Ecological Research

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RESEARCH ARTICLE OPEN ACCESS

Leaf Litter Decomposition Along an Elevation Gradient Across Two Contrasting Forest Types: Implications for Future Climate Change

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Received: 31 March 2025 | **Revised:** 24 August 2025 | **Accepted:** 11 October 2025

Keywords: climate change | decomposition rate per unit cumulative temperature | elevation | functional trait | soil

ABSTRACT

Understanding elevational changes in ecosystem processes is important for predicting ecosystem responses to global warming. Plant litter decomposition is expected to increase with increasing temperature as elevation decreases. However, how decomposition varies along elevation gradients within and across forests dominated by different species remains unclear. We investigated in situ and downward-transplanted leaf litter decomposition of two dominant species, deciduous broad-leaved beech (*Fagus crenata*) dominating at lower elevations and evergreen coniferous Maries fir (*Abies mariesii*) dominating at higher elevations, in a montane range. For the downward-transplanted treatment, litter from the highest elevation of each species' distribution was decomposed at lower elevations. Elevational changes in soil properties and litter traits of the two species were measured alongside. Within each species' range, the in situ decomposition generally increased with decreasing elevation, and the slopes of these relationships were not altered by the species-specific elevational changes in litter traits. In contrast, the decomposition of *A. mariesii* litter was more temperature-sensitive than that of *F. crenata*. Across forest types, *A. mariesii* at higher elevations had a greater in situ decomposition rate than *F. crenata*, possibly due to its lower lignin content compared to *F. crenata*. When the transplanted litter of *A. mariesii* was decomposed in *F. crenata*-dominated forests, its decomposition rate dropped to a level similar to *F. crenata* despite warmer conditions and its lower lignin. This study underscores the significance of considering plant traits and plant–soil interactions in predicting the responses of carbon and nutrient cycles in forest ecosystems to future climate change.

1 | Introduction

Understanding the responses of ecosystems to environmental changes is crucial for predicting the effects of future climate changes on ecosystem functioning. To predict the long-term, large-scale responses of communities and ecosystems to climate change, many studies have investigated changes in above- and below-ground species, communities, and ecosystem processes along elevation gradients because air temperature often changes linearly with elevation (Bahram et al. 2012; Berger et al. 2015; Djukic et al. 2010; Körner 1989; Körner 2007; Mayor et al. 2017; Salinas et al. 2011; Sundqvist et al. 2013). Litter decomposition, one of the fundamental biogeochemical processes in carbon and nutrient cycles in plant and soil systems, is expected to be faster at lower elevations with warmer conditions (Salinas et al. 2011; Vitousek et al. 1994; Wang et al. 2010) because metabolic activity is enhanced under warmer conditions (Prescott 2010). However, litter decomposition is also directly affected by litter traits and soil properties, which can vary across and within plant species or vegetation types (Berger et al. 2015). For example, nutrient concentration in leaf litter is often positively correlated with decomposition rate, while leaf mass per area (LMA) or recalcitrant chemicals such as lignin and phenolics are negatively correlated with decomposition in many ecosystems (Cornwell et al. 2008). Higher soil moisture and decomposer abundance, activity, and diversity can enhance decomposition, while higher soil pH may retard it (Coûteaux et al. 1995; Gavazov 2010; Berg and McClaugherty 2003; Kitz et al. 2015).

Higher elevations are often associated with stress-tolerant plant characteristics due to relatively harsh conditions (e.g., low temperature, low nutrient availability, strong wind) (Sundqvist et al. 2013). In general, with increasing elevation, LMA increases (Hikosaka et al. 2002; Salinas et al. 2011; Sundqvist et al. 2011) and foliar nutrient content decreases (Körner 1989; Salinas et al. 2011; Tanner et al. 1998; Vitousek et al. 1988) across and within species. Some anti-herbivore or structural chemicals, such as total phenolics, condensed tannins, and lignin, are also hypothesized to have greater concentrations in plant tissues at higher elevations, because plants in nutrient-poor, harsh conditions tend to have greater concentrations of them (Coley et al. 1985). These functional trait changes with elevation could slow decomposition at higher elevations. However, changes in leaf and litter traits with elevation can vary depending on plant species or vegetation type (De Long et al. 2015; Salinas et al. 2011; Sundqvist et al. 2011). Along an elevation gradient in northern Japan, Hikosaka et al. (2021) found contrasting trends in leaf traits between two dominant tree species. In *Fagus crenata* Blume, which dominates at lower elevations, LMA increased with elevation, while foliar nitrogen (N) decreased. In contrast, in *Abies mariesii* Mast., which dominates at higher elevations, LMA decreased with elevation, but foliar N remained unchanged. Notably, *A. mariesii* exhibited a much higher overall LMA than *F. crenata*. Similarly, Sundqvist et al. (2012) showed that concentrations of total phenolics and tannins in some species increased, decreased, or remained unchanged along an elevation gradient in northern Sweden. Thus, the elevational dependence of leaf litter decomposition can differ depending on species or vegetation type, especially across different vegetation types with distinct traits (Sundqvist et al. 2011; Mayor et al. 2017). Further, soil biotic and abiotic properties which affect decomposition may vary with elevation. Soil moisture is often reported to increase, and soil pH to decrease, with increasing elevation (Griffiths et al. 2009; Smith et al. 2002; Tsui et al. 2004). The ratio of fungal to bacterial biomass in soils, which is an indicator of substrate quality, can increase with elevation associated with low temperature and less decomposable organic matter (Pietikäinen et al. 2005; Wagai et al. 2011; Wardle et al. 2004). It is therefore important to investigate the response of leaf litter decomposition to elevational gradients together with leaf litter traits and soil properties to better understand how decomposition will respond to future climate changes.

In this study, we investigated leaf litter decomposition along an elevation gradient in the Hakkoda mountains in northern Honshu, Japan. In those mountains, the vegetation type shifts drastically with increasing elevation from cool temperate deciduous broad-leaved forests dominated by *F. crenata* to subalpine evergreen coniferous forests dominated by *A. mariesii*, with mixed forests in transition zones (Hikosaka et al. 2021). The objective of this study was to elucidate how the leaf litter decomposition rates of two contrasting dominant species change with elevation within and across species, and how the elevational pattern is modified depending on soil properties (e.g., pH, moisture, and fungi to bacteria ratio) and leaf litter chemicals (e.g., N, lignin, and phenolics), which may affect decomposition. We conducted two types of litter-bag experiments (Figure 1). By incubating the leaf litter of the dominant species in situ (Figure 1a), we evaluated the natural decomposition rates along an elevation gradient. By incubating the transplanted leaf litter from the highest elevation for each dominant species translocated downward within the same forest types and in the *F. crenata*-dominated forests for *A. mariesii* (Figure 1b), we evaluated the effect of warming on litter decomposition independent of intraspecific changes in litter traits associated with elevation. As well as the usual calculation of decomposition rate per unit time, the decomposition rate was calculated relative to cumulative temperature (i.e., temperature-independent decomposition rate) during the experiment, to reveal the effects of leaf litter traits and soil properties on decomposition independent of temperature. We hypothesized that: (1) Within each species, the natural decomposition rate (i.e., the in situ decomposition rate per unit time) generally increases with decreasing elevation. However, the slope of this increase may vary among species, being either steepened or flattened by species-specific elevational changes in leaf litter traits. (2) Across species, the in situ decomposition rate per unit time is slower for *A. mariesii* than for *F. crenata* because *A. mariesii* naturally occurs at higher elevations with colder conditions and has a much higher LMA than *F. crenata* (Hikosaka et al. 2021). (3) For both species, the transplanted decomposition rate per unit time increases at lower-elevation plots, likely due to the warmer conditions, even for *A. mariesii* decomposing in the *F. crenata*-dominated forests. (4) Across species, the slower decomposition rate of *A. mariesii* persists in the temperature-independent decomposition of both in situ and transplanted litter, although the interspecific difference is reduced compared to decomposition influenced by temperature. We also investigated how temperature, leaf litter traits, and soil properties affect the natural decomposition rates along the elevation gradient.

