil bacterial abundance and community structures because the amount of labile organic matter is scarce. Various patterns of the relationships between organic matter content and fungal communities have been reported (Rousk and Nadkarni 2009), but there is no general trend. Also, in forest ecosystems, because the absolute amount of soil organic carbon is abundant, it is unlikely that organic carbon content has an influence on soil microbial communities compared to other ecosystems (Pei et al. 2014). Rather, the availability of carbon strongly governs the activities of specific microbes and their functions. Indeed, since the carbon source utilization can be applicable in classifying isolates of soil microbes, microplates containing different carbon sources such as Biolog can be used to determine the functional diversity of soil microbes. (Preston-Mafham et al. 2002). The diversity of plant traits reflecting the various characteristic of organic matter may also influence the diversity and community structures of soil microbes in forests.

As reviewed above, soil properties play an essential role in influencing soil microbial diversity and community structures, but there are many reports showing different patterns from those in general trends (e.g., Zhou et al. 2016 for soil pH). Although analytical methods may affect soil microbial communities, considering spatial and temporal changes in plant communities can be able to generalize the relationships between microbial communities and soil properties.

1-3-1. Spatial variability of soil microbial communities

In forest ecosystems, soil microorganisms can vary significantly in both space and time (Ettema and Wardle 2002; Bardgett et al. 2005). Spatially explicit approaches for studying soil microbes have revealed spatial patterns at scales ranging from millimeters to hundreds of kilometers, meaning that patterns emerge in a nested manner across a wide range of scales (Ettema and Wardle 2002; O'Brien et al. 2016). On the order of millimeters, it is assumed that moisture in soil pores and the distribution of plant roots significantly affect soil microbial communities (Ettema and Wardle 2002). For example, the distribution of bacteria capable of oxidizing ammonium and nitrate reflects those of fine roots (Grundmann and Debouzie 2000). The recent studies showed that the abundance of soil microbes varied horizontally at the centimeter to meter scales and was often elevated in activity hotspots (Baldrian et al. 2010; Anderson et al. 2014). The microbial activity in these hotspots may be up to 20 times higher than in bulk soil (Kuzyakov and Blagodatskaya 2015). Although activity hotspots may be responsible for a large proportion of forest ecosystem processes, the extent of their contribution remains unknown. On the plot-to field scale, plant species and communities, as well as soil animals, can influence soil microbial communities. For instance, spatial heterogeneity of methanogenic bacteria is associated with the patchiness of plant litter at a field scale (Wachinger et al. 2000). The role of plant species effect in driving soil ecosystem processes is most apparent when plant species with different functional traits occur together in a landscape (Schlesinger and Pilmanis 1998). Even within relatively large plots, the spatial distribution of soil microorganisms reflects those of plants (Klironomos et al. 1999).

On the order of kilometers or more, soil microorganisms can examine the patterns of community structures and diversity using the same concept as macroorganisms. For example, a latitudinal diversity gradient has been considered a consequence of a shift in the effects of abiotic and biotic factors that limit species distributions form the poles to the equator. Thus, the diversity of most fungal groups peaked in tropical regions although some fungal groups such as ectomycorrhizal fungi were most diverse in temperate and boreal regions (Tedersoo et al. 2014). On the other hand, for soil bacterial communities, spatial differences in community structures could be explained by soil pH, shaping latitudinal diversity patterns (Fierer and Jackson 2006). However, according to Baas-Becking's "everything is everywhere" hypothesis, the biogeography has shown distinctly different patterns between soil microorganisms and macroorganisms such as plants and animals because of differences in their strategies of dispersal and reproduction (Fierer et al. 2011). Elevational gradients are also suitable for examining how soil microbial communities respond to the environment because environmental changes equivalent to latitude gradients can be observed even on a relatively narrow geographical scale such as several kilometers. According to the framework of Ettema and Wardle (2002), climate, vegetation and soil properties can influence soil biota, potentially affecting soil microbial communities, but these interactions are not sufficiently considered to explain spatial patterns of soil microbial communities.

