Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient
Fujii, Saori; Cornelissen, Johannes H. C.; Berg, Matty P.; Mori, Akira S.

Published in:
Functional Ecology

DOI:
10.1111/1365-2435.13027

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2018

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient

Saori Fujii1,2,3 | Johannes H. C. Cornelissen2 | Matty P. Berg2,4 | Akira S. Mori1

1Department of Environment and Natural Sciences, Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama, Japan
2Department of Ecological Science, Faculty of Science, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands
3Hakubi Center for Advanced Research / Field Science Education and Research Center, Kyoto University, Kyoto, Japan
4Conservation and Community Ecology Group, Groningen Institute for Evolutionary Life Sciences, Groningen University, Groningen, The Netherlands

Correspondence
Saori Fujii
Email: sao@itak.or.jp

Funding information
JSPS Fellowship, Grant/Award Number: 13J00547 and 25850115; JSPS Overseas Research Fellow, Grant/Award Number: 847; the Mitsui & Co., Ltd. Environment Fund, Grant/Award Number: the Japanese Ministry of Education, Culture and Sports

Handling Editor: Sergio Rasmann

Abstract
1. Plant litter decomposition is key to carbon and nutrient cycling in terrestrial ecosystems. Soil fauna are important litter decomposers, but how their contribution to decomposition changes with alterations in plant composition and climate is not well established.
2. Here, we quantified how soil mesofauna affect decomposition rate interactively with climate and leaf and root traits. We conducted an in situ decomposition experiment using eight dominant tree species per forest site across four elevations (50, 400, 600 and 1,000 m a.s.l.) in northern Japan. We used litterbags with different mesh sizes to control litter accessibility to soil mesofauna.
3. We found stronger effects of plant litter quality on both decomposition rates and faunal contribution thereto, and perhaps of local variation in soil nutritional and moisture regimes, than climatic effects of elevation. This suggests that changing climate likely alters forest litter decomposition rates indirectly through shifts in tree community composition more than directly through changing abiotic regimes. Considering both leaves and roots as litter resources enlarged the overall contribution of variation in litter quality to decomposition rates and faunal effects thereupon, because litter quality and decomposition rate varied more between leaves and roots overall than among leaves within and across elevations.
4. The contribution of mesofauna to litter decomposition was larger in nutrient-rich litter than in recalcitrant litter across the elevational gradient, suggesting amplification of the effect of litter traits on decomposition through preference of soil fauna for their food resources.
5. Our findings highlight the importance of considering synergistic influences of soil faunal activities with litter traits of both leaves and roots for better understanding biogeochemical processes across environmental gradients over space or time.

KEYWORDS
altitudinal gradient, biogeochemical process, fine root, forest ecosystem, invertebrates, leaf litter, litter chemical traits, soil microarthropods

1 INTRODUCTION

Plant litter decomposition is a fundamental biogeochemical process through its regulation of carbon sequestration and nutrient supply to plants in terrestrial ecosystems (Swift, Heal, & Anderson, 1979). Hence, changes in litter decomposition rates have profound effects on ecosystem functioning, especially in mature forest ecosystems with a closed nitrogen cycle, in which plant growth is strongly dependent...
on nitrogen availability (Chapin, Matson, & Vitousek, 2011). Litter decomposition is well known to be driven by multiple interactive determinants including climate, litter traits and soil organisms (Aerts, 1997; Lavelle et al., 1993; Swift et al., 1979). Disentangling the effects of these factors and their interactions on decomposition across spatial and temporal scales is still an important challenge to predict possible consequences of global climate change for the stability vs. dynamics of ecosystem functions (Bradford et al., 2016; García-Palacios, Shaw, Wall, & Hättenschwiler, 2016; Handa et al., 2014). While climate has long been considered the primary broadscale control on litter decomposition rates (Berg et al., 1993; Lavelle et al., 1993), recent studies suggest that effects of plant litter traits at local to regional scale may predominate (Bradford et al., 2016; Cornwell et al., 2008). However, it is still difficult to generalize the role of soil fauna as decomposers in relation to climate and litter traits (Kutsch, Bahn, & Heinemeyer, 2009). Although the direct effect of soil fauna on decay rates is often lower than those of the other factors (Fujii, Makita, Mori, & Takeda, 2016a; Makkonen et al., 2012; Wall et al., 2008), they strongly mediate the effects of abiotic environment and litter traits on decomposition processes via microbial activity (Lavelle et al., 1993; Wardle, 2002). Therefore, elucidating the role of soil fauna in litter decomposition is necessary to better understand and predict changes in decomposition.