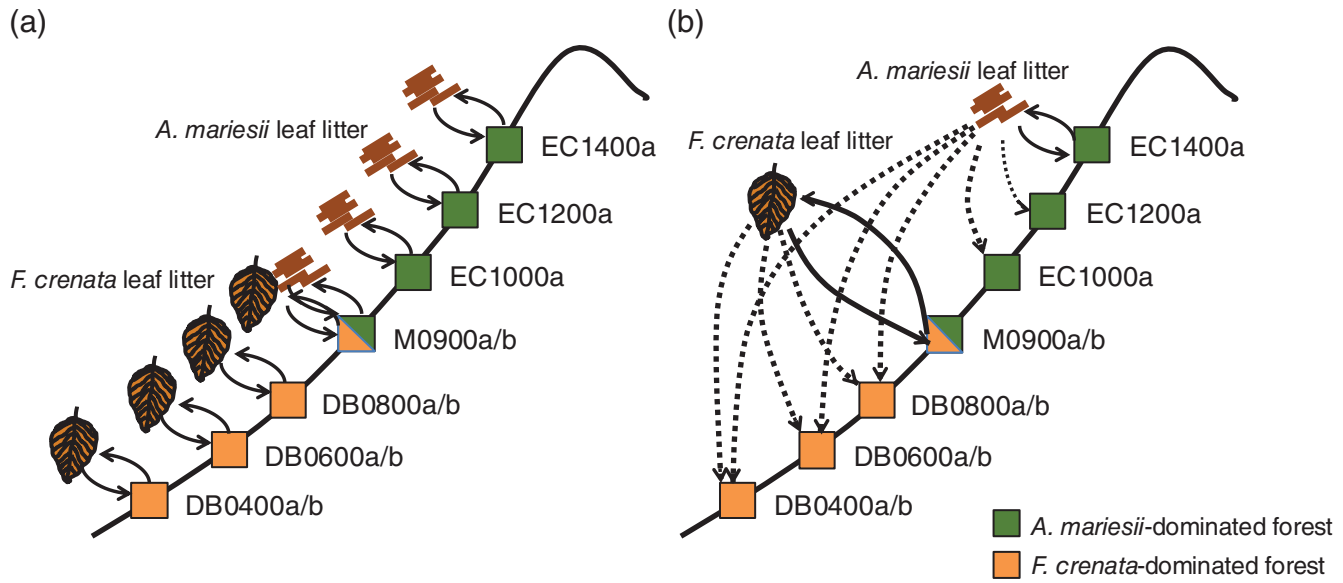

FIGURE 1 | Two types of litter-bag experiments in this study. (a) The leaf litter of each dominant species was decomposed in the same plots where the leaf litter samples collected (in situ litter-bag experiment). (b) The transplanted leaf litter from the highest elevation for each dominant species was decomposed downward within the same forest types (indicated by dotted arrows) and in the *Fagus crenata*-dominated forests for *Abies mariesii* leaf litter (transplanted litter-bag experiment).

2 | Material and Methods

2.1 | Study Site and Plant Species

The study site is in the Hakkoda mountains in Aomori Prefecture, northern Honshu, Japan. The Hakkoda mountains include several peaks higher than 1200 m above sea level, and the highest one (Mt. Ohdake, 40°41′ N, 140°52′ E) is 1584 m. The annual mean temperature, annual precipitation, and maximum snow depth between 1990 and 2009 at the Sukayu meteorological station (40°39′ N, 140°51′ E, 900 m) ranged from 4°C to 6°C, 1300–2300 mm year^{-1}, and 3–5 m, respectively (Nakashizuka et al. 2016; Shimazaki et al. 2011). Snow cover disappears in late April at elevations from 400 to 600 m but remains in June above 1200 m. In these mountains, the natural vegetation is relatively well preserved above 300 m. At elevations from 400 to 800 m, deciduous broad-leaved forests are dominated by *F. crenata*, and at altitudes from 1000 to 1400 m, subalpine coniferous forests are dominated by *A. mariesii*, with mixed forests dominated by both species in transition zones from 800 to 1000 m. Dwarf bamboo, *Sasa kurilensis* (Rupr.) Makino and Shibata, dominates the forest understory, especially at higher elevations.

In this area, we established a total of 14 permanent research plots (0.05–0.25 ha) (Figure S1 and Table 1). Seven of these plots were located on the west slope of Mt. Akakura, spanning over different forest types along an elevation gradient (line a). In the deciduous broad-leaved (DB) forests, plots DB0400a, DB0600a, and DB0800a were situated at elevations of 400, 600, and 800 m, respectively. A transitional plot (M0900a) was located at approximately 900 m in a mixed (M) forest. In the evergreen coniferous (EC) forests, plots EC1000a, EC1200a, and EC1400a were positioned at 1000, 1200, and 1400 m, respectively. Another seven plots (line b: DB0400b, DB0600b, and DB0800b in the DB forests, M0900b in the mixed forests, and EC1000b, EC1200b, and EC1400b in the EC forests) were located on the east slope of Mt. Takada-Otake with the same elevation intervals in line a. In these plots, a summer tree census was conducted annually from 2007 to 2019. The litter fall was collected monthly during the growing season (from July to October or November depending on elevation) by using 5 litter traps (each with an area of 0.5 m^2) set every 10 m in each plot from 2009 to 2012. The litter was sorted into *F. crenata* leaf litter, *A. mariesii* leaf litter, reproductive organs of each species, and other deciduous leaf litter, for dry weight determination. The temperature on the soil surface in each plot was measured (Hobo Pendant, Onset Computer Corporation, Bourne, MA, USA) hourly from October 2009 to November 2012. Based on the soil surface temperature, we deduced the starting and ending dates for snow cover each year; the soil surface temperature is stable around 0°C during snow cover. We calculated the duration (days) of the growing season as days without snow cover. We also calculated the mean annual soil temperature (MAT) through the years, and the mean and cumulative daily-mean soil temperatures during the growing season (MTG and CTG, respectively; Table 1). The range of MAT within each forest type along the elevation gradient is about 2°C, which is comparable to the temperature increase predicted by the year 2100 (IPCC 2023). MAT, MTG, and CTG decrease linearly with elevation (Pearson's correlation coefficients are −0.964, −0.918, and −0.964 for $n = 14$, respectively).

2.2 | Soil Property Measurements

Soil samples were collected at three subplots in each plot (the three subplots were apart at least 10 m from each other) during the mid-growing season in August 2013. Surface mineral soils were collected from 0 to 5 cm depth with a soil core (φ50 × 51 mm, DIK-1801; Daiki Rika Kogyo Co. Ltd., Japan) and kept refrigerated until further processing. Samples were sieved through a 4 mm mesh to avoid destroying soil

TABLE 1 | Plot description with climatic and vegetation parameters.