1-3-2. Temporal variability of soil microbial communities

Soil microbial communities are influenced not only spatially but also temporally by plant communities (Bardgett et al. 2005). The relationships between forest plants and soil microorganisms operate over a spectrum of temporal scales, ranging from days to seasons. On a relatively short scales, a "hot moment" is known to have a significant impact on nutrient cycling of forest ecosystems through the activities of soil microbial communities (McClain et al. 2003). A freeze-thaw cycle in forest soils is one example of hot moments that change rapidly microbial communities (Groffman et al. 2009). At longer time-scales such as decades to centuries, it has been recognized that forest succession affects community structures of soil microbes. In primary succession, the colonization of soil microbial communities leads those of plants (Schmidt et al. 2008). Following the development of plant communities, both root-associated and free-living microbes are significantly changed. For root-associated microbes, arbuscular mycorrhizal fungi dominate at an early stage of succession although ectomycorrhizal fungi dominate at late successional stage (Read 1994). In addition, the availability of N to plants decreases and the subsequent decline in plant productivity in aging boreal forests is linked to high carbon allocation from plant roots to ectomycorrhizal fungi (Blaško et al. 2015). Although few studies have revealed the relationship between free-living bacteria and forest succession, soil fungal dominated ecosystem often becomes increasingly crucial as succession proceeds (Bardgett et al. 2007). Recently, He et al. (2016) found that saprotrophic fungal communities were influenced by stand age in temperate secondary forests. In this case, the fungal genus *Lachnum* was more dominant in 20 years old stands, whereas the fungal genus *Fusarium* was more abundant in 40 years old stands (He et al. 2016).

Interactions between plants and soil microorganisms are influenced by seasonal changes in the availability of soil resources (Bardgett et al. 2005). In particular, plant phenology can, directly and indirectly, influence the seasonal variability of soil microbial communities because plant affects carbon and nitrogen availability for soil microbes as a result of exudation of labile carbon through roots and substrate input by litterfall (Bardgett et al. 2005). According to a study comparing soil microbial community functions between summer and winter, summer was characterized by high transcription of ligninolytic and cellulolytic enzymes produced mainly by fungi although the transcription of genes encoding enzymes degrading starch and trehalose was high in winter (Žifčáková et al. 2017). However, most of the studies on the seasonal variability of soil microbial communities were conducted on specific forest types (Voříšková et al. 2014; Žifčáková et al. 2017), no studies are investigating how soil microbial communities change in response to plant phenology in various forest types.

1-4. Idiosyncratic relationships between soil microbial communities and litter decomposition in forest ecosystems

Litter decomposition is a fundamental process for carbon and nutrient cycling in temperate forests and can be controlled by litter quality and climate through decomposer communities (Coûteaux et al. 1995; Keiser et al. 2014). Indeed, it has been widely recognized that the structural and chemical complexity of plant litter regulates degradation by microbial communities (e.g., Christensen 2001; Cotrufo et al. 2013). Also, soil temperature and water contents can be significant factors influencing litter decomposition rate either directly by microbial activity (Fierer et al. 2005) or indirectly by feedback processes via microbial communities (Bardgett et al. 2008). In the study of litter decomposition rates along elevational gradients, moisture rather than temperature is likely to be an essential factor

(Murphy et al. 1998). However, biogeochemical models based only on litter quality and climate parameters not explain about 30 % of the variation in litter decomposition (Gholz et al. 2000; Trofymow et al. 2002). In spite of more than 25 years of litterbag experiments designed to examine litter quality and climate effects on decomposition, there is still substantial debate as to the importance of microbial communities on litter decomposition processes.

Understanding how soil microbial communities maintain ecosystem functioning is a central theme in microbial ecology. As mentioned above sections, the interactions between plants and soil microbial communities show a direct pathway through plant roots and indirect pathway through soil food webs. Although the direct pathway has strong specificity, idiosyncratic relationships between soil microbial communities and plants are not fully clarified in the indirect pathway. In forest ecosystems, one idiosyncratic relationship that is particularly relevant for litter decomposition has been identified as home-field advantage (HFA; Gholz et al. 2000; Ayres et al. 2009). Namely, soil microbial communities may become specialized in breaking down litter that they are associated with, resulting litter decomposing more rapidly in its 'home' environment than in an 'away' environment (Ayres et al. 2009). Clarifying the mechanism of HFA can fully explain variations of litter decomposition and solve the problem of biogeochemical models. However, in previous studies, there are considerable variations in the strength and direction of HFA effects, and there are many cases in which HFA does not occur (Ayres et al. 2009; Freschet et al. 2012). For example, Veen et al. (2015) found that vegetation type and climate are essential for litter mass loss, but not necessarily to determine the HFA effects. In spite of the most likely explanation for HFA effects is soil microbial identity (e.g., Ayres et al. 2009; Keiser et al. 2014), it is surprising that there have been few studies that have investigated the contribution of microbial communities to HFA (Strickland et al. 2009; Fanin and Bertrand 2016). Focusing on microbial community identity helps us understand how immense microbial diversity plays a role in maintaining forest ecosystem functioning.