A recent meta-analysis of litterbag experiments based on the presence vs. absence of soil fauna showed that the effects of soil fauna on decomposition rates are generally positive across different biomes (García-Palacios, Maestre, Kattge, & Wall, 2013; but see Kampichler & Bruckner, 2009), while they also vary with climatic factors at the global scale. Several papers have suggested that the faunal contribution to decomposition is high under warm and humid conditions (Makkonen et al., 2012; Wall et al., 2008; Wang, Ruan, & Wang, 2009), where biological activity and metabolic rates are considered to be less constrained by climatic factors (Lavelle et al., 1993). Interactions between litter traits and soil fauna have also been mentioned as important determinants of decomposition at the local scale (Carrillo, Ball, Bradford, Jordan, & Molina, 2011; Hättenschwiler & Jørgensen, 2010; Smith & Bradford, 2003), where climatic variance is relatively small. However, in the current literature a large inconsistency still exists in the relationship between the effects of soil fauna and litter quality. While soil fauna have been predicted to facilitate the decomposition of especially recalcitrant litters (Coleman, Crossley, & Hendrix, 2004; Fülsler, 2002; Seastedt, 1984), empirical evidence has shown stronger faunal enhancement of decomposition rates for litter of higher quality (Fujii et al., 2016a; Schädler & Brandl, 2005). On the other hand, some papers show that the direction and strength of interaction between the effects of litter traits and soil fauna vary among biomes (i.e. different climatic regimes) and sites (García-Palacios et al., 2013; Milcu & Manning, 2011; Perez, Aubert, Decaëns, Trap, & Chauvat, 2013). This context dependency among studies suggests that faunal effects on decomposition cannot be predicted easily, because the mesoфаunal contribution will change in association with changes in climate, litter traits and soil biota.

Global climate warming is likely to increase decomposition rates of given litter materials, as implied by faster decomposition under warmer conditions across latitudinal or altitudinal temperature gradients (e.g. Berg et al., 1993; Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Vitousek, Turner, Parton, & Sanford, 1994). However, besides temperature, also plant and soil faunal communities will shift in response to climate change (Berg et al., 2010; Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), which could affect decomposition rates. Shifts in ecosystem process rates with climate change through the consequences of shifts in biological community composition are poorly understood for terrestrial ecosystems (Van der Putten, Macel, & Visser, 2010), but ecosystem responses to temperature along elevational gradients can serve as proxies through space for time substitution (Sundqvist, Sanders, & Wardle, 2013). Global warming will result in an upward move of most taxonomic groups along mountain slopes in response to increasing temperature (Sheldon, Yang, & Tewksbury, 2011), although dispersal ability varies among taxa (Berg et al., 2010; Mori et al., 2015). Thus, with the caveat that other factors than temperature (e.g. moisture regimes, soil structure and chemistry) may interfere with the temperature gradient, in situ decomposition experiments using a natural elevational gradient give us the first step to predict the shift in decomposition rates in association with both direct warming effects and concomitant shifts in biological communities.

Particularly, a shift in plant functional trait composition in response to climate changes could have critical effects on the decomposition through changing litter traits (Aerts, 1997; Cornelissen et al., 2007). Increasing elevation can result in a shift, both among and within predominant species, towards traits enhancing tolerance of more stressful environments, such as cold-induced nutrient limitation, at the expense of growth rate potential (Sundqvist, Giesler, & Wardle, 2011; Vitousek, Matson, & Turner, 1988). Through trait "afterlife" effects, such a shift may lead to declining plant litter quality with elevation (Kitayama et al., 2004; Tanner, Vitousek, & Cuevas, 1998; Vitousek et al., 1994); this in turn can affect communities of soil biota and their functions in conjunction with climatic factors (Bardgett & Wardle, 2010). However, previous studies on this issue have focused exclusively on above-ground leaf litter, which is generally of relatively high quality compared to that of fine roots (Freschet et al., 2013), while input of fine-root litter into the soil is almost equivalent in quantity to that of leaf litter (Norby, Ledford, Reilly, Miller, & O’Neill, 2004; Vogt et al., 1996). Recent studies have shown that interspecific variation in fine-root tissue quality is often correlated with that in leaf tissue quality (summarized in Freschet, Cornelissen, van Logtestijn, & Aerts, 2010b; Reich, 2014), leading to a positive correlation between leaf and root litter decomposition rates across different plant species (Freschet et al., 2013; Fujii, Makita, Mori, & Takeda, 2016b). This implies that the shifts in the effects of root litter traits on decomposition in response to changing climate may have the same patterns with that in leaf litter. However, the difference in substrate quality between leaf and root litter overall is easily as large, if not larger, than the variation between leaves of different species (Freschet, Aerts, & Cornelissen, 2012; Zhang, Hui, Luo, & Zhou, 2008). Thus, effects of litter quality based on quality changes of each given organ along elevation may be cancelled out by the greater overall difference in litter quality between different organs, for instance between leaves and roots. However, these relationships between different organs are poorly known.
To fill this research gap and improve insight in future temperature responses of decomposition rates, we aim to quantify how soil fauna affect decomposition rate interactively with climate and litter traits of leaves and roots along an elevational gradient. We conducted an in situ decomposition experiment using eight dominant tree species per site across four elevation sites (50, 400, 600 and 1,000 m a.s.l.) in the northern forests of the Shiretoko Peninsula, Japan. We used litterbags with different mesh sizes to control for the accessibility of the litter to soil fauna. Here, we focused on mesofauna represented by soil microarthropods (e.g. Collembola and Oribatida), which are the most abundant soil fauna in most terrestrial ecosystems (Bardgett & Cook, 1998; Petersen & Luxton, 1982). Soil mesofauna are considered to contribute to decomposition directly through consumption of litter and humus and indirectly through association with micro-organisms (Hanlon, 1981; Seastedt, 1984). Here, we test the following hypotheses: (1) with increasing elevation, plant tissue quality decreases both within and among plant species, leading to slower decomposition rates and a lesser faunal contribution thereto at higher elevations synergistically with a negative effect of low temperature, and (2) interaction between the effects of fauna and litter quality on decomposition rate is stronger at lower elevations, where a more favourable abiotic environment stimulates faunal activity.

