

Research article

What makes decomposition faster under conspecific trees? The factors controlling the magnitude of home-field advantage

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Oikos

2024: e10532

doi: [10.1111/oik.10532](https://doi.org/10.1111/oik.10532)

Subject Editor:

Gerlinde B. De Deyn

Editor-in-Chief:

Gerlinde B. De Deyn

Accepted 1 June 2024



The 'home-field advantage (HFA)' for decomposition means that leaf litter decomposes faster on soils under the conspecific species (i.e. the home field) than on soils under different species (i.e. 'away'). Many previous studies have demonstrated the HFA, but the underlying mechanisms remain unclear. We conducted a reciprocal litter-decomposition experiment using two species with different leaf traits: *Abies mariesii*, an evergreen conifer, and *Fagus crenata*, a deciduous broad-leaved tree. Dominance of these species shifts along an elevation gradient with a transition zone where both species coexist. In mixed forests of the transition zone along the elevation gradient, we explored how the magnitude of HFA between these two species was influenced by temperature, soil properties, or leaf litter traits which could directly affect the decomposition rate. The magnitude of HFA observed between the two species varied widely from −3.89 to 28.3%. Our modeling showed that the magnitude of HFA increased with decreasing soil pH and leaf litter N, i.e. in more acidic soil and for less decomposable litter. Soil pH affected leaf litter decomposition in the home plots of each species, whereas leaf litter N did not. The magnitude of the HFA increased as the difference in soil pH between the *F. crenata* and *A. mariesii* plots at the same elevation became greater, but decreased as the difference in soil C became greater. Thus, the response of leaf litter decomposition to environmental changes might vary not only through direct effects of vegetation traits but also through indirect effects of the HFA. This highlights the importance of considering HFA for accurately predicting the response of local carbon and nutrient cycles to climate change, particularly in communities where a replacement of dominant species by others is expected due to climate change.

Keywords: functional traits, home-field advantage, litter decomposition, mountain forest, plant–soil interaction, reciprocal transplant



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Introduction

Decomposition of plant litter plays an important role in recycling and storage of carbon and nutrients, which affect primary productivity and ecosystem composition around the world (Swift et al. 1979, Wardle et al. 2004, Berg and McClaugherty 2014, Veen et al. 2018). Decomposition is controlled by three fundamental factors: the abiotic environment (e.g. mean temperature, moisture), the decomposer community (e.g. bacteria and fungi), and the substrate quality (e.g. lignin and N contents) (Ball et al. 2009, Swift et al. 1979, Aerts 1997, Berg and McClaugherty 2014, Zhou et al. 2015, Bradford et al. 2016, Veen et al. 2018). About 70% of the global variation in leaf litter decomposition can be explained by climate and litter quality (Johansson et al. 1995, Gholz et al. 2000, Parton et al. 2007, Cornwell et al. 2008, Zhou et al. 2015). However, on a local scale, site- or ecosystem-specific conditions can greatly influence decomposition processes. A deeper understanding of such effects could improve global models used to predict the complex impacts of future climate change on ecosystem functions such as carbon sequestration and CO₂ fluxes (Salinas et al. 2011, St. John et al. 2011, Bradford et al. 2016), particularly in communities where replacement of a dominant species by others is expected.

The ‘home-field advantage (HFA)’ for litter decomposition results from specific plant–soil affinity that controls the decomposition process at a local scale (Gholz et al. 2000, Ayres et al. 2009b, Kagata and Ohgushi 2013). As the aboveground vegetation is a major resource for soil biota, plants may impose selection pressure on the decomposers by creating soil conditions conducive to organisms that specialize in the litter contributed by this vegetation (Perez et al. 2013). As a result, plant litter can decompose faster than expected under the plant from which it originates (i.e. ‘at home’) than it does ‘away’ from that plant (Ayres et al. 2009b, Kagata and Ohgushi 2013, Wang et al. 2013, Keiser et al. 2014). The HFA is different from stimulatory effects of high litter quality and/or high soil fertility independent of its origin (e.g. priming effects, Kuzyakov 2010). Many reciprocal litter-transplant experiments and recent meta-analyses have demonstrated that the HFA often occurs in forest ecosystems (Ayres et al. 2009b, Milcu and Manning 2011, Wang et al. 2013, Veen et al. 2015a), yet the magnitude of the HFA varied greatly among studies and ecosystems (Ayres et al. 2009b, Freschet et al. 2012, Perez et al. 2013, Van Der Putten et al. 2013, Wang et al. 2013, Veen et al. 2015a). This suggests that the HFA is site- or ecosystem-specific but the underlying mechanisms are still poorly understood.