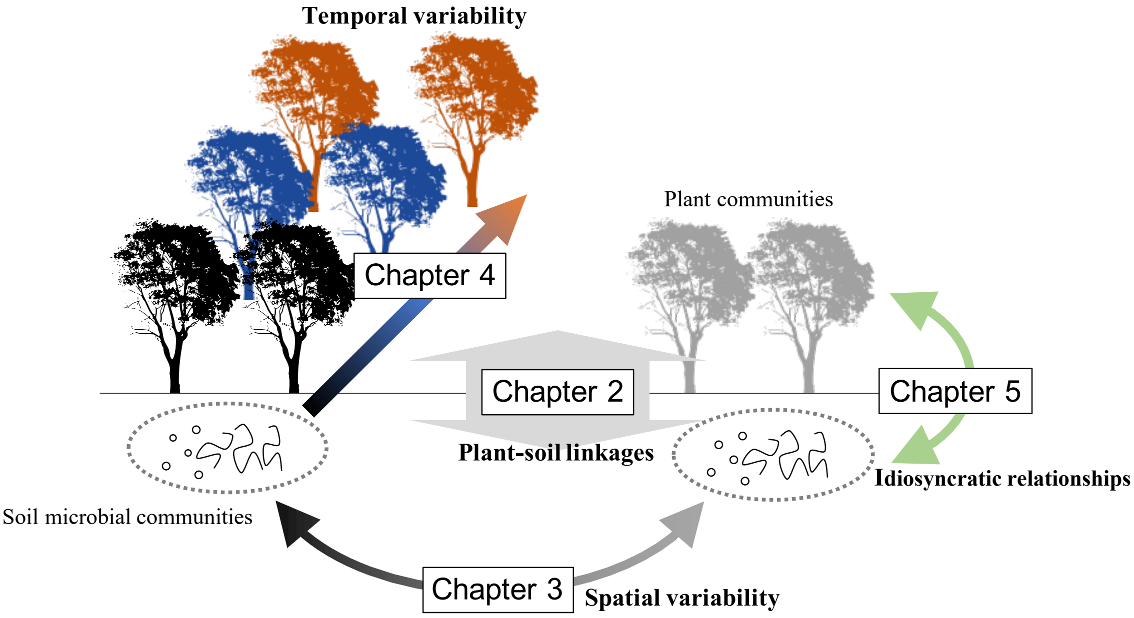

Fig. 1-1 Outline of the thesis. Chapter two reveals the importance of relationships between plant communities and soil properties along elevational gradients. The following chapters also focus on two major spatio-temporal scales where aboveground ecosystem components mainly influence soil microbial communities. The first is elevational change, which is covered in chapter three. The second is seasonal change, which is handled in chapter four. Chapter five clarifies the idiosyncratic relationships between HFA for litter decomposition and soil microbial communities.

1-5. Aim and thesis outline

Considering HFA for litter decomposition in forest ecosystems, microbial community identity for litter decomposition could potentially exist in soil microbial communities, depending on environmental factors. However, it is not clear how these idiosyncratic microbial communities are positioned in the whole community and how it responds to environmental changes. Therefore, it aims to verify how soil microbial communities exhibit spatio-temporal variability and identity to litter decomposition (Fig. 1-1). Chapter two clarifies the importance of relationships between plant communities and soil properties along elevational gradients. The following chapters also focus on two major spatio-temporal scales where aboveground ecosystem components mainly influence soil microbial communities. The first is elevational change, which is covered in chapter three. The second is seasonal change, which is handled in chapter four. Chapter five deals with the relationships between HFA for litter decomposition and soil microbial identity. This thesis consists of the general introduction (chapter 1), four chapters presenting the main research of the doctoral thesis (chapters 2-5), and the general discussion of the key findings (chapter 6). Each of the four research chapters is either published or intended for publication as independent research articles in international peer-reviewed journals.