2 MATERIALS AND METHODS

2.1 Site description

This study was conducted at four sites across an elevational gradient (50, 400, 600 and 1,000 m a.s.l.) on the west-facing slope of Mount Raus (1,661 m), the highest peak in Shiretoko National Park, located in north-eastern Hokkaido, Japan (latitude 44°08’ to 11’, longitude 145°03’ to 08’). Approximately 90% of the park’s terrestrial area is covered with pristine natural vegetation, mostly mixed conifer–hardwood forest. The mean annual precipitation of the lowland area was c. 1,090 mm and the mean temperature was 6.8°C during the study period. The maximum temperature in August and minimum temperature in February are c. 22°C and −16°C, respectively. The vegetation varies from mixed deciduous and coniferous forest dominated by Picea jezoensis, Abies sachalinensis and Quercus crispula at low elevation to deciduous broadleaved forest dominated by Q. crispula, Betula ermanii and Sorbus commixta higher up the altitudinal gradient (Mori et al., 2013). The soil type is Andosol (US Soil Taxonomy) with moder humus. Soil properties are shown in Table 1 (see the methods in Supporting Information 1). To evaluate and visualize the variation in soil environment across an elevational gradient, we performed a principal components analysis (PCA) using ln-transformed data of all measured soil properties (Supporting Information 2). The first axis (PC1), accounting for 52.3% of the variance, was related to soil temperature, inorganic N and pH. The second axis (PC2), accounting for 19.8% of the variance, was involved in $A_h$ horizon depth, soil respiration rate, water content and total C and N contents.

### 2.2 Litter decomposition experiment

We used litterbags to quantify the contribution of mesofauna to leaf and root litter decomposition. We collected leaves and roots of eight typical tree species at each elevation as litterbag materials (Supporting Information 3, 20 species in total). These species were selected to account for more than 80% of canopy cover at each elevation (Cornelissen et al., 2003), based on both basal area and...
leaves and roots were air-dried at room temperature for 14 days. We selected the fine roots (≤1.0 mm diameter) from each species. The leaves and roots were carefully washed with tap water to remove soil and leaves with herbivory or disease symptoms from litter samples. We removed sorption (i.e. N, P and K; Supporting Information 4). We removed robust to exclusion of data for the nutrients strongly related to resorption. In addition, we confirmed that our results based on a multivariate litter quality index as predictor of decomposition patterns were similar in initial and harvested litter samples, thereby avoiding errors in calculation of mass loss on a dry mass basis. Subsequently, we weighed the dry mass of litter for leaf or root material to determine the mass loss per sample as % of initial mass.

2.3 | Control experiment

As we incubated different plant species at different elevations, we wanted to assess the effect of elevation on substrate of a constant quality for reference. Therefore, we incubated litterbags filled with cellulose filter paper to check the environmental effects associated with elevation on decomposition rates. Amounts of 1.0 g and 0.5 g of cellulose filter paper (filter paper no. 5B: ADVANTEC, Tokyo, Japan) were enclosed in 10 cm × 10 cm and 5 cm × 10 cm nylon mesh bags, respectively, with the same mesh sizes as the leaf and root bags. In June 2016, we placed six sets of four bags each randomly in the four plots. The bags were placed analogous to the leaf and root litterbags, that is, bags filled with 1 g cellulose on the soil surface, and bags filled with 0.5 g cellulose placed vertically into the soil. In total, we used 96 litterbags (two positions × two mesh sizes × six replicates × four sites). In August 2016, we collected all bags after about 50 days of incubation and determined mass loss in the same way as in the main litterbag experiment (Supporting Information 5). The incubation was relatively short and only in the summer period, because we anticipated relatively fast decomposition of the filter paper. The summer represents the period in which much of litter mass loss usually occurs and when the effects of the altitudinal temperature gradient should be the strongest.

2.4 | Measurement of the initial litter quality

We prepared an additional set of litter subsamples for 64 litter types (eight species × two plant organs × four sites) to quantify the initial tissue chemistry. We selected one litterbag randomly from all prepared litterbags for each litter type before incubation. Leaves and roots were finely ground using a laboratory mill (BEAD CRUSHER T-01, TAITEC, Koshigaya, Japan) for chemical analysis. We analysed total C and N contents, lignin (acid-insoluble fraction, AIS) content, total carbohydrate (TCH) content and contents of individual nutrients (P, K, N) using an elemental analyser (CARLO ERBA NA 1500, Carlo-erba, Rome, Italy) and a lignin analyser (LIGNOlab, LEHMANN INSTRUMENTS, Sertig, Switzerland). We used 50 g of litter and 30 g of cellulose filter paper (filter paper no. 5B: ADVANTEC, Tokyo, Japan) for chemical analysis. We analysed total C and N contents, lignin (acid-insoluble fraction, AIS) content, total carbohydrate (TCH) content and contents of individual nutrients (P, K, N) using an elemental analyser (CARLO ERBA NA 1500, Carlo-erba, Rome, Italy) and a lignin analyser (LIGNOlab, LEHMANN INSTRUMENTS, Sertig, Switzerland).
K, Ca and Mg). We measured total C and N contents using the combustion method (Vario EL III CHNOS Elemental Analyzer, Elementar, Hanau, Germany) and AIS content by gravimetry following the standard method of hot sulphuric acid digestion (King & Heath, 1967). We extracted samples with alcohol–benzene (99.9% ethanol (v/v); benzene = 1: 2) at room temperature, with the residue treated with 72% sulphuric acid (v/v) for 2 hr at room temperature. The mixture was diluted with distilled water to make a 2.5% sulphuric acid solution and autoclaved at 120°C for 60 min. After cooling for two hours, the residue was filtered and washed with 30 ml water through a porous crucible (G4), dried at 105°C for 24 hr and weighed to evaluate the AIS. We used the filtrate (autoclaved sulphuric acid solution) for analysis of total carbohydrate (TCH) using the phenol–sulphuric acid method (Dubois, Gilles, Hamilton, Rebers, & Smith, 1956). We added 5% phenol (v/v) and 98% sulphuric acid (v/v) to the sulphuric acid solution derived from the hot sulphuric acid digestion, and then, the optical density of the solutions was measured using a spectrophotometer (490 nm) (UV-1800; Shimadzu Co., Kyoto, Japan) and compared with known concentrations of D-glucose as standards. We quantified the contents of P, K, Ca and Mg using an inductively coupled plasma atomic emission spectrometer (ICPE-9000; Shimadzu Co., Kyoto, Japan) after acid wet oxidation by gradual heating in hot plates with nitric acid and perchloric acid in the ratio of 2:1.