Plot	Elevation (m)	MAT (°C)	Growth duration (days)	Snow cover start date	Snow melt date	MTG (°C)	CTG (°C)	Dominant species	Total basal area (cm^2/ha)	Leaf litter fall (t/ha)
DB0400a	491	8.46 (0.20)	215 (4.73)	6 Dec	11 May	13.8 (0.09)	3092 (70.6)	*Fagus crenata*	40.2	1.66
DB0400b	379	8.96 (0.19)	232 (9.91)	5 Dec	22 Apr	13.6 (0.26)	3273 (67.1)	*F. crenata*	43.4	1.34
DB0600a	600	7.50 (0.28)	192 (10.50)	29 Nov	26 May	13.7 (0.16)	2738 (102.0)	*F. crenata*	47.1	2.08
DB0600b	636	7.86 (0.22)	213 (6.93)	6 Dec	12 May	13.0 (0.06)	2871 (79.3)	*F. crenata*	52.0	2.28
DB0800a	805	7.36 (0.33)	194 (11.80)	26 Nov	26 May	13.1 (0.11)	2689 (119.0)	*F. crenata*	47.0	1.46
DB0800b	776	7.01 (0.28)	191 (9.24)	1 Dec	31 May	12.8 (0.16)	2560 (101.0)	*F. crenata*	47.3	1.74
M0900a	911	6.92 (0.21)	181 (7.09)	22 Nov	2 Jun	13.4 (0.49)	2527 (76.9)	*F. crenata*/*Abies mariesii*	30.0	1.46
M0900b	891	6.09 (0.26)	169 (5.77)	24 Nov	13 Jun	12.5 (0.16)	2225 (92.2)	*F. crenata*/*A. mariesii*	54.7	1.96
EC1000a	985	6.47 (0.12)	197 (9.02)	26 Nov	19 May	11.6 (0.23)	2364 (45.8)	*A. mariesii*	30.8	1.39
EC1000b	971	6.22 (0.19)	179 (6.24)	25 Nov	6 Jun	12.1 (0.20)	2274 (68.1)	*A. mariesii*	43.2	1.04
EC1200a	1200	5.54 (0.16)	180 (2.03)	15 Nov	25 May	11.2 (0.38)	2046 (59.5)	*A. mariesii*	23.2	0.57
EC1200b[a]	1213	6.00 (0.18)	202 (3.21)	23 Nov	12 May	10.7 (0.33)	2206 (53.0)	*A. mariesii*	29.5	NA
EC1400a	1312	4.93 (0.18)	176 (1.76)	15 Nov	24 May	10.5 (0.39)	1884 (52.0)	*A. mariesii*	22.1	0.55
EC1400b	1440	5.09 (NA)	163 (NA)	5 Nov	25 May	10.9 (NA)	1863 (NA)	*A. mariesii*	29.3	0.72

Note: The letters DB, M, and EC in the plot names stand for deciduous broad-leaved forest, mixed forest, and evergreen coniferous forest, respectively. The letters a or b at the end of each plot name indicate lines a or b in which the plots were set up (Figure S1). Growth duration is the length of the growing season without snow cover. The values for MAT, growth duration, snow-cover start date, snow melt date, MTG, and CTG are means and standard errors (in parentheses) for 3 years of observations (2009–2012) during the litter bag experiments. Total basal area and leaf litter fall were obtained in 2011. Plot size varied from 0.05 to 0.25 ha depending on the situation in each forest.
Abbreviations: CTG: mean annual cumulative daily-mean soil temperature during the growing season; MAT: mean annual soil temperature; MTG: mean soil temperature during the growing season; NA: not available.
[a]Data of EC1200b for 2012 was obtained in a newly established plot because EC1200b was moved in summer 2012 due to the difficulty of access to the old plot. Data of EC1400b was available only for 2012.

aggregate structure and fungal hyphae for further analyses (e.g., Urakawa et al. 2016; Wardle 1993). Soil bulk density and soil moisture were determined after drying at 105°C for 24 h. Soil pH (H_2O) was measured with the suspension of 10 g of the sieved fresh soil extracted in 25 mL of ion-exchanged water for 1 h. Total soil N and C concentrations (%) were determined with dried and ground soils using a vario EL III Element Analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany).

Fungal and bacterial biomasses were determined using ester-linked fatty acids as biomarkers (Schutter and Dick 2000; Gass and Binkley 2011). The entire surface organic layer including litter and humus was sampled with a polyvinyl chloride core (volume 100 cm^3, surface area 20 cm^2) in October 2013 at the three locations in each plot where soil sampling for abiotic properties was conducted. Briefly, 0.2 M KOH in methanol was added to 3 g of sieved fresh soil in a glass centrifuge tube. The methanol and soil were mixed well and incubated to release ester-linked fatty acids and methylate them. After neutralizing the tube contents with 1.0 M acetic acid, the fatty acid methyl esters (FAMEs) were partitioned into an organic phase with 10 mL of hexane. After centrifuging, the hexane layer was evaporated under anaerobic conditions. Finally, FAMEs were dissolved in hexane/methyl tert-butyl ether containing an internal standard and analyzed by gas chromatography (Agilent 7890A gas chromatograph) with an HP-ULTRA 2 capillary column with a 100% dimethylpolysiloxane phase (Agilent Technologies, Santa Clara, CA) using an automated MIDI (Microbial ID Inc., Newark, DE) system based on GC-FID separation. The fatty acid 18:2ω6,9 was used to estimate fungal biomass, and the sum of 15:0iso, 15:0anteiso, 15:0, 16:0iso, 16:1u7c, 17:0iso, 17:0anteiso, 17:0cyclo, 17:0, 18:1ω7, and 19:0cycloω8c was used to estimate bacterial biomass (Frostegård and Bååth 1996; Stahl and Klug 1996; Miura et al. 2013).

2.3 | Litter-Bag Experiments

Litter-bag experiments were conducted over 3 years to measure the decomposition rates of *F. crenata* and *A. mariesii* leaf litter along the elevation gradient. These experiments were carried out in all seven plots on line a, as well as in three DB plots and one M plot on line b (Figure 1). For these experiments, fresh *F. crenata* litter was collected from the forest floor in each DB and M plot on both lines between October and November 2009. Similarly, fresh *A. mariesii* litter was collected from each EC plot on line a between September and October 2009. The collected fresh leaf litter was sorted, air-dried in a dry chamber, and 3 g (dry weight) samples were placed in 12 × 12 cm polyester mesh bags (1-mm netting). Each litter bag contained a sample from a single species, including bags with samples from the mixed forests. The 1-mm mesh size was sufficiently small to prevent losses of litter caused by breakage, and excluded macrofaunal decomposers, such as worms and coleoptera.

We conducted two types of litter-bag experiments. To evaluate natural leaf litter decomposition rates of the two dominant species along an elevation gradient, the litter bags with dried leaf-litter samples of a single species were incubated at the plots from where the samples had been collected (in situ litter-bag experiment, Figure 1a). To assess changes in litter decomposition under warmer conditions while controlling for intraspecific variation in leaf litter traits along the elevation gradient, litter bags containing leaf litter from the highest elevation for each species (*F. crenata*: DB0900a and DB0900b; *A. mariesii*: EC1400a) were placed in plots at lower elevations within the same line from which they were originally collected (transplanted litter-bag experiment, Figure 1b). In both experiments, one or two litter bags per species were placed at five subplots (they were set every 10 m so that they contained the three subplots for soil property measurements) in each plot, depending on the amount of collected leaf litter available, for four sampling times. That is, (litter bags) × (subplots) × (sampling times) = (1 or 2) × 5 × 4 litter bags were prepared for each decomposition experiment in each plot. In total, 622 litter bags were installed on the soil surface between October 30 and November 26, 2009. The litter bags were harvested after 7 (June 8–11, 2010), 12 (November 5–9, 2010), 24 (October 14–November 16, 2011), or 36 (October 18–22, 2012) months. Three to 10 litter bags for each species for each experimental treatment were harvested from each plot on each date. The soil on the outside of each sampled litter bag was brushed away, and the litter was dried at 40°C for 72 h to determine dry weight.

The decomposition rate was calculated by fitting a simple exponential decay function (Olson 1963) using the mass loss over time at each subplot for each experimental treatment:

$$M_t = M_0 e^{-ktime\ t}, \quad (1)$$

where M_0 is the initial leaf litter mass; M_t is the remaining leaf litter mass after time t (y) expressed as a proportion of the initial dry leaf litter mass; k_{time} is the decay constant expressed in unit y^{-1}. k_{temp}, the decay constant expressed in unit $day^{-1}\ °C^{-1}$, was calculated by fitting a simple exponential decay function:

$$M_t = M_0 e^{-ktempT}, \quad (2)$$

where T (day °C) is the cumulative daily-mean temperature above 0°C after time t.