Chapter 2:

Relationships between understory plant diversity and soil properties along elevational gradients

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Chapter 3:

Elevational diversity gradients of soil microbes

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Chapter 4:

Seasonal dynamics of soil microbial communities

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Chapter 5:

Soil microbial identity in home-field advantages for litter decomposition

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Chapter 6:

General discussion

6-1. Introduction

Microbial ecologists have long sought to understand what factors govern soil fungal and bacterial communities (Swift et al. 1979; Fierer 2017). Climate and soil conditions have been regarded as the main factors determining soil microbial communities (Fierer and Jackson 2006; Zhou et al. 2016; Fierer 2017). However, based on a number of observations that plant community structures also drive forest ecosystems (Morin et al. 2011; Gamfeldt et al. 2013), plant-soil linkages may affect soil fungal and bacterial communities. In particular, litter decomposition through microbial communities is a fundamental determinant of carbon and nutrient cycling in temperate forests (Melillo et al. 2002). Given home-field advantage (HFA) for litter decomposition, soil microbial communities may become specialized in breaking down plant litter that they are associated with, resulting in accelerated decomposition (Ayres et al. 2009). Therefore, the objective of the thesis was to understand the spatio-temporal variability of soil microbial communities and their identity for litter decomposition. This final chapter firstly recaptures and discusses the results obtained in the main researches of the doctoral thesis (Chapters 2-5) and combines these findings (Section 6-2). Following this, the next section discusses future directions and challenges for research (Section 6-3). Finally, this chapter ends with a concluding remark for this thesis (Section 6-4).

6-2. Synthesis of research findings

Chapter 2: Relationships between understory plant diversity and soil properties along elevational gradients

Elevational diversity gradients (EDGs) of vegetation can be shaped by the evolutionary histories of plants as well as by ecological factors (Nogué et al. 2013; Merckx et al. 2015). However, few studies of EDGs have focused on the roles of phylogenetic constraints and the associations with complicated interactions among environmental factors (Schreeg et al. 2010; Ulrich et al. 2014). Chapter two examined the direct and indirect roles of environmental factors in forming EDGs of forest understory vegetation. In this research, taxonomic and phylogenetic diversities of tree seedlings increased monotonically with elevation, and the same pattern was found for the taxonomic diversity of herbs. Structural equation modeling indicated that both the taxonomic and phylogenetic diversity of tree seedlings were most associated with soil properties, although the phylogenetic diversity of herbs was related to light conditions. These results highlight the importance of environmental filtering by soil properties in shaping EDGs of tree seedlings. This research implies that phylogenetic constraints in adaptation to soil properties should be considered when predicting changes in EDGs under environmental fluctuations.

The relationships between understory vegetation and soil properties observed in chapter two can also be formed through litter decomposition. Indeed, but not surprisingly, plant litter composition often reflects the diversity and community structures of understory vegetation (Barbier et al. 2008; McIntosh et al. 2016). According to the results of chapter three, as soil microbial communities relate to leaf traits of trees, the composition of litters may influence understory vegetation via soil microbial communities. Similarly, McIntosh et al. (2016) found that understory vegetation can be affected by plant litters of overstory vegetation through decomposer microbial communities. On the other hands, the importance of understory vegetation on soil ecosystem processes is frequently ignored due to low contribution of this layer to overall biomass. Although understory vegetation can contribute significantly to the nutrient cycling of temperate forest ecosystems because litters of understory vegetation decompose more than twice as rapidly as those of trees (Muller 2003; Gilliam 2007), contributions of litters of understory vegetation to forest ecosystems through microbial communities are thoroughly unclear. These indicate that future studies are necessary to understand how overstory and understory plant litters affect forest ecosystem functioning through soil microbial communities.

Chapter 3: Elevational diversity gradients of soil microbes

Chapter three examined how plant functional diversity, soil properties, and soil temperature affect EDGs of soil bacteria and fungi at different soil depths. The diversity of bacteria decreased with elevation in surface soils but showed no relationship with elevation in deep soils. Structural equation modeling showed that soil bacterial diversity across elevational gradients was directly affected by plant functional diversity, especially where leaf C:N ratio diversity had stronger effects than soil properties. Chapter three found that EDGs of soil bacteria as a consequence of the total effect of elevation were determined by the degree of negative indirect effects of soil temperature, via plant functional diversity and soil properties, against a positive direct effect of soil temperature on bacterial diversity. These findings demonstrate that community assembly of soil microbes is causally linked with the climate, plant functional diversity and soil properties, which determine EDGs.