To improve our understanding of the mechanisms that control the HFA, it is necessary to explore the factors that determine its magnitude. Some previous studies suggested that litter quality should be an important factor. Low-quality, persistent litter potentially induces a stronger HFA, because persistent organic matter may require specialized decomposers for decomposition to proceed (Milcu and Manning 2011, St. John et al. 2011, Kagata and Ohgushi 2013, Perez et al. 2013, Keiser et al. 2014, Veen et al. 2018). In contrast,

high-quality litter generally appears to promote the activity of the decomposer community without necessarily inducing the HFA (Keiser et al. 2014). In addition, the magnitude of the HFA may decrease when microsite conditions become more favorable for leaf litter decomposition; that is, warmer, moister, and less acidic conditions favor higher activity of soil decomposers, thereby accelerating litter decomposition irrespective of its quality (Aerts 1997). However, observations of the influence of litter quality or microsite conditions on the magnitude of the HFA are contradictory. It has also been suggested that the HFA increases with increasing dissimilarity in litter quality and microsite conditions between home and away (Freschet et al. 2012, Veen et al. 2015a). However, it remains unknown how litter quality, microsite conditions, and their differences between home and away together influence the magnitude of the HFA.

To understand the underlying mechanisms controlling the magnitude of the HFA, we conducted a reciprocal litter-transplant decomposition experiment along an elevation gradient in the Hakkoda Mountains, Aomori, Japan. In the Hakkoda Mountains, forests are dominated by *Fagus crenata*, a deciduous broad-leaved tree, at lower elevations (400–800 m a.s.l.), by *Abies mariesii*, an evergreen coniferous tree, at higher elevations (1000–1400 m a.s.l.), and by both species together in the mixed forests of the transition zone (800–1000 m a.s.l.). The reciprocal litter-transplant decomposition experiment was conducted in the mixed forest of the transition zone to explore how temperature, litter traits and soil properties, and the differences in these factors between home and away, affect the magnitude of the HFA between the two species. The mixed forest of the transition zone is ideal for such an experiment because of the mosaic of soil conditions induced by varying tree species occurring at all elevations within the same temperature range. The higher contents of phenolic compounds in *A. mariesii* may lead to acidified soil under this species, and the higher lignin content in *F. crenata* tends to lead to accumulation of litter materials on the forest floor and humus in soils under this species (Berg and McClaugherty 2014). Such differences between the two dominant species are expected to cause the large HFA between them, which will provide an opportunity to experimentally test how the magnitude of the HFA is affected by 1) changes in temperature, leaf litter traits, and soil properties along an elevation gradient and 2) differences in those factors between microsites dominated by different species at the same elevation. In addition, it is important to understand the HFA in transition zones between forest types, because tree species in alpine areas are shifting to higher elevations in response to global climate warming, resulting in changes of species composition and ecosystem processes along elevation gradients (Dullinger et al. 2004, Salinas et al. 2011, Du et al. 2018). *Fagus crenata* is expected to expand its distribution to higher elevations in response to a warming climate (Matsui et al. 2004), which may cause it to invade *A. mariesii*-dominated forests at higher elevations. Therefore, it is urgent to understand how specific plant–soil interactions affect decomposition processes in a context where altered climate conditions

and associated changes in forest composition may decouple such interactions.

In this study, we asked the following specific questions: 1) how does the leaf litter decomposition of *F. crenata* and *A. mariesii* differ between home and away along an elevation gradient? Does a positive HFA occur between the two species? 2) How do the factors controlling leaf litter decomposition, such as temperature, leaf litter traits, and soil properties, which could change along an elevation gradient, influence the magnitude of the HFA between the two species? This question is critically important to understand the direct and indirect effects through the HFA of those factors on leaf litter decomposition in the context of climate change. We expect the HFA to be stronger for persistent litter traits, such as higher contents of secondary compounds or lower N content, as persistent traits may require specialized decomposers to promote decomposition (Milcu and Manning 2011, Veen et al. 2015b). The HFA might also be stronger under unfavorable decomposition conditions, such as colder, drier, and more acidic soils, because specialized decomposers may be needed in such conditions. At the same time, we tested how differences in temperature, leaf litter quality, or soil properties between home and away affect the magnitude of HFA at the same elevation (Ayres et al. 2009b, Freschet et al. 2012).