To calculate the decay constants k_{time} (y^{-1}) or k_{temp} ($day^{-1}\ °C^{-1}$), data on remaining litter mass at 7 months were excluded. The data at 7 months deviated from the simple exponential relationship between time and remaining leaf litter mass, because decomposition progressed slowly under snow for the first 7 months after initiating the decomposition experiment, particularly for *F. crenata* litter (Figure S2). Thus, only data from the initial time point, as well as at 12, 24, and 36 months, were used for the calculations. The decay constants at each subplot were obtained for each experimental treatment of each species at each plot.

2.4 | Litter Trait Measurements

For two subsamples of fresh leaf litter collected at each plot for each species, the concentrations of total phenolics (TPh), condensed tannins (CT), and lignin were measured. A Folin–Ciocalteu method was used to determine the total phenolic

content (Waterman and Mole 1994) using tannic acid as the standard. A proanthocyanidin assay was used to determine the condensed tannin content with cyanidin chloride, a commercially available anthocyanidin, as the standard (Julkunen-Tiitto 1985). An improved acetyl bromide procedure (Fukushima and Hatfield 2001; Iiyama and Wallis 1990) was used to determine the lignin content. The concentration of lignin was calculated to fit the equation derived from Fukushima and Hatfield (2001). Total C and N concentrations in *F. crenata* and *A. mariesii* leaf litter were measured using a vario EL III Element Analyzer for the samples collected in litter traps in November 2010 and October 2011.

2.5 | Statistical Analyses

All statistical analyses were performed using R statistical software v. 4.1.1 (R Development Core Team 2021). We used a generalized linear mixed-effects model (GLMM) to analyze the effect of elevation on leaf litter traits (total C, total N, lignin, TPh, and CT), soil properties (pH, moisture, total C, total N, and fungi to bacteria ratio (F/B)), and the leaf litter decomposition rates (k_{time} and k_{temp}) of in situ and transplanted litter with leaf litter species or forest type (i.e., *F. crenata* vs. *A. mariesii*) as grouping factors. The data of subplots were used for the decomposition rates, and the plot-mean values were used for leaf litter traits and soil properties. In addition, to investigate the effects of the species-specific elevational changes in leaf litter traits on the natural decomposition, we analyzed the interaction effect between elevation and litter bag type (in situ and transplanted) on k_{time} within the species. These analyses were performed using the generalized linear mixed models (GLMMs) with the *glmmTMB* package (ver. 1.1.11) in R (Brooks et al. 2017), with plot ID as a random effect. We used a gamma distribution with a log-link function as the error distribution. Before fitting the model, we scaled elevation to have mean = 0 and standard deviation (SD) = 1. Soil properties of the mixed forests, which were influenced by both dominant species, were excluded from these analyses. We also used ANOVA to analyze the effect of the combination of decomposed litter species and dominant forest species on log-transformed $k_{time\ \text{transplanted}}$ and $k_{temp\ \text{transplanted}}$. This analysis was necessary because transplanted *A. mariesii* leaf litter decomposed in both *A. mariesii*-dominated and *F. crenata*-dominated forests. The Tukey HSD method was used for post hoc multiple comparisons among *F. crenata* leaf litter decomposed in *F. crenata*-dominated forests, *A. mariesii* leaf litter decomposed in *F. crenata*-dominated forests, and *A. mariesii* leaf litter decomposed in *A. mariesii*-dominated forests.

A principal component analysis (PCA) was performed to explore the relationships among the leaf litter traits averaged for each plot. The variables for this analysis included LMA for green leaves and the leaf litter traits listed above. The LMA data were obtained from Hikosaka et al. (2021). The first component (PC1) with more than 1 eigenvalue explains 86.3% of the total variation in leaf and leaf litter traits (Table S1). PC1 is positively associated with leaf litter N and lignin concentrations and negatively associated with LMA and the concentrations of C, TPh, and CT (Table S1). Another PCA was performed to explore the relationships among soil properties averaged for each plot. The first two components with more than 1 eigenvalue each explain 65.7% (PC1) and 21.3% (PC2) of the total variation in soil properties (Table S2). PC1 is negatively associated with soil moisture, C, N, and F/B (Table S2). PC2 is negatively associated with soil pH (Table S2). Before performing these analyses, we scaled all variables to have mean = 0 and SD = 1.

To investigate the factors that best explain the variation in leaf litter decomposition along an elevation gradient, we implemented a GLMM using the *glmmTMB* package with plot ID as a random effect. The GLMM analysis for in situ leaf litter decomposition per unit time ($k_{time\ \text{in situ}}$) included MAT, leaf litter species, PC1 and PC2 for soil properties, the interactions of these factors with leaf litter species, and PC1 for leaf traits as explanatory variables. The data from subplots were used for the decomposition rates, and the plot-mean values were used for the explanatory variables. We used only the PC scores for leaf traits or soil properties that had more than one eigenvalue (Tables S1 and S2). The interaction between PC1 for leaf traits and leaf litter species was not included in this analysis because PC1 was distinctly separated between the two species (Figure S3a). We used a Gamma error distribution with a log-link function. Before constructing the model, we scaled continuous explanatory variables to have mean = 0 and SD = 1 to compare the relative strengths of the effects of the explanatory variables on decomposition. The combinations of explanatory variables that achieved the best predictive ability were selected on the basis of Akaike's information criterion (AIC), the lowest value of which indicates the best fit. We used the *dredge* function in the *MuMIn* package in R (Bartoń 2020) to find the set of explanatory variables with the lowest AIC value.

3 | Results

3.1 | Leaf Litter Traits Along an Elevation Gradient

In general, leaf litter traits differed greatly between *F. crenata* and *A. mariesii*. Compared to *A. mariesii* litter, *F. crenata* litter had significantly lower C, TPh, and CT and significantly greater

TABLE 2 | Summary statistics for the analysis of the generalized linear mixed-effects model to identify the best-fit model to explain the in situ leaf litter decomposition rate per unit time. Coefficients, standard errors (in parentheses), and *z* values are shown for each variable.

$k_{time\ \text{in situ}}$ (y^{-1})		
Selected explanatory variables	**Coefficient**	***z***
Intercept	−0.628 (0.096)	−6.56***
Mean annual soil temperature (MAT) (°C)	0.265 (0.069)	3.87***
Soil PC1	0.114 (0.047)	2.39*
Species	−0.445 (0.101)	−4.40***
MAT × Species	−0.241 (0.101)	−2.39*

Note: Significance: *$p < 0.05$, ***$p < 0.001$.