2.5 | Data analyses

To characterize and position each type of litter along a single axis of litter traits, we performed a principal components analysis (PCA) using multiple ln-transformed chemical trait data (Figure 1). The first axis (PC1), accounting for 71.7% of variance in litter quality, was strongly related to the contents of total C, lignin and other nutrients (N, P, K, Ca and Mg). The second axis (PC2), related to the content of TCH, accounted for only 13.2% of variance. We thus used the PC1 scores to represent a synthetic variable incorporating multiple trait variables as an index of litter quality in the subsequent analyses. We calculated mesofaunal contribution to mass loss as: (mass remaining in 42-μm-mesh bag – mass remaining in 1-mm-mesh bag)/mass remaining in 42-μm-mesh bag. To evaluate factors determining litter mass loss and mesofaunal contribution, we used linear mixed-effects models (LMM) with subplots and litter types as random effects. We used linear models because dependent variables take continuous values, and their variances are not influenced by average values. We checked for normality and homogeneity of the residuals by making a histogram of the standardized residuals and a graph of fitted values and standardized residuals, respectively (Supporting Information 6). To assess the determinants of litter mass loss, we included the following four single factors: elevation (four levels: 50, 400, 600 and 1,000 m elevation), litter quality, plant organ (two levels: leaf and root) and mesofauna (two levels: presence and absence), and their first-order interactions as fixed effects in the full model. For the mesofaunal contribution, we included the effects of elevation, plant organ, litter quality and their first-order interactions in the full model. We selected the most parsimonious models on the basis of backward stepwise regression using the likelihood ratio test for random effects (significance level: \( p < .1 \)) and the F test for fixed effects based on Satterthwaite’s approximation for denominator degrees of freedom (significance level: \( p < .05 \), but the lower order effects were not tested for significance if the highest order interactions were significant) (Bolker et al., 2009). To compare the relationships between litter traits and mesofaunal contribution to decomposition under different climate conditions, we ran the LMM with subplots and litter types as random effects for mesofaunal contribution as an independent variable for each elevation. We included two fixed effects (litter quality and plant organ) and their interaction for each elevation in the full model and selected the most parsimonious models as described above. The performance of the final models was assessed based on the marginal and conditional R squares, which indicate the proportion of variance explained by the fixed effects alone (\( R^2_m \)) and the proportion of variance explained by the whole model (\( R^2_c \)), respectively (Nakagawa & Schielzeth, 2013). There were no collinearities among explanatory variables except for the relationship between litter quality and plant organ (nested ANOVA with litter types nested, \( F = 109.4, \ p < .001 \)). All factors were standardized (\( M = 0, \ SD = 1 \)) before analysis. We used R software 3.0.2 (http://www.r-project.org/), with “vegan”, “lmerTest” and “MuMn” libraries.

**FIGURE 1** Plot of all types of litter ordinated by principal components analysis (PCA) using initial chemical trait data of both leaves and roots (Supporting Information 3) to produce the first axis (PC1) scores as a synthetic index of litter quality in the subsequent analyses. Species abbreviations are shown in Supporting Information 3. Filled circles and open circles show leaves and roots, respectively. Circle colour shows elevation: red, 50 m; green, 400 m; blue, 600 m; purple, 1,000 m.
3 | RESULTS

3.1 | The relative importance of elevation, litter quality and soil mesofauna for litter decomposition rate