Material and methods

Research site and plot properties

The study site is located in the Hakkoda Mountains in Aomori, Japan. This range contains many peaks that are higher than 1200 m a.s.l. The highest one (Mt Ohdake) is 1584 m a.s.l. (40°41'N, 140°52'E). The annual mean precipitation here ranges from 1300 to 2300 mm and the mean annual air temperature ranges from 4 to 6°C. The maximum snow depth ranges from 3 to 5 m as a result of heavy snow from November to May. These data were obtained from the Sukayu meteorological station (40°38.9'N, 140°50.9'E, 900 m a.s.l.) between 1990 and 2009 (details in Shimazaki et al. 2011). The soil is classified as Andosol (FAO classification). The lower elevations (400 to 800 m a.s.l.) are dominated by *F. crenata* and the higher elevations (1000 to 1400 m a.s.l.) by *A. mariesii*. The transition zone between 800 and 1000 m a.s.l. is a mixed forest where each species forms patches (Fig. 1a).

We established six pairs of plots along an elevation gradient in patches of the mixed forest, in which one plot in the pair was dominated by *F. crenata* (*F. crenata* plots) and the other was dominated by *A. mariesii* (*A. mariesii* plots) (Fig. 1b). The plots within each pair were at the same elevation. Each

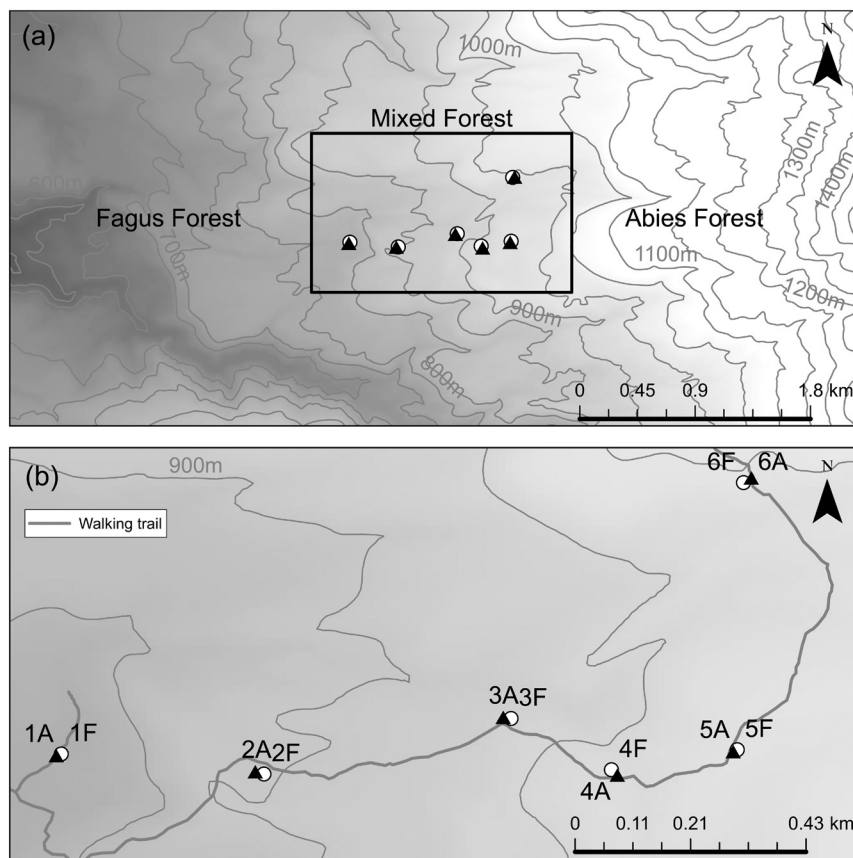


Figure 1. Locations of the studied plots. (a) Overview of the study area. The plots were located in mixed forest in the transition zone between the two species. (b) Enlarged map of the plot locations. ○ *Fagus crenata* dominant; ▲ *Abies mariesii* dominant. Numbers in (b) represent pairs of plots dominated by *A. mariesii* (A) or by *F. crenata* (F). See the Supporting information for details.

plot was circular, with a 7 m radius. Each paired plot position was located at least 200 m from adjacent positions and the two members of each pair were within 10 m of each other at the same elevation. All trees greater than 10 cm in diameter at breast height (DBH) were identified and their DBH were recorded. The ratio of *F. crenata* basal area to total basal area (FBA/TBA) was stable at 1 in the *F. crenata* plots except 5F, where it was 0.87. On the other hand, *F. crenata* was abundant in the *A. mariesii* plots at lower elevations but became less abundant at higher elevations; therefore, FBA/TBA decreased with increasing elevation (Supporting information).