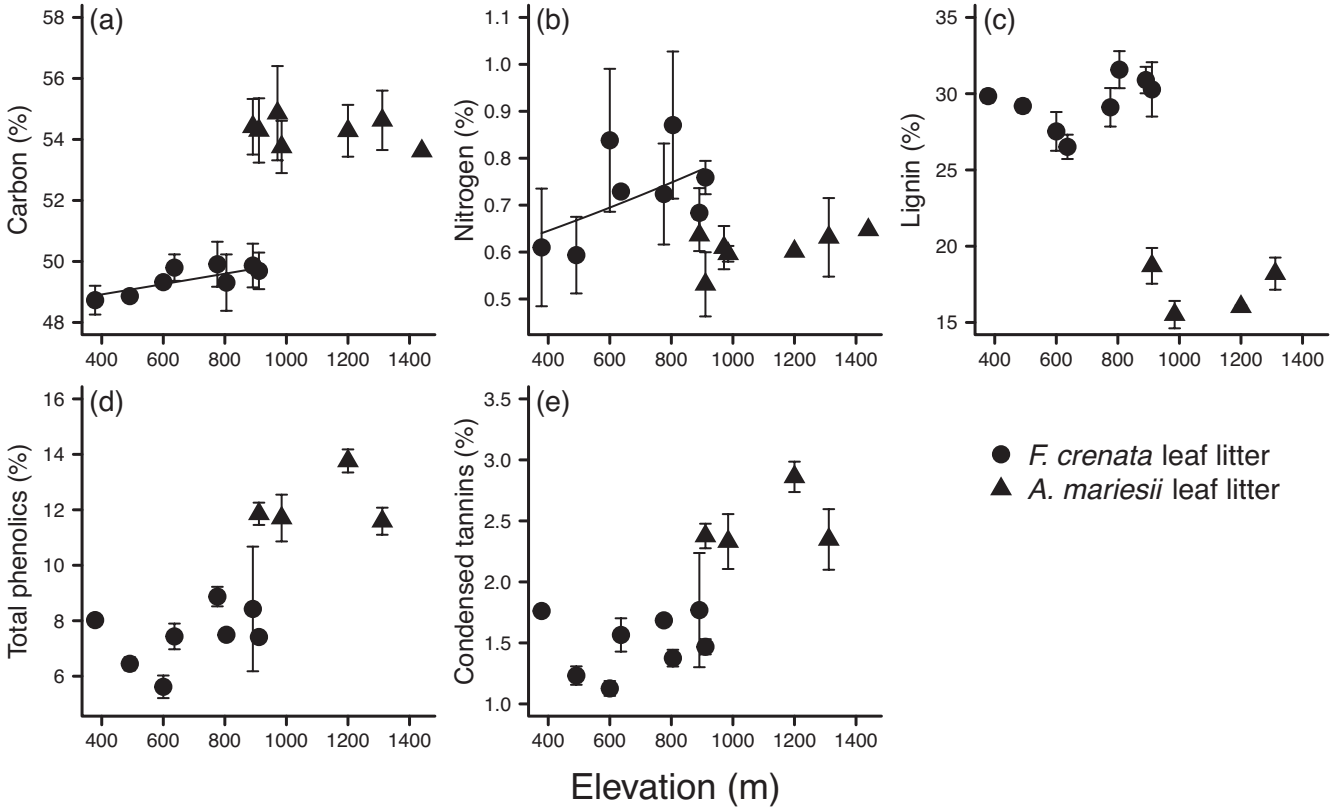

FIGURE 2 | Leaf litter chemistry along an elevation gradient in the Hakkoda mountain range. Means and standard errors of the 2-year plot means with five litter traps for (a) carbon, (b) nitrogen, and of the two leaf litter samples for (c) lignin, (d) total phenolics, and (e) condensed tannins in each plot are indicated. All concentrations were % dry weight. Closed circles indicate *Fagus crenata* leaf litter, and closed triangles indicate *Abies mariesii* leaf litter. Data for carbon and nitrogen were not obtained for plot EC1200b. Data for *A. mariesii* leaf litter lignin, total phenolics, and condensed tannins were not obtained for plots M900b, EC1000b, EC1200b, or EC1400b. Solid lines indicate significant relationships ($p < 0.05$) between traits and elevation within each species derived from Table S3.

N and lignin concentrations (Figure 2, statistical results are shown in Table S3). The response of leaf litter traits to elevation varied between *F. crenata* and *A. mariesii*. For *F. crenata* litter, the C and N concentrations were significantly higher in plots at higher elevations (Figure 2a,b and Table S3), while the concentrations of TPh, CT, and lignin were similar along the elevation gradient (Figure 2c–e and Table S3). For *A. mariesii*, all leaf litter traits studied did not change significantly with elevation (Figure 2 and Table S3).

3.2 | Soil Properties Along an Elevation Gradient

The changes in soil properties along elevation gradients were sometimes opposite between *F. crenata*-dominated forests and *A. mariesii*-dominated forests. Within *F. crenata*-dominated forests, soil C and N were significantly higher and soil pH was marginally significantly lower in plots at higher elevations (Figure 3a,c,d and Table S3). In contrast, within *A. mariesii*-dominated forests, soil C, soil N, and F/B were significantly lower in plots at higher elevations (Figure 3c–e and Table S3). That is, the concentrations of soil C and N had unimodal patterns with peaks at around 1000 m a.s.l. Compared to *A. mariesii*-dominated forests, *F. crenata*-dominated forests had significantly lower soil C ($p < 0.05$), soil N ($p < 0.05$), and F/B ($p < 0.001$). Soil moisture was similar along the elevation gradients within each type of forest, and between the two types of forests (Figure 3b and Table S3).

3.3 | Leaf Litter Decomposition Rate Along an Elevation Gradient

In situ leaf litter decomposition rates per unit time ($k_{time\ \text{in situ}}$) were significantly and marginally significantly lower at higher elevations within the *A. mariesii* and *F. crenata* ranges, respectively (Figure 4a and Table S3). There were no significant differences in the slopes of k_{time} with elevation between in situ and transplanted litter for both species within each species' range (Figure S4; *F. crenata*: $z = -0.471$, $p = 0.638$; *A. mariesii*: $z = 0.426$, $p = 0.670$). On the other hand, *F. crenata* had significantly lower $k_{time\ \text{in situ}}$ than did *A. mariesii* (Table S3), although temperature was higher at lower elevations independent of forest types. For *F. crenata* litter, $k_{time\ \text{transplanted}}$ was significantly lower at higher elevations, but for *A. mariesii* litter, it was similar among the plots in the ranges of *A. mariesii* and *F. crenata* along the elevation gradient (Figure 4b and Table S3). The ANOVA showed that the leaf litter species–species range combination had no significant effect on $k_{time\ \text{transplanted}}$ ($F = 0.397$, $p = 0.674$), indicating that there were no significant differences in $k_{time\ \text{transplanted}}$ among the three combinations: *A. mariesii* transplanted litter decomposed in the *A. mariesii* range, *A. mariesii* transplanted litter