Elevational gradients represent model systems for understanding the relationships between soil microbial communities and environmental factors (Bryant et al. 2008; Fierer et al. 2011; Peay et al. 2017), but the multiple influences of plant-soil linkages and the climate on EDGs of soil microbes have never been explored. As mentioned in chapter one, soil properties play a crucial factor in affecting soil microbial communities (Fierer and Jackson 2006; Fierer et al. 2017). However, given the results of chapter five, the patterns of soil microbial diversity may have been reinforced by litter decomposition through biotic interactions between plant traits and microbes. For example, some studies support the link between soil microbial community composition and organic matter decomposition (Fanin et al. 2011; Fanin and Bertrand 2016). These findings suggest that the high chemical diversity of leaf litters could form a relationship between microbial diversity in forest soils and plant organic matter inputs to soil. For clarifying the role of biotic interactions between plants and soil microbial communities in shaping these diversity patterns, further studies are required to investigate the relationships between plant leaf litters and their decomposer microbes along elevational gradients.

Chapter 4: Seasonal dynamics of soil microbial communities

Chapter four aimed to evaluate the importance of seasonality, elevation, and soil depth in determining soil fungal and bacterial communities, given the influence of climate conditions, soil properties, and plant traits. Seasonal diversity and abundance patterns did not match between fungi and bacteria, where the peak of fungal diversity and bacterial abundance was observed in April, but those of bacterial diversity occurred in January. Model-based clustering found taxonomic groups associating carbon and biogeographical cycles that were paralleled with seasonality, implying that they are indispensable taxa driving ecosystem processes in temperate forests. Furthermore, bacterial communities were profoundly explained by both spatial and seasonal changes in soil water contents, while many taxonomic groups of soil fungi were related to plant traits along elevational gradients. These findings suggest that the contribution of the seasonal variability of climate conditions, soil properties, and plant traits are equal to or greater than those of spatial changes for microbial communities in forest soils at mid-to-high latitudes.

Both aboveground and belowground properties operate over seasonal timescale in forest ecosystems at the mid-to-high latitude (Bardgett et al. 2005), but the seasonality of soil fungal and bacterial communities in this area has not been fully understood. Consistent with the assumption of chapter one, the seasonal variability of soil microbial communities may have been regulated by tree phenology in temperate forests. However, both litter decomposition and photosynthate allocation can represent essential factors that contribute to the observed seasonal variability. For achieving a further understanding of the seasonal variability of soil microbial communities, it would be necessary to complement the current knowledge with functional analyses for metatranscriptomes.

Chapter 5: Soil microbial identity in home-field advantages for litter decomposition

Chapter five aimed to understand the relationships between HFA for litter decomposition and soil microbial communities. Given the "community-by-environment" interaction in microbial ecology (Matulich and Martiny 2015; Glassman et al. 2018), it is assumed that both soil and climate affinity strongly influenced litter decomposition, but this hypothesis was not supported. Rather, HFA effects of litter decomposition highly depended on the source soil via fungal and bacterial identity. Although a home-climate advantage for litter was significant in the early stage of decomposition, it was not a strong limiting factor as compared with a soil advantage. These suggest that litter decomposition in temperate forests was explained by microbial communities that are not functionally redundant, but these relationships may have the robustness to climate change. As mentioned in chapter one, HFA for litter decomposition plays an essential role in understanding overall decomposition processes that have implications for global climate and biogeochemical models (Ayres et al. 2009a; Austin et al. 2014; Palozzi and Lindo 2018). These findings contribute to an understanding of the impacts of global climate changes on belowground ecosystem processes and the role of microbial communities in biogeochemical cycles of forest ecosystems. Chapter five also implies that ignoring home-soil advantages for litter decomposition could lead to misinform biogeochemical models and potential cascading consequences for forest management.

This thesis found that: (1) plant-soil linkages were significant along elevational gradients in cool-temperate montane forests (Chapter 2); (2) Community assembly of soil fungi and bacteria was linked with the climate, plant traits, and soil properties, which determine elevational and seasonal diversity patterns (Chapters 3 and 4); (3) Identity of soil microbial communities for litter decomposition has the robustness to climate change (Chapter 5). For synthesizing these findings, the thesis highlights that soil microbial communities have spatio-temporal variability in response to environmental changes, but their identity for litter decomposition has robustness to environmental perturbations, which is explained by plant-soil linkages in forest ecosystems (Fig. 6-1). These findings are significant because the impacts of plant-soil linkages on soil microbial community structures and dynamics are still mostly underexplored. Only recently have studies began to focus on microbial community structures scrutinized by high-throughput sequencing to predict home-field advantages for litter decomposition (Asplund et al. 2018; Glassman et al. 2018; Lin et al. 2018).