In September and October 2016, we collected freshly fallen litter in a randomly selected 50 × 50-cm area on the forest floor of each plot, then air-dried and sorted it into *F. crenata* leaf litter, *A. mariesii* leaf litter, *F. crenata* fruits, *A. mariesii* fruits, dwarf bamboo *Sasa kurilensis* branches and leaves, tree branches, and other. We determined the total fresh litter (g m⁻²) and the ratio of *F. crenata* leaf litter to the total (Fagus/total fresh litter).

Leaf litter traits

Freshly fallen *F. crenata* and *A. mariesii* leaf litter was collected from the study plots on 23 September and 16 October 2014 to determine the leaf litter traits. We obtained three samples from each plot, which were dried in a vacuum freezer and ground into a powder for further analyses. In each powdered sample, the concentrations of carbon (C), nitrogen (N), total phenolics, condensed tannins, and lignin were measured. Carbon and nitrogen concentrations were measured with an NC analyzer (Vario EL III; Elementar). We used the Folin–Ciocalteu method to determine the total phenolics concentration (Waterman and Mole 1994), using tannic acid to create a laboratory standard curve. We used a proanthocyanidin assay to determine the condensed tannins concentration, using cyanidin chloride, a commercially available anthocyanidin, to create a standard curve (Julkunen-Tiitto 1985). We used an improved acetyl bromide procedure (Iiyama and Wallis 1990, Fukushima and Hatfield 2001) to determine the lignin concentration. The concentration of lignin was calculated to fit the equation derived from Fukushima and Hatfield (2001).

Soil properties

Soil cores were collected with a stainless-steel soil-sampling core with a volume of 100 ml (ø 50 × 51 mm) at a 5 cm depth below the soil surface, just below the organic layer, at three spots in each of three subplots per plot on 8 September 2014, during the growing season. Soil cores were kept in plastic bags at 4°C until they could be processed, which occurred within 24 h. The three soil cores from each subplot were homogenized, weighed, and then sieved through a 2 mm mesh to provide a single composite sample for further analysis. We obtained a total of 36 samples (3 samples per plot × 12 plots). Part of each sample was oven-dried at 100°C to determine the soil moisture content and was subsequently used for CN analysis with a Vario EL III analyzer to determine the total C

and N contents. Fresh soil was used for pH and inorganic N measurements. The soil pH was measured via water extraction. We added 25 ml of distilled water to 10 g of sieved, fresh soil and shook the solution for 1 h before measuring the pH with a pH meter. To determine the ammonium (NH₄⁺) and nitrate (NO₃⁻) concentrations, we suspended 30 g of sieved fresh soil in 300 ml of 0.5 M KCl solution and shook the solution for 1 h. We then filtered the suspension, obtaining at least 60 ml of supernatant from each sample, which we froze. We measured the NH₄⁺ and NO₃⁻ concentrations using the methods of Ueda et al. (2017). We did not detect any NO₃⁻, so we do not discuss this form of N further.