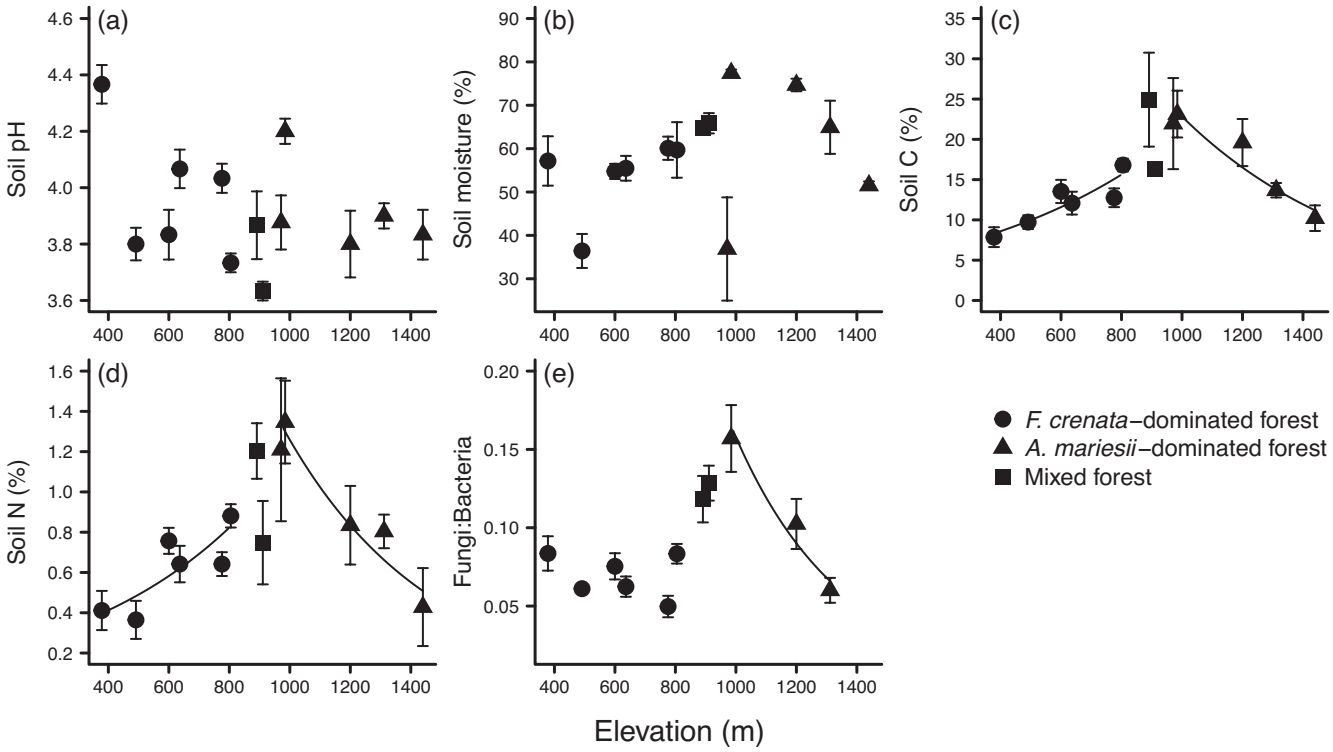

FIGURE 3 | Soil properties along an elevation gradient. Means and standard errors of three samples for soil (a) pH, (b) moisture, (c) C, (d) N, and (e) Fungi/Bacteria in each plot are indicated. Closed circles indicate forest dominated by *Fagus crenata*, closed squares indicate mixed forest, and closed triangles indicate forest dominated by *Abies mariesii*. Data for soil pH, moisture, C, and N were not obtained for plot EC1200b. Data for soil Fungi/Bacteria were not obtained for plots EC1000b, EC1200b, or EC1400b. Solid lines indicate significant relationships ($p < 0.05$) between soil properties and elevation within each species derived from Table S3.

decomposed in the *F. crenata* range, and *F. crenata* transplanted litter decomposed in the *F. crenata* range.

The in situ leaf litter decomposition rate per unit temperature ($k_{temp\ \text{in situ}}$) was similar among plots along the elevation gradient within each species' range (Figure 4c and Table S3). *F. crenata* had significantly lower $k_{temp\ \text{in situ}}$ than did *A. mariesii* (Table S3). The $k_{temp\ \text{transplanted}}$ of *F. crenata* litter was similar among the plots along elevations within the *F. crenata* range (Figure 4d and Table S3). That of *A. mariesii* litter was significantly higher at higher elevations within the ranges of both species, because it decreased greatly in the *F. crenata* range (Figure 4d and Table S3). The ANOVA showed that the effect of the leaf litter species-species range combination on $k_{temp\ \text{transplanted}}$ was significant ($F = 9.45$, $p < 0.001$). The subsequent Tukey HSD test showed that the $k_{temp\ \text{transplanted}}$ of *A. mariesii* litter decomposed in the *A. mariesii* range was significantly greater than that of *A. mariesii* litter and *F. crenata* litter decomposed in the *F. crenata* range ($p < 0.001$ for both), while there was no significant difference between the $k_{temp\ \text{transplanted}}$ of *F. crenata* litter and *A. mariesii* litter decomposed in the *F. crenata* range ($p = 0.469$).

3.4 | Factors Affecting Leaf Litter Decomposition

The best model to explain $k_{time\ \text{in situ}}$ included MAT, soil PC1, leaf litter species, and the interaction between MAT and leaf litter species (Table 2). The predicted positive slope of the $k_{time\ \text{in situ}}$ to MAT was steeper for *A. mariesii* litter (Figure 5a). Soil PC1 had predicted positive relationships with the $k_{time\ \text{in situ}}$ for *F. crenata* litter and for *A. mariesii* litter (Figure 5b).

4 | Discussion

The natural leaf litter decomposition rate of *A. mariesii* increased with decreasing elevation (i.e., increasing temperature) within its range, consistent with some previous studies (Kitayama and Aiba 2002; Salinas et al. 2011; Vitousek et al. 1994; Wang et al. 2010), while that of *F. crenata* only showed a marginal increase with decreasing elevation (Figure 4a). However, partially contrary to our first hypothesis, the slopes of these relationships were not altered by the elevational changes in leaf traits for both species (Figure S4), even though the two studied species showed different trends in elevational trait changes (Figure 2; Hikosaka et al. 2021). Across species, the leaf litter decomposition rate was not necessarily slower for *A. mariesii* with higher LMA distributed at higher elevations (i.e., colder conditions) compared to *F. crenata* with lower LMA distributed at lower elevations (i.e., warmer conditions), in contrast to our second hypothesis (Figure 4a). Interestingly, and partially contrary to our third hypothesis, when *A. mariesii* leaf litter decomposed at lower elevations in *F. crenata*-dominated forests beyond the *A. mariesii* range, its decomposition rate did not increase despite the higher temperatures at lower elevations (Figure 4b). Moreover, contrary to our fourth hypothesis, the temperature-independent decomposition rate of *A. mariesii* leaf litter in *A.*