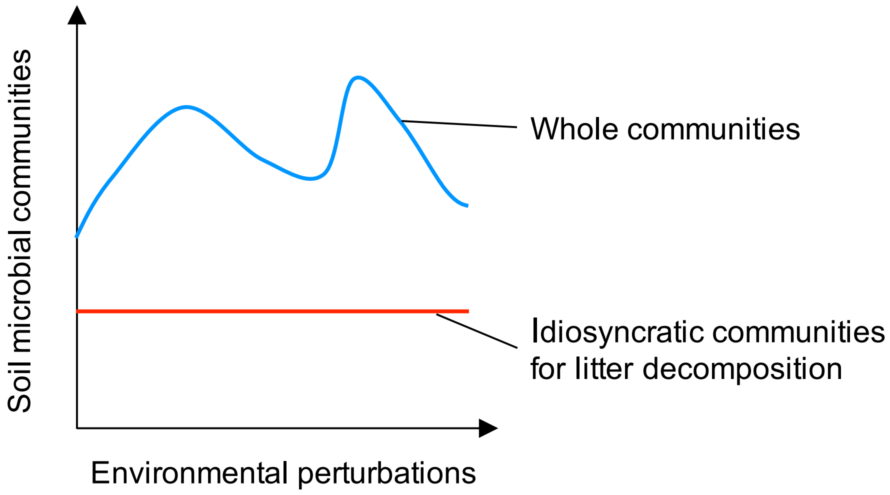

Fig. 6-1 Schematic diagram of the synthesis of the research findings. Soil microbial communities have spatio-temporal variability in response to environmental changes, but their identity for litter decomposition has the robustness to environmental perturbations, which explained by plant-soil linkages in forest ecosystems

6-3. Future research perspectives

Functional scales of microbial identity for litter decomposition

Significant spatio-temporal scales of microbial identity for litter decomposition are unclear in this thesis. According to the results of chapter five, elevational differences of 1000 m showed soil microbial identity for litter decomposition, but the significant elevational range was unknown. Likewise, idiosyncratic microbial communities were significant during the first one and a half years of litter decomposition, but it was unclear whether it was effective over a more extended period. Indeed, as discussed in chapter five, the HFA effects of litter decomposition can decrease with time (Freschet et al. 2012; Pearse et al. 2014; Ayres et al. 2009b). In order to solve these problems, it is necessary for future research to conduct further experiments along elevational gradients and over a more extended period.

Clarifying boundaries of idiosyncratic microbial communities is also essential for conservation strategies of forest ecosystems. In a global scale, defining an ecoregion to represent a more ecologically relevant planning unit than political boundaries is fast becoming a standard tool for conservation planning (e.g., McDonald et al. 2005; Lamorex et al. 2006; Dinerstein et al. 2016). Recently, Smith et al. (2018) analyzed the global patterns of species accumulation and turnover in various taxa including soil fungi and examined whether ecoregion borders represent exact delineations between distinct communities. Then, they found that there were relatively sharp boundaries for soil fungi (Smith et al. 2018). Given the results of chapter five, this implies that there are sharp boundaries of microbial identity for litter decomposition along elevational gradients in cool-temperate forests. Since idiosyncratic communities rather than whole communities can designate ecoregions, further research may generalize forest conservation policy and planning.

Influence of other organisms on microbial identity for litter decomposition

In forest ecosystems, not only the direct contribution of soil microbial communities but also other biological communities can, directly and indirectly, influence soil microbial identity for litter decomposition. Although not considered in chapter five, soil fauna may directly contribute to HFA for litter decomposition. For example, Milcu and Manning (2011) found that HFA effects of litter decomposition was stronger in plots dominated by more recalcitrant litter inputs and suggested that a range of size class of soil fauna contributed to this HFA effects. In addition, soil fauna can influence the identity of soil microbial communities indirectly for litter decomposition. Indeed, microbial-feeding nematodes in soils can affect soil fungal and bacterial activities, indirectly regulating the litter decomposition rate (Griffiths

1994; García-Palacios et al. 2016). In order to solve these points, it is necessary for the future study to perform similar experiments using litterbags with different mesh size (Milcu and Manning 2011).