Decomposition experiment

The studied plots for the leaf litter decomposition experiment (Fig. 1b) covered a range of values for pH (3.6–4.5), soil moisture (59.9–80.7%), and elevation (828–1000 m a.s.l.). In each plot, we obtained fresh leaf litter of the dominant species (i.e. *F. crenata* or *A. mariesii*) on 23 September and 26 October 2014. The collected litter was air-dried, then mixed carefully to produce a homogeneous single-species sample for each plot. The sample was not sterilized to avoid changing labile leaf litter traits, particularly secondary metabolites such as total phenolics and condensed tannins, but soil and visible soil fauna were removed. From this sample, we placed an amount equivalent to a dry weight of 3 g in a 12 × 12-cm plastic 1-mm-mesh litterbag. Each litterbag contained litter from a single species. Litterbags of *F. crenata* from a given elevation were placed in three subplots under *F. crenata* trees in the *F. crenata* plots where the sample was collected (home) and in three subplots under *A. mariesii* trees in paired *A. mariesii* plots at the same elevation (away). The reciprocal placements were made for *A. mariesii* litterbags. This enabled us to consider four litter decomposition treatments: 1) *F. crenata* litter that decomposed in *F. crenata* plots (Fagus/Fagus), 2) *F. crenata* litter that decomposed in *A. mariesii* plots (Fagus/Abies), 3) *A. mariesii* litter that decomposed in *F. crenata* plots (Abies/Fagus) and 4) *A. mariesii* litter that decomposed in *A. mariesii* plots (Abies/Abies). All litterbags were installed between 27 and 30 October 2014. Litterbags from all subplots in these treatments were sampled on 16 June and 27 October 2015 and on 16 September 2016, which were 0.7, 1.0, and 2.0 years after the experiment began. As there were six plot pairs and litterbags were retrieved at three times after placement, there were 216 litterbags (6 plot pairs (12 plots) × 2 species × 3 sampling dates × 3 subplots). The litterbags were opened carefully, and soil was removed with a brush. The litter was then dried (at 40°C for 3 days) and weighed to calculate the mass loss.

Statistical analyses

Changes in leaf litter traits and soil properties along the elevation gradient

We analyzed the effects of elevation, leaf litter species (*A. mariesii* and *F. crenata*), and their interactions on leaf litter

traits (C, N, C/N, total phenolics, condensed tannins, lignin). We also analyzed the effects of elevation, plot species (*A. mariesii* versus *F. crenata*), and their interactions on soil properties (pH, moisture, total C, total N, C/N, NH_4^+). We used generalized linear models (GLMs) rather than generalized linear mixed models (GLMMs) because we couldn't obtain convergent GLMMs in many cases due to an undetectably small variance for the random effect (plot identity). This could cause several problems (Bates et al. 2015, please see the documentation of 'isSingular' in the 'lme4' package). We used a Gamma distribution with a log-link function as the error distribution. We tested the significance of each explanatory variable by a type-II likelihood-ratio test (LR test) using the *Anova* function of the 'car' package in R (Fox and Weisberg 2011).

Calculation of the decay rate constant

To calculate the litter decay rate constant (k), we used the leaf litter mass remaining at each time t . To calculate k (year^{-1}), we used an exponential decay function (Olson 1963):

$$X_t = X_0 e^{-kt} \quad (1)$$

where X_0 is the initial leaf litter mass (3 g) and X_t is the residual leaf litter mass at time t . The curves for each subplot were fitted using the *nlm* function of the 'nlme' package in R. Because some litterbags were lost or damaged, k values were not calculated for two of the 72 subplot-species combinations.

Changes in litter decomposition along the elevation gradient

To test for differences in the decomposition rate among the four treatments (*A. mariesii* leaf litter decomposed in an *A. mariesii* plot, *A. mariesii* litter decomposed in a *F. crenata* plot, *F. crenata* leaf litter decomposed in a *F. crenata* plot, and *F. crenata* litter decomposed in an *A. mariesii* plot) along the elevation gradient, we analyzed the k values using a GLM. The response variable was k and the explanatory variables were elevation, the decomposed litter species ('litter species'), and the dominant species in the plot ('plot species'). Interactions among the elevation, dominant species, and litter species were also included in the models. We tested for significance of the explanatory variables using the LR test.

Calculation of the home-field advantage index

The ratio of the decomposition rate at home to away of a given species for a litter-transplant decomposition experiment between only two species does not allow us to distinguish between the HFA and variation in decomposition due to site conditions (e.g. temperature, nutrient availability, soil decomposer communities) (Ayres et al. 2009a, Keiser et al. 2014). Therefore, we adopted the home-field advantage index (HFAI) developed to quantify the magnitude of the HFA between two species (Ayres et al. 2009b). The HFAI is defined as:

HFAI

$$= \left[\left(\frac{A_{\text{RML}a} + B_{\text{RML}b}}{2} \right) / \left(\frac{A_{\text{RML}b} + B_{\text{RML}a}}{2} \right) \right] \times 100 - 100 \quad (2)$$

$$A_{\text{RML}a} = \frac{Aa}{Aa + Ba} \times 100 \quad (3)$$

where $A_{\text{RML}a}$ represents the relative mass loss of litter from species A at site a , and Aa and Ba represent the percent mass loss of leaf litter from plant species A and B decomposing at site a . Litter mass loss by each species was expressed as relative mass loss (i.e. a percentage of total mass loss at that site for both species) because some sites have inherently faster decomposition rates than others due to site conditions. HFAI represents the percentage change in the rate of mass loss of litter when it decomposes at home versus away and is a net value for both species (A and B) involved in the reciprocal transplants. A positive HFAI represents a faster decomposition at home from away and a negative HFAI represents a faster decomposition at away from home.