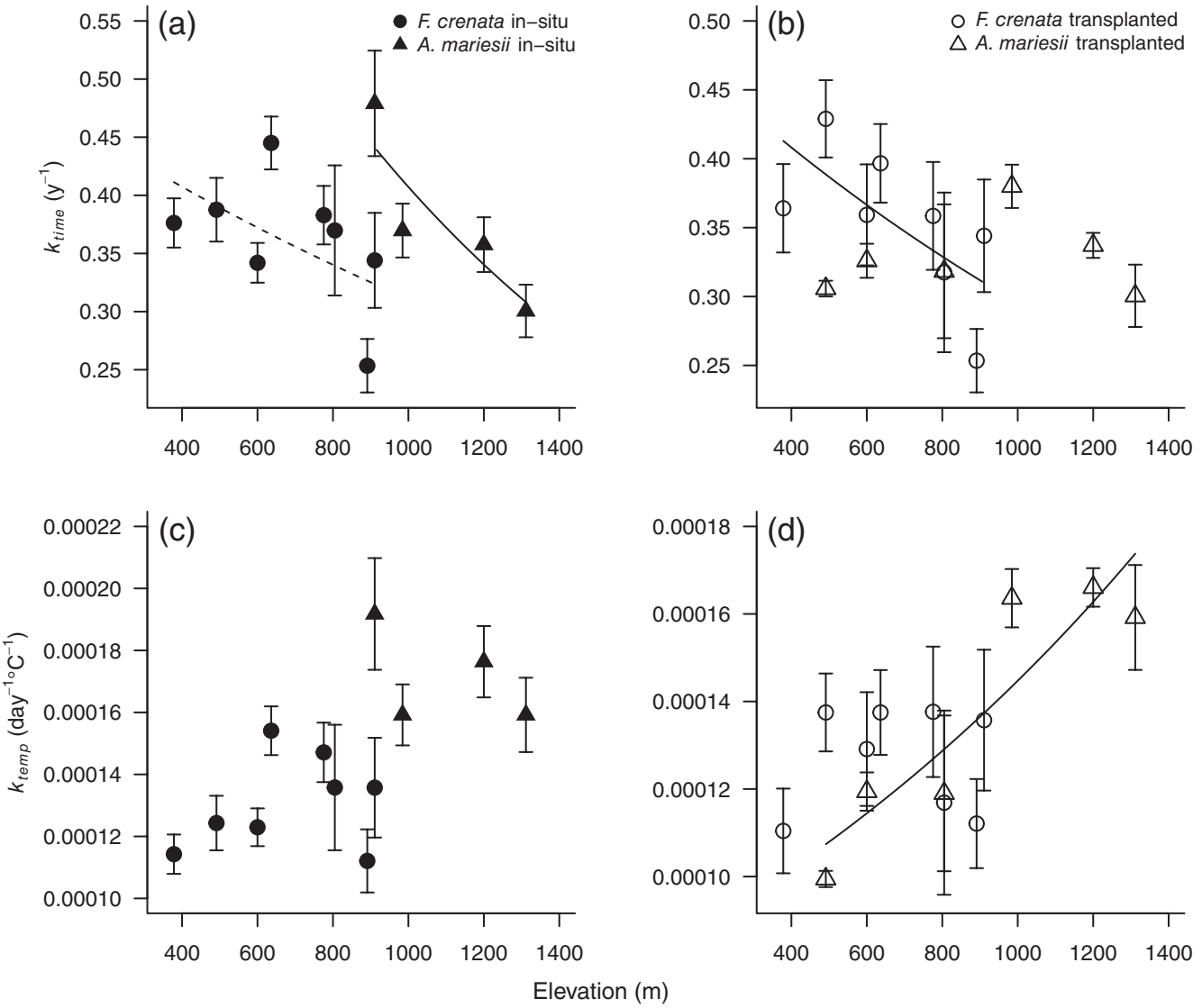

FIGURE 4 | Leaf litter decomposition rate along an elevation gradient for 3 years of (a) in situ litter per unit time, (b) transplanted litter per unit time, (c) in situ litter per unit temperature, and (d) transplanted litter per unit temperature. Means and standard errors for the three to five subplots in each plot are indicated. Closed (in situ, left panels) and open (transplanted, right panels) circles indicate *Fagus crenata* leaf litter and triangles indicate *Abies mariesii* leaf litter. Solid and dashed lines indicate significant ($p < 0.05$) and marginally significant ($p < 0.1$) relationships, respectively, between decomposition rates and elevation within each species, derived from Table S3.

mariesii-dominated forests was greater than that of *F. crenata* leaf litter in *F. crenata*-dominated forests (Figure 4c,d). However, when *A. mariesii* leaf litter decomposed in *F. crenata*-dominated forests, its temperature-independent decomposition rate declined to levels similar to that of *F. crenata* leaf litter (Figure 4d). Our study clearly demonstrated that leaf litter decomposition along an elevation gradient was intricately affected by vegetation traits and soil properties in addition to temperature. We discuss detailed possible reasons for these observed patterns in the following sections.

4.1 | Different Relationships of Leaf Litter Decomposition to Elevation Between the Two Contrasting Species

Although the elevational changes in LMA and leaf litter N were different in *F. crenata* and *A. mariesii* (Figure 2b; Hikosaka et al. 2021), the elevational changes in natural decomposition ($k_{time\ \text{in situ}}$) were not different from those of transplanted litter, which is independent of intraspecific elevational changes in litter traits, for both species. One possible reason is that leaf litter lignin, which is largely responsible for and often associated with slower decomposition (Cornwell et al. 2008), did not change with elevation in either species (Figure 2c). However, the sensitivity of decomposition to temperature was different between the species: the decomposition of *A. mariesii* was more responsive to warming (Table 2 and Figure 5a). From their leaf litter translocation experiment with 15 species along an elevation gradient in Peruvian forests, Salinas et al. (2011) also showed that the sensitivity of leaf litter decomposition to temperature varied sevenfold across species, although they found no leaf litter trait (e.g., SLA and N) related to this sensitivity. In our study, *F. crenata* leaf litter consistently exhibited higher lignin concentrations than *A. mariesii* leaf litter (Figure 2c). This trait difference may make the leaf litter decomposition of *F. crenata* less responsive to warming.

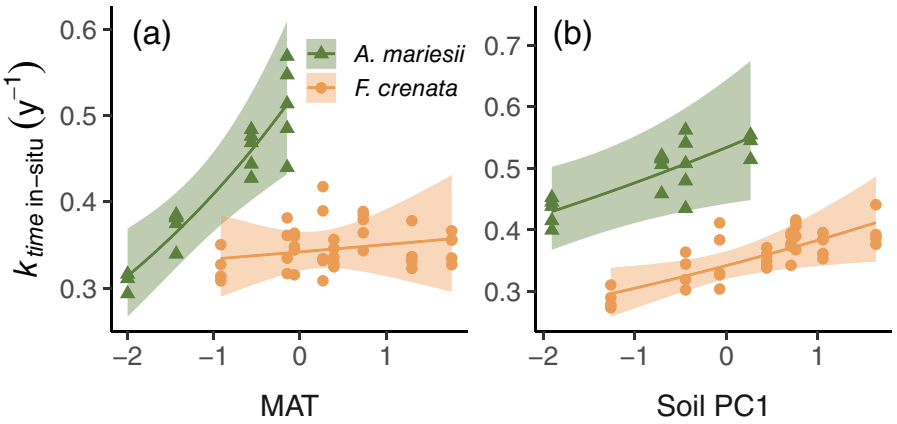

FIGURE 5 | Predicted relationships between explanatory factors selected in the generalized linear mixed-effects model analysis, namely (a) mean annual soil temperature (MAT) and (b) soil PC1, with in situ leaf litter decomposition rate per unit time in *Fagus crenata* (orange) and *Abies mariesii* (green) across study plots along an elevation gradient. Points represent partial residuals of $k_{time\ \text{in situ}}$ at each decomposition location, lines represent predicted relationships, and shaded areas represent 95% confidence intervals of the relationships. Partial residuals of $k_{time\ \text{in situ}}$ and predicted relationships were calculated assuming the selected explanatory factors other than the focal factors were constant at their mean values between the two forest types. Note that the *x*-axes denote standardized trait values and the relationships' slopes denote each factor's effect sizes.

In addition, the elevational relationship between decomposition and soil properties differed between the two species. The GLMM analysis showed that the soil PC1 positively affected $k_{time\ \text{in situ}}$ in both species (Figure 5b). This indicated that the natural decomposition rate was greater at lower soil moisture, soil C, soil N, and F/B ratio for both species if the effect of MAT was set at a constant. However, the elevational changes in soil PC1 showed contrasting patterns for each forest type; soil PC1 decreased from a positive value toward zero within *F. crenata*-dominated forests but increased from a negative value toward zero within *A. mariesii*-dominated forests with elevation (Figure S3b). As a result, the relationship between decomposition and soil properties related to soil PC1 seemed switched for *A. mariesii* along an elevation (Figures 3 and 4a). This may be because *A. mariesii* can be more responsive to the elevational change in MAT. The relationship and importance of soil properties on leaf litter decomposition with elevation can be different depending on plant species, probably through the species' traits (Berger et al. 2015). These complex relationships and the different responses to increasing MAT explained above could make the elevational dependence of $k_{time\ \text{in situ}}$ species-specific (Figure 4a).

4.2 | Importance of Differences in Species Traits on Leaf Litter Decomposition Rates With Elevation

Although the trait PC1 was not selected in the best model, species identity (i.e., species' difference) strongly explained the variation in $k_{time\ \text{in situ}}$ (Table 2). The differences in their traits may be represented by the species difference in the best model, because leaf litter traits were distinctly different between the two species (Figures 2 and S3a). This result suggested that trait differences between the species may be important for explaining the decomposition, while the effects of intraspecific trait variation with elevation on the elevational changes in decomposition were weaker than those of MAT or soil properties as discussed above. The importance of trait differences between the two species was clearer when we focused on the temperature-independent decomposition rate (k_{temp}). The $k_{temp\ \text{in situ}}$ values suggested that the decomposition rate would be greater in *A. mariesii* if the effect of temperature was removed (Figure 4c). Greater $k_{temp\ \text{in situ}}$ of *A. mariesii* than that of *F. crenata* in the same plot (same soil properties) (M0900a, $t = 2.21$, $p = 0.063$) further confirmed that the differences in leaf litter traits between the two species accounted for the differences in the intrinsic decomposition rate (Figure 4c). These results also showed that the decomposition rate of *A. mariesii* was greater when MAT and soil PC1 were set at the same value for both species (Figure 5a,b). *A. mariesii* leaf litter tends to have more soluble phenolics, such as total phenolics and condensed tannins (Figure 2d,e), which are easily leached away in the early stages of decomposition processes (Berg and McClaugherty 2003). The decomposition of *A. mariesii* leaf litter progressed even under the snow, while that of *F. crenata* progressed very little, especially in the first winter after the experiment began (Figure S2a). This may suggest that decomposing fungi, which are particularly needed for lignin degradation, are less active during winter when the temperature is low, while physical leaching of soluble phenolics due to precipitation accounted for the mass loss independent of temperature (Cleveland et al. 2006; Powers et al. 2009; Wieder et al. 2009). These results support the findings of Berger et al. (2015), in which the mass loss of coniferous pine (*Pinus nigra* J.F.Arnold) was generally greater than that of deciduous beech (*Fagus sylvatica* L.) along an Alpine elevation gradient from 900 to 1900 m a.s.l. They found that the release of C, which was tightly related to mass loss, was higher in pine litter than in beech litter. The differences in chemical composition in leaf litter between the two study species may account for the greater decomposition rates per unit temperature of *A. mariesii* leaf litter, which maintains relatively higher decomposition rates per unit time at higher elevations with colder temperatures (Figure 4a).