For considering whole forest ecosystem, food-web dynamics can affect the spatio-temporal variability of soil microbial communities and their identity for litter decomposition through abiotic and biotic interactions. For example, in coniferous forests in the Pacific Northwest of the United States, small mammals such as mice and moles contribute to plant litter decomposition by mixing soils (Carey and Harrington 2001). Flying squirrels in this area are also important dispersal agents for hypogeous fungi, which are a major part of their diet (Maser et al. 1978). Recent range expansion of the barred owl (*Strix varia*) onto the Pacific Northwest of the United States decreases the abundance of native prey species, causing significant changes in avian predator communities with cascading effects on food-web dynamics and litter decomposition processes (Holm et al. 2016). Because the population density of sika deer (*Cervus nippon*) has recently been increasing and potential effects of browsing on vegetation have been reported in western regions adjacent to this study area (Ohashi et al. 2014), it is required in future works to monitor how declining vegetation affects the identity of soil microbial communities for litter decomposition.

Influences of soil environments and microbial identity on forest plant communities

Given plant-soil feedback in forest ecosystems, soil microbial communities can affect plant communities through their identity for litter decomposition. Indeed, the structure and activity of soil microbial communities involved in decomposition processes alter plant productivity and community composition through physicochemical conditions of soil and carbon supply to the soil (Bardgett et al. 2008). However, much remains unknown about how idiosyncratic microbial communities for litter decomposition drive interactions between soil properties, other microbes such as root-associated microbes, and plant communities. Here, the following reviews the influence of soil abiotic and biotic conditions on plant communities, as not mentioned chapter one.

Soil physicochemical properties, such as soil pH, moisture, and nutrient status, have been widely studied as factors influencing plant diversity and community structures. Soil pH is often recognized as an indicator of soil properties because of the simplicity for measurement. Indeed, soil pH indicates a high correlation with the quality and quantity of soil nutrients although it does not represent nutrients available for plants. There are various trends in observed relationships between plant communities and soil pH, and various mechanisms have been proposed (Grime 1979; Pärtel 2002). For example, a mechanism underlying the hump-shaped plant diversity and soil pH relationships is physiological stress limiting the number of plant species adapted to the extreme ends of the pH gradients (*sensu* intermediate stress hypothesis by Grime 1979; physiological tolerance hypothesis by Currie et al. 2004). That is, on acidic soils ($pH < 4$), plant diversity could be constrained by high phytotoxicity (high concentrations of Al^{3+}, Fe^{2+}, Fe^{3+}, and Mn^{2+}; Abedi et al. 2013) and nutrient limitation (low concentrations of Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}; Rorison 1980). On the contrary, on high pH soils ($pH > 7$), phosphorus and iron become limiting nutrients due to their decreased solubility (Tyler 1996; Zohlen and Tyler 2000).

Soil moisture also directly affects plant diversity and community structures because plants acquire minerals and nutrients through soil water. A series of studies by Silvertown and colleagues (Silvertown et al. 1999; Araya et al. 2011; Garcia-Baquero et al. 2016) focused on understanding the patterns of plant diversity and community composition in grasslands. They define the hydrological niche segregation as resource partitioning of soil water through different acquisition strategies, such as different phenology and root depths (Araya et al.

2011). Although niche differentiation by water availability is frequently reported in arid regions with low precipitation, competition among coexisting plants for water resources can affect vegetation succession (Kozlowski 2002). Besides soil properties, various factors, such as temperature, topography and light environment, are also crucial for shaping plant diversity and community structures (Beatty 1984; Gilbert and Lechowiz 2004; Grace et al. 2011). Forest plant-soil feedback can change both positively and negatively depending on these abiotic factors. Indeed, Smith and Reynolds (2015) found that plant-soil feedbacks change from negative to positive with decreasing light intensity in forest understory plants. For understanding plant-soil feedbacks in forest ecosystems, it is essential to clarify the effects of complicated interactions between abiotic factors and plant-soil linkages.

Not only soil abiotic factors but also soil microbes also play an essential role in influencing plant diversity and community structures. There are several distinct groups of soil microbes associated with plant roots, affecting plant communities. The arbuscular mycorrhizal fungi are related to about 80 % of angiosperm species (Brundrett 2002) and dominate in temperate and tropical forests. Plants are also coexisting with ectomycorrhizal fungi and ericoid mycorrhizal fungi in a temperate to a boreal nutrient-rich forest (Read and Perez-Moreno 2003). The presence of these types of fungi is of critical importance for plant diversity and ecosystem functioning. For example, using an experimental mycorrhizal-plant system, Maherali and Klironomos (2007) found that functional complementarity among arbuscular mycorrhizal fungi enhances plant productivity, shaping plant community assembly. For bacteria, plant growth promoting rhizobacteria (PGPR), which increases plant growth and fitness (Vessey 2003), can affect plant diversity and community structures. In particular, in forests, mycorrhization helper bacteria, which promote mycorrhizal development, can influence plant diversity and community structures (Frey-Klett and Garbaye 2005; Kurth et al. 2013) although the importance of such bacterial effects on forest ecosystems has seldom been explored.