The values of PC1 axis were largely different between plant organs (i.e., leaves and roots) instead of between elevations (Figure 1). Coniferous litter exhibited low quality (high lignin and low nutrient content) both for leaves and roots (Supporting Information 3). The range in litter quality of the eight predominant species at each elevation overlapped across elevations for both leaf and root litter, except for root litter at 1,000 m (Figure 2b). As determinants of litter mass loss, all single variables, that is, elevation, litter quality, plant organ and mesofauna, were selected in the final model ($R^2_m = .86, R^2_c = .95$, Table 2). The effects of litter quality, plant organ and presence vs. absence of mesofauna on decomposition were stronger than that of elevation (Table 2). The average value for litter mass loss of the eight predominant species at each elevation was consistently higher for leaf litter than for root litter across elevations (Figure 2c). On the other hand, neither the change in mass loss of leaf litter nor that of root litter showed a consistent trend with elevation (Figure 2c); this was also observed for litter quality in terms of trait composition (Figure 2b), contrary to our hypothesis. Significant and strong correlation between litter quality and mass loss was found both within (Figure 2a; Pearson’s correlation coefficient; $50 \text{ m}, r = -.93, p < .001; 400 \text{ m}, r = -.90, p < .001; 600 \text{ m}, r = -.96, p < .001; 1,000 \text{ m}, r = -.92, p < .001$) and across the elevational gradient (Figure 2a; Pearson’s correlation coefficient; $r = -.92, p < .001$). Mass loss was larger in nutrient-rich litter than in recalcitrant litter with high lignin content, regardless of the elevation. The effect of presence vs. absence of mesofauna on both leaf and root decomposition was generally positive at each elevation except for root decomposition at 600 m (Figure 2c). The effect of presence of mesofauna interacted significantly with litter quality and elevation (Table 2).

3.2 | Determinants of mesofaunal contribution to decomposition across and within elevations

The contribution of soil mesofauna to litter mass loss was regulated by litter traits rather than by the elevational gradient, because the final model ($R^2_m = .30, R^2_c = .65$) only included the fixed factors related to litter quality and plant organ (Table 2). The much higher value of $R^2_c$ than $R^2_m$ indicates that the variance of the dependent variable was well explained by random factors. The mesofaunal contribution was higher in nutrient-rich litter than in recalcitrant litter including root litter across the entire elevational gradient (Figure 3a; Pearson’s correlation coefficient; $r = -.57, p < .0001$). However, the interaction between litter quality and plant organ was also selected in the final model (Table 2), and the effect of litter quality on mesofaunal contribution showed different patterns between plant organs (Figure 3a; Pearson’s correlation coefficient; leaves, $r = -.55, p < .01$; roots, $r = .58, p < .001$). The effect of elevation on mesofaunal contribution was not selected in the final model (Table 2), but the average value of mesofaunal contribution tended to be larger at higher sites (Figure 3b). The relationships between litter quality and mesofaunal contribution within each elevation showed that mesofaunal contribution tended to be higher in nutrient-rich litter than in recalcitrant litter including root litter for all elevations (Supporting Information 7). This correlation between litter quality and mesofaunal contribution was stronger at high elevation sites (Supporting Information 7a; Pearson’s correlation coefficient; $50 \text{ m}, r = -.61, p < .05; 400 \text{ m}, r = -.38, \text{ ns}; 600 \text{ m}, r = -.72, p < .01; 1,000 \text{ m}, r = -.70, p < .01$; Supporting Information 7b).

4 | DISCUSSION

Our in situ litterbag experiment using an elevational gradient to mimic future climate change is the first attempt to examine the contribution of mesofauna to both leaf and root decomposition of multiple plant species under different climatic conditions. We found strong effects of plant litter quality rather than elevation on both litter decomposition rates and the mesofaunal contribution thereto, leading to a contradiction to our hypotheses. We will discuss below how our findings shed new light on the non-negligible roles of soil mesofauna as regulators of decomposition through strong interactions with litter quality.

4.1 | Stronger control of decomposition by litter quality than climate

Temperature is a well-known driver of litter decomposition, and litter mass loss rates are often greater at lower latitudes (Berg et al., 1993) or at lower elevations due to warmer conditions (Sundqvist et al., 2013). Our control experiment using filter paper, that is a substrate of a constant quality, showed that decomposition rates increased as elevation decreased for both above-ground and below-ground decomposition (Supporting Information 5), supporting findings from previous decomposition experiments using the same litter material across elevations (Salinas et al., 2011; Vitousek et al., 1994; Wang, Ruan, & Han, 2010). While soil variables may have played a role as well (see below), climatic factors, notably temperature, were likely direct drivers of decomposition along this gradient.

On the other hand, the elevational effects on decomposition were not clear in our in situ litterbag experiment using diverse species, which means that the effect of litter quality on decomposition dominated over the climate effect (Table 2). First, we hypothesized that a decline in temperature with increasing elevation produces poor-quality litter (Kitayama et al., 2004; Tanner et al., 1998; Vitousek et al., 1994), which would amplify the decline in decomposition rate with elevation. However, changes in litter quality of the dominant tree species were not consistently explained by the elevational gradient, and the ranges of litter quality mostly overlapped across elevations for both leaf and root litter. While temperature can strongly influence the structure of plant communities along a mountain slope by affecting plant photosynthesis and metabolism (Hoch & Körner, 2012) as well as by possible changes in soil nutrient availability with increasing elevation, it is likely that mesofauna adds another level of control to decomposition along a gradient.

In conclusion, our results suggest that both mesofauna and litter quality play a major role in the decomposition of different species under different climatic conditions. Mesofauna showed a significant positive effect on decomposition across elevations, except at 600 m. The importance of mesofauna and litter quality suggests that the decomposition of litter is likely to be strongly controlled by the quality of the litter itself and the presence of mesofauna, while elevation shows a smaller and less consistent effect. These findings have implications for the future of decomposition processes in mountain ecosystems as climate changes and elevational gradients are modified.
responded to other abiotic (e.g. moisture) or biotic factors (e.g. microbial community composition) that varied in idiosyncratic ways with elevation (Supporting Information 2). These multiple, possibly interacting environmental factors together might have resulted in the large variation in litter quality through enabling various species to coexist at each elevation. This variation could have overruled the small differences in average litter quality across elevations, which may explain why litter quality effects per se were dominant in this study; especially for leaf litter, dominance of evergreen coniferous/broadleaf species, which produce recalcitrant leaf litter (Cornwell et al., 2008), at lower elevation could also cancel out any underlying pattern of decline in litter quality with elevation. While climate has long been considered the primary broadscale control on decomposition rates, recent evidence has suggested that litter traits often predominate at local to regional scale (Bradford et al., 2016; Cornwell et al., 2008; Makkonen et al., 2012). Although the relative importance between climate and litter traits on decomposition is still debated because it depends on spatial scale and range of trait variability (Bradford et al., 2016), our results emphasize the importance of considering functional traits of plants actually living under natural conditions to predict shifts in decomposition in response to climate changes.