4.3 | Importance of Plant–Soil Interactions on Leaf Litter Decomposition With Elevation

On the other hand, when the transplanted *A. mariesii* leaf litter decomposed at lower elevations in *F. crenata*-dominated

forests beyond the *A. mariesii* range, its $k_{temp\ \text{transplanted}}$ dropped to levels similar to *F. crenata* leaf litter (Figure 4d), despite *A. mariesii* leaf litter having much lower concentrations of lignin compared to *F. crenata* leaf litter. This emphasized the importance of soil properties, in addition to differences in leaf litter traits between the species, in the patterns of decomposition found in this study. This result suggested "home-field advantage" in litter decomposition (Ayres, Steltzer, Simmons, et al. 2009; Gholz et al. 2000); some soil properties in the "home," such as the soil biotic community, have a higher affinity for litter decomposition of the "home" than "away" species. In reality, a home-field advantage was observed between *F. crenata* and *A. mariesii* coexisting in the mixed forests at our study site (Daumal et al. 2024). Such a home-field advantage may facilitate higher decomposition rates of *A. mariesii* leaf litter in *A. mariesii*-dominated forests even under the cooler conditions at higher elevations (Ayres, Steltzer, Berg, et al. 2009; Keiser and Bradford 2017; Veen et al. 2015).

4.4 | Implications for the Effect of Future Climate Change on Ecosystem Functions

The leaf litter decomposition rates of the two dominant tree species will increase with future warming within the current ranges of each species (Figure 4a). However, the decomposition of *A. mariesii* litter may be more responsive to warming than *F. crenata* litter (Figure 5a). Moreover, the temperature-independent decomposition rate of *A. mariesii* was greater than that of *F. crenata* (Figure 4c,d), due to a species difference probably depending on leaf litter lignin and soluble phenolics (Figure 2). Thus, the impact of future climate warming on leaf litter decomposition in this mountain range may be more severe for coniferous *A. mariesii* distributed at higher elevations than for broad-leaved *F. crenata* distributed at lower elevations. A previous study at this site showed that the response of relative production per unit biomass to temperature is also species-specific; it remains stable with elevation for *F. crenata*-dominated forests, while it increases as temperature increases down with elevation for *A. mariesii*-dominated forests (Hikosaka et al. 2021). Thus, the organic material stock (roughly the difference between production and decomposition) in forest ecosystems may decrease for *F. crenata*-dominated forests, while it may remain stable for *A. mariesii*-dominated forests during future climate change. Further study is needed to investigate the linkage between production, decomposition, and organic material stock above and below ground with consideration of the differences between forest types. More importantly, we should note that the expected responses to temperature of parameters related to ecosystem functions have often been investigated within the current distribution of each species (but see Mayor et al. 2017). However, our study clearly showed that the effect of temperature along an elevation gradient on the leaf litter decomposition rate of a species can be drastically modified, especially across distinct forest types with different soil properties (e.g., Figure 4b). These results highlight the importance of considering species leaf litter traits and plant–soil interactions for accurately predicting the response to future climate change of carbon and nutrient cycles in forest ecosystems, particularly where specific plant–soil interactions would be decoupled due to a replacement of dominant species and changes in tree species distribution because of climate change (Bardgett et al. 2013; Mayor et al. 2017; Hiura et al. 2019; Joly et al. 2023).

Acknowledgments

We thank Dr. C. Kamiyama for helping with field work and Dr. Gaku Takimoto for critical comments on this manuscript. This research contributes to the Japan Long Term Ecological Research Network (JaLTER) and the International Long Term Ecological Research Network (ILTER). This study was supported by the Environment Research and Technology Development Fund, Ministry of the Environment of Japan (no. D-0904); a research grant from The Mitsui & Co. Environment Fund (no. R11-G4-1046); the Green Network of Excellence (GRENE) Program of the Ministry of Education, Culture, Sports, Science and Technology (MEXT), Japan; and JSPS KAKENHI (26281049, 17H03835, and 20H04380). Masatoshi Katabuchi was supported by the Xingdian Talent Support Program of Yunnan Province (E5YNR03B01), the Xishuangbanna State Rainforest Talent Support Program (E4BN041B01), and the Chinese Academy of Science President's International Fellowship Initiative (2020FYB0003).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets used during the current study will be reposited in the JaLTER database in DIAS.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Variable loadings of PCA with leaf and leaf litter traits averaged for each plot. **Table S2:** Variable loadings of PCA with soil properties averaged for each plot. **Table S3:** The effect of elevation on fresh leaf litter chemistry, soil properties, and leaf litter decomposition rate was analyzed using a nested GLMM model that included forest type or leaf litter species as grouping factors. Coefficients, standard errors (in parentheses), and z values are shown for each variable. "*F. crenata against A. mariesii*" indicates the differences of each response variable of *Fagus crenata* leaf litter or *F. crenata*-dominated forest to those of *Abies mariesii* leaf litter or *A. mariesii*-dominated forest; positive coefficient indicates that each response variable is higher in *F. crenata* leaf litter or *F. crenata*-dominated forest than in *A. mariesii* leaf litter or *A. mariesii*-dominated forest, and negative coefficient indicates the opposite pattern. Elevation within each species indicates the effect of elevations on the response variables within each leaf litter species or forest type. Significance: $+p < 0.10$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. CT: condensed tannins; TPh: total phenolics. **Figure S1:** Study plots in the Hakkoda mountains in northern Honshu, Aomori, Japan. The line-a plots are on the west slope of Mt. Akakura and the line-b plots are on the east slope of Mt. Takada-Otake. Circles indicate *Fagus crenata*-dominated forest, triangles indicate *Abies mariesii*-dominated forest, and squares indicate mixed forest. **Figure S2:** Examples of means and standard errors of three to five samples of leaf litter mass declines against (a) time (year), and (b) cumulative daily mean temperature (day °C). Circles indicate in situ *Fagus crenata* leaf litter decomposed at plot DB0400a and triangles indicate in situ *Abies mariesii* leaf litter decomposed at plot EC1000a. **Figure S3:** Relationships with elevation of (a) PC1 for leaf and litter traits, (b) PC1 for soil properties, and (c) PC2 for soil properties. **Figure S4:** Leaf litter decomposition rate along an elevation gradient for three years. (a) *Abies mariesii* litter decomposition rates per unit time. (b) *Fagus crenata* litter decomposition rates per unit time. Means and standard errors for the three to five subplots in each plot are indicated. Points are slightly jittered along the x-axis for clarity. Closed and open circles represent in situ and transplanted treatments, respectively. Solid and dashed lines indicate fitted relationships for in situ and transplanted litter bags, respectively. Slope differences between in situ and transplanted litter bags were not significant for either species. A significant relationship between decomposition rate and elevation was found for *A. mariesii* ($p < 0.001$), but not for *F. crenata*.