Although values of mass loss are customarily used for estimation of HFAI, it depends only on the final litter weight in a litter bag. Therefore, we calculated HFAI for each elevation using the estimated values of k for each subplot and species with Eq. 2 because more accurate estimations of the decomposition process rate would be obtained when incorporating information from multiple collections of litter bags along time. For the estimation of HFAI, first we calculated the mean values of k for each plot and species and then we calculated the percent mass loss after two years for each plot and species. Next, we applied the resultant values to Eq. 2 and obtained values of HFAI for each plot pair (*A. mariesii* plot-*F. crenata* plot) for the reciprocal transplant at each elevation.

Factors affecting home-field advantage

To identify the factors that affected the HFA, we estimated the effects of environmental factors, soil properties, and litter traits on HFAI. First, we assumed that the litter decay rate constant k (Eq. 1) is a function of multiple factors as:

$$k_{lpi} = \exp \left(\sum_{f=1}^N \beta_{fip} \times X_{fi} + P_p + L_l + LP_{lp} + \alpha + \varepsilon_i \right) \quad (4)$$

where k_{lpi} is the decay rate constant for the i -th litter bag containing litter species l decomposed in species p dominant forests, β_{fip} is the slope of the relationship between the f -th factor ($f=1-N$) and the decay rate constant for litter species l decomposed in p dominant forests, X_{fi} is the value of the f -th factor for the i -th litter bag, P_p is the difference in the decay rate constant between litter bags decomposed in species p dominant forests and *Abies* forests (P_p is always 0 for *Abies* dominant forests), L_l is the difference in the decay rate constant between litter of species l compared to *Abies* litter (L_l is always 0 for *Abies* litter), LP_{lp} is the interactive effect between

litter species and forest type, α is the intercept of the relationship, and $\mathcal{E}_i$ is the residual for the i -th litter bag. Because we did not consider interactions among the factors, when other factors are fixed at certain values (e.g. means), the mean decay rate constant for litter species l decomposed in p dominant forests can be described as a function of a factor F as:

$$k_{lp} = \exp(\beta_{F|p} \times x + P_p + L_l + LP_{lp} + \alpha + c_{lp}) \quad (5)$$

where x is a value of factor F and c_{lp} is a constant representing the effect of other factors for litter species l decomposed in p dominant forests. By substituting the constant part of Eq. 5 as C_{lp} , the equation becomes:

$$k_{lp} = \exp(\beta_{F|p} \times x + C_{lp}) \quad (6)$$

Using Eq. 1 and 6, the relationship between factor F and percent mass loss after t years for litter species l decomposed in p dominant forests is:

$$\begin{aligned} \% \text{Mass loss}_{lp,t} &= \frac{X_0 - X_t}{X_0} \times 100 \\ &= \frac{X_0 - X_0 e^{-kt}}{X_0} \times 100 \\ &= \frac{X_0 - X_0 e^{-\exp(\beta_{F|p} \times x + C_{lp}) \times t}}{X_0} \times 100 \end{aligned} \quad (7)$$

Using Eq. 7, we estimated the relationships between factor F and mass loss of *Abies* and *Fagus* litter decomposed in the home and away conditions. By applying the resultant relationships, Eq. 7 to Eq. 3, we estimated the relationships between factor F and relative mass loss under four conditions. Finally, we estimated the relationship between factor F and HFAI by applying the relationships between relative mass loss and factor F to (Eq. 2).

Estimation of parameters of the model described above was conducted by estimating the parameters in Eq. 4. This was done using a GLM with a Gamma error distribution with a log-link function to describe the relationships between k (as the response variable) and the environmental factors, soil properties, and litter traits. As the explanatory variables, we used mean annual soil temperature (MAT), soil pH, soil moisture, soil NH_4^+ , soil C, leaf litter N, condensed tannins, lignin