Furthermore, using both leaf and root litter contributed greatly to the dominant effects of litter quality on decomposition. Litter quality and decomposition rate varied between leaves and roots as much or more compared to the variation in leaf litter quality and decomposition rate within and across elevations (Figure 2b,c). Still, within the leaf subset there was a strong correlation between mass loss and litter quality (Supporting Information 8a,c,e). In contrast, roots were generally...
of low litter quality with a smaller range of values and showed a less clear trend with mass loss, although litter quality was selected as a significant factor affecting mass loss (Supporting Information 8b,d,f). Indeed, decomposition rates of root litter below-ground were lower than those of leaf litter on top of the soil surface at all elevations, even though below-ground decomposition was consistently more rapid than above-ground decomposition when we compared the same litter substrates (i.e. sheets of cellulose filter paper) (Supporting Information 5). This means that the effects of litter quality between leaves and roots were so strong that they overruled the effects of soil depth position on decomposition (see Freschet et al., 2013; Fujii & Takeda, 2010). Considering that nutrient resorption efficiencies are higher in leaves than in fine roots (Freschet et al., 2010a), the difference between leaf and root litter quality in this experiment, using fresh materials, might have been somewhat amplified. However, the strong effects of litter quality as well as the difference between leaf and root litter were retained even if the nutrients strongly related to resorption were excluded from litter chemical trait data (Supporting Information 4). Thus, our results demonstrate the importance of considering litter of other plant organs than just leaves to assess the effects of plants on decomposition along environmental gradients.

4.2 Soil mesofaunal contribution to decomposition interacts with litter quality and elevation effects

Our study has shown that mesofauna have positive effects on litter decomposition irrespective of the strong abiotic variation across the elevational gradient (Table 2). This relative importance of the mesofaunal contribution against climate seemed to be larger compared to previous studies including multiple climatic conditions (Garcia-Palacios et al., 2013; Makkonen et al., 2012). This may be because the influence of local-scale factors on mass loss was large due to the large variation in plant litter quality within elevations. Indeed, the mesofaunal contribution was strongly regulated by litter traits, being higher in nutrient-rich and less lignified litter than in recalcitrant litter across elevations (Figure 3a). This finding supports some previous empirical evidence for the mesofaunal contribution (Fujii et al., 2016a; Schädler & Brandl, 2005) and shows an analogy with the contribution of (meso- and) macrofauna to decomposition (Coq, Souquet, Meudec, Cheynier, & Hattenschwiler, 2010; Garcia-Palacios et al., 2013; Liu et al., 2015). However, other papers reported a greater role for mesofauna in more recalcitrant litter or nutrient-poorer sites (Milcu & Manning, 2011; Perez et al., 2013; Yang & Chen, 2009). We offer