Personalized nutrition and its implications for the management of forest ecosystems

Findings derived from studies of human microbiomes can be expected to improve understanding the role of soil microbial communities in forests and the perspective for forest management. In particular, the relationships between gut microbiomes and personalized nutrition will develop this work and lead to an understanding of forest ecosystem processes through soil microbial communities. Personalized nutrition is an approach that assists individuals in achieving a lasting dietary behavior change that is beneficial for health, but it is a problem that improving dietary behavior based only on genetic information does not contribute to sustained health (Zmora et al. 2016). For example, elevated blood glucose levels after meals are known as a significant risk factor for diabetes, but existing methods for regulating them have limited efficacy (Nathan et al. 2007). Zeevi et al. (2015) focused on gut microbiomes which differed among individuals and performed microbiome-association analyses to clarify the relationships between postprandial (post-meal) glycemic responses (PPGR; Gallwitz 2009) and gut microbial communities. They also developed a machine-learning model that integrates blood parameters, dietary habitats, anthropometrics, physical activity, and gut bacterial community composition and functions. Finally, they showed that personally tailored dietary interventions based on the model resulted in significantly improved PPGRs accompanied by consistent alterations to the gut microbiome (Zeevi et al. 2015).

Because carbon sequestration programs are gaining attention globally, whether productivity increases in afforestation areas is a major practical problem (Marland and Schlamadinger 1997; FAO 2015). According to the concept of personal nutrition, tailored litter composition for each afforestation area may improve soil ecosystem functioning through microbial communities, resulting in high productivity. However, in order to clarify this point, it is necessary to explain how soil microbial identity for litter decomposition affects plant growth rate, as mentioned above. Similar to the study of Zeevi et al. (2015), developing a model that integrates climate, soil properties, litter quality and composition, and soil fungal and bacterial communities can predict the productivity of each forest through soil microbial communities. Based on the results of the model, litter content contributing to the growth rate for each forest would be devised. Finally, examining whether the inputs of these litters to afforestation can improve productivity. Further studies may suggest guidelines for the management of afforestation based on soil community identity for litter decomposition.

6-4. Concluding remarks

This thesis found that: (1) plant-soil linkages were significant along elevational gradients in cool-temperate montane forests; (2) Community assembly of soil fungi and bacteria was linked with the climate, plant traits, and soil properties, which determine elevational and seasonal diversity patterns; (3) Identity of soil microbial communities for litter decomposition has the robustness to climate change. The findings of the doctoral thesis highlight that soil microbial communities have spatio-temporal variability in response to environmental changes, but their identity for litter decomposition has the robustness to environmental perturbations, which explained by plant-soil linkages in forest ecosystems. The further elucidation of the linkages between microbial identity and forest ecosystem functionings may simplify an understanding of the manner how plant-soil linkages shape ecosystem processes.

Acknowledgements

First and foremost, I would like to thank Dr. Toshihide Hirao for supervising me as a doctoral student and for his support during all stages of this thesis. His outstanding guidance, astute feedback, incredible generosity, and tremendous patience cannot be credited adequately within the scope of this acknowledgments section. I am especially grateful to Dr. Kiyoshi Umeki for his help, discussion, and critical view at various stages of the thesis. I would also thank Dr. Haruka Ohashi and Dr. Kiyokazu Kawada for help with fieldwork and Dr. Terumasa Takahashi for laboratory analysis. Furthermore, I would like to thank Dr. Susumu Goto and Dr. Naoko Miura for their help at various stages of the thesis through monthly seminar. I would also deeply thankful to all the members of Education and Research Center, the University of Tokyo Forests. I am grateful to the staffs of the University of Tokyo Chichibu Forest, namely Takeshi Chishima (present affiliation: The University of Tokyo Chiba Forest), Koji Fujihira, Ryusei Haraguchi, Yuji Igarashi, Kazuya Omura, Michio Saiki, Michihiro Takano, Kae Takatoku, Saito Toshihiro, and Yumiko Yoshida for their assistance in the field. This study was supported by a Grant-in-Aid for JSPS Fellows from the Japan Society for the Promotion of Science (no. 18J14438) and the Sasakawa Scientific Research Grant from the Japan Science Society (no. 28-628).

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Supplementary materials

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