<table>
<thead>
<tr>
<th>Litter mass loss</th>
<th>Litter type</th>
<th>Random effects</th>
<th>Chi.sq</th>
<th>Chi.df</th>
<th>p</th>
<th>Fixed effects</th>
<th>Sum.sq</th>
<th>df</th>
<th>F value</th>
<th>p</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subplot</td>
<td>19.40</td>
<td>1</td>
<td>.0000</td>
<td>Elevation</td>
<td>0.08</td>
<td>63</td>
<td>1.68</td>
<td>.1992</td>
<td>-0.053</td>
<td>0.041</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(R²m = .86)</td>
<td>Litter quality</td>
<td>959.54</td>
<td>1</td>
<td>.0000</td>
<td>3.39</td>
<td>60</td>
<td>68.48</td>
<td>.0000</td>
<td>-0.603</td>
<td>0.073</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(R²m = .95)</td>
<td>Plant organ (leaf/root)</td>
<td>1.15</td>
<td>59</td>
<td>23.27</td>
<td>.0000</td>
<td>-0.335</td>
<td>0.069</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesofauna (presence/absence)</td>
<td>9.06</td>
<td>1,175</td>
<td>182.76</td>
<td>.0000</td>
<td>0.084</td>
<td>0.006</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation: Litter quality</td>
<td>0.15</td>
<td>57</td>
<td>2.94</td>
<td>.0919</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation: Plant organ</td>
<td>0.12</td>
<td>58</td>
<td>2.38</td>
<td>.1283</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation: Mesofauna</td>
<td>1.41</td>
<td>1,175</td>
<td>28.37</td>
<td>.0000</td>
<td>0.033</td>
<td>0.006</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter quality: Plant organ</td>
<td>0.41</td>
<td>59</td>
<td>8.22</td>
<td>.0057</td>
<td>0.214</td>
<td>0.075</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter quality: Mesofauna</td>
<td>3.43</td>
<td>1,175</td>
<td>69.23</td>
<td>.0000</td>
<td>-0.052</td>
<td>0.006</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant organ: Mesofauna</td>
<td>0.16</td>
<td>1,174</td>
<td>3.17</td>
<td>.0751</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesofaunal contribution</td>
<td>Subplot</td>
<td>4.22</td>
<td>1</td>
<td>.0400</td>
<td>Elevation</td>
<td>0.15</td>
<td>63</td>
<td>0.40</td>
<td>.5276</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(R²m = .30)</td>
<td>Litter type</td>
<td>260.79</td>
<td>1</td>
<td>.0000</td>
<td>Litter quality</td>
<td>0.71</td>
<td>61</td>
<td>1.98</td>
<td>.1641</td>
<td>-0.205</td>
<td>0.146</td>
<td></td>
</tr>
<tr>
<td>(R²m = .65)</td>
<td>Plant organ (leaf/root)</td>
<td>0.88</td>
<td>60</td>
<td>2.45</td>
<td>.1228</td>
<td>-0.219</td>
<td>0.140</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation: Litter quality</td>
<td>0.36</td>
<td>58</td>
<td>0.99</td>
<td>.3232</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation: Plant organ</td>
<td>0.06</td>
<td>57</td>
<td>0.16</td>
<td>.6893</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter quality: Plant organ</td>
<td>5.04</td>
<td>60</td>
<td>14.00</td>
<td>.0004</td>
<td>0.545</td>
<td>0.146</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
three plausible explanations for this inconsistency among studies. First, interaction between nutritional status of litter and site can affect faunal contribution (Milcu & Manning, 2011; Perez et al., 2013). Faunal food preference and the subsequent contribution to decomposition could vary with their stoichiometric constraints as determined by soil nutrient condition (Marichal et al., 2011; Martinson et al., 2008); for example, soil fauna might choose easily decomposable (i.e. non-recalcitrant and nutrient-rich) litter in nutrient-limited environments such as late-successional forests. This phenomenon can also be caused by energy limitation in soil (Hättenschwiler, Coq, Barantal, & Handa, 2011; Orwin, Wardle, & Greenfield, 2006), as decomposition of recalcitrant compounds is often controlled by available, labile C compounds including root exudates (Fontaine et al., 2007; Kuzyakov, 2010). Second, the contribution of a specific faunal group can be altered by the soil community structure or interactions within/among trophic levels in the site (González & Seastedt, 2001). High variability of mesofaunal feeding attributes including both microbivores and detritivores can also amplify this complexity (Rusek, 1998). Litter accumulation in nutrient-poor sites can provide much habitat for soil mesofauna, which can enhance the faunal contribution to decomposition through an increase in faunal abundance or diversity (Perez et al., 2013). Third, different timing of sampling among studies also creates inconsistencies, because determinants of decomposition including faunal effects shift along decomposition stages (Fujii et al., 2016a; García-Palacios et al., 2016; Smith & Bradford, 2003). Testing these or further hypotheses is still needed to better understand the apparent context dependence of the interactive effects of mesofauna and litter quality on decomposition.

The greater importance of litter quality than climatic regulation for the contribution of mesofauna to litter decomposition may be partly due to inclusion of root litter in our study, which mostly had lower litter quality compared to leaf litter and made the overall range of litter quality broader. Actually, the effect of elevation on mesofaunal contribution was detected in root decomposition if we analysed the data separately for leaf and root material (Supporting Information 8), although the effects of litter quality were still stronger than that of elevation for both leaf and root decomposition. The contribution of mesofauna to root decomposition was lower than that to leaf decomposition (Figure 3a), which supports a previous study comparing mesofaunal effects on leaf and root decomposition in a warm-temperate forest (Fujii et al., 2016a). However, there was significant interaction between the effects of litter quality and plant organ on the mesofaunal contribution to decomposition (Table 2): the mesofaunal contribution was higher in nutrient-rich litter for leaves, while it was higher in recalcitrant litter for roots. Besides the lower nutrient and higher lignin concentrations in root than in leaf litter (Figure 1), there are differences in chemical composition and tissue structure; for example, roots possess an epidermis and exodermis high in lignin and suberin, which protect inner nutrient-rich tissues against microbial attack (Esau, 1964; Fujii & Takeda, 2010). Substrate differences including structural properties can attract different faunal communities colonizing decomposing litter (Fujii & Takeda, 2012, 2017), likely leading to the different relationships between litter quality and mesofaunal contribution. The different vertical spatial positions (i.e. on vs. in the soil) of the litter can also have led to the different contributions of mesofauna to the decomposition of leaves and roots, because faunal species composition as
well as microclimate is different between above-ground and below-ground (Berg, Kniese, Bedaux, & Verhoef, 1998; Fujii & Takeda, 2010; Krab, Oorspong, Berg, & Cornelissen, 2010). However, litter traits were probably still the predominant factor to determine mesofaunal function in our study, because there were no significant effects of mesofauna on mass loss of filter paper, that is a substrate with a constant quality, neither when incubated above-ground nor below-ground (Supporting Information 5). Fujii and Takeda (2017) showed that over two times more soil mesofauna were involved in root decomposition than in leaf decomposition and that especially oribatid mites, which include species to tunnel into coniferous needles or woody substrates and ingest the internal mesophyll, are primarily involved in root litter decomposition. While in our and most previous studies the mesofaunal contribution has been derived indirectly from exclusion treatments via mesh size, a deeper understanding would benefit from combining such experiments with direct identification and quantification of the actual fauna involved in litter decomposition.

Although the direction of litter quality effects on the mesofaunal contribution to decomposition was similar among elevational sites (i.e. lack of interaction between elevation and litter quality on mesofaunal contribution across elevations; Table 2), the correlation between litter quality and contribution of mesofauna within elevation tended to be stronger at the higher elevations (Supporting Information 7). This contradicted our hypothesis, that the faunal contribution to decomposition should be higher under warmer climatic conditions, such as in tropical biomes (González & Seastedt, 2001; Makkonen et al., 2012; Wall et al., 2008) and at low elevations (Wang et al., 2009, 2010). Indeed, faunal functioning has been considered to be strong in environments where biological activity is less constrained by climatic factors (Lavelle et al., 1993; Swift et al., 1979). However, the nutrient status of soil can also affect soil fauna as mentioned above (Lavelle et al., 1993). Soil nitrogen content is generally low in tropical areas (Chapin et al., 2011), and Wang et al. (2010) also showed that lower elevational areas exhibited lower soil fertility. In the present study, inorganic N content was lower at higher elevations (Table 1; Supporting Information 2), as most of the previous studies showed (Sundqvist et al., 2013). In view of the above, the soil faunal contribution to decomposition may increase under low soil fertility, where microbial activities are limited and soil organic matter can accumulate, as characterized by the relatively high soil carbon content, lower soil pH and higher soil water-holding capacity at the high (1,000 m) elevation site in our study (Supporting Information 2). Our findings certainly merit in-depth study of the importance of other environmental factors in addition to temperature as regulators of interactive effects of litter quality and mesofauna on decomposition.

While our in situ litterbag experiment has elucidated plausible decomposition patterns for both leaf and root litter of many species under natural conditions, as an important first step to predict changes under climate change, some caveats are necessary. With our method, we could not assess the relative importance of various determinant factors (i.e. climate, litter trait, soil community and soil properties) strictly, because they interact and covary. In addition, we did not focus on the impact of soil community composition, which although smaller than other factors, can change with climate and the accompanying plant community (Fanin & Bertrand, 2016; Fujii et al., 2017; Keiser & Bradford, 2017). Further analyses combining the soil community composition and fully factorial studies considering litter substrates of different organs, which was the most important contributor to variance in litter traits and decomposition rates, will be necessary to disentangle the mechanisms underpinning the patterns observed here.

### 4.3 The role of soil mesofauna in decomposition in future climates

Our study has shown stronger regulation of the faunal contribution to decomposition by plant litter quality than by climate. The larger contribution of mesofauna to decomposition rates in nutrient-rich than in recalcitrant litter means that the effects of plant litter traits on decomposition might be emphasized through the preference of soil fauna for high-quality, palatable food resources. If increasing temperature might enhance plant litter quality (i.e. richer in nutrients and lower in lignin) in the future (Tanner et al., 1998; Vitousek et al., 1994), according to our findings the faunal contribution to decomposition might increase. However, a broad range of litter traits will remain under global warming, partly because litter quality diverges strongly between leaf and root litter (and woody debris, not studied here) regardless of plant species and elevation. In that case, soil fauna will contribute to decomposition mainly by positive feedback to the effects of litter quality as influenced by soil temperature, moisture or nutritional regimes. Recent recognition of the predominance of litter quality effects on decomposition within sites and regions at larger spatial scales (Bradford et al., 2016; Cornwell et al., 2008) may eventually mean that there can be more significant impact of mesofauna on decomposition than previously expected. Thus, the faunal feedback to decomposition, via shifts in biological communities in response to climate changes, may need to be incorporated into global decomposition models for better predictions of decomposition rates as the climate changes.

### ACKNOWLEDGEMENTS

This study was supported by the Mitsui & Co., Ltd. Environment Fund, the Japanese Ministry of Education, Culture and Sports (No. 23770083), and a JSPS Fellowship for Japanese Young Scientists (No. 25850115 and No. 13J00547). SF was funded by a JSPS Overseas Research Fellowship (No. 847, 2015–2017). Logistical support for the field study was provided by the Shiretoko Foundation. We thank Mizuki Maeda and laboratory members at Yokohama National University for their assistance with field and laboratory work. We thank Dr. Toko Tanikawa for her support with chemical analyses. The authors have no conflicts of interest to declare.

### AUTHOR’S CONTRIBUTIONS

S.F. conceived the ideas and designed the methodology. S.F. and A.S.M. set up the experiment and mainly collected the data, but all authors joined the field sampling. S.F. analysed the data and wrote the manuscript with critical inputs from J.H.C.C., M.P.B. and A.S.M.
DATA ACCESSIBILITY

All litter decomposition data were archived in Dryad Digital Repository https://doi.org/10.5061/dryad.q09g2 (Fujii, Cornelissen, Berg, & Mori, 2018).

ORCID

Saori Fujii http://orcid.org/0000-0002-2501-5626
Akira S. Mori http://orcid.org/0000-0002-8422-1198

REFERENCES


Sundqvist, M. K., Giesler, R., & Wardle, D. A. (2011). Within- and across-


FUJI ET AL.

How to cite this article: Fuji S, Cornelissen JHC, Berg MP, Mori AS. Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. Funct Ecol. 2018;32:840–852. https://doi.org/10.1111/1365-2435.13027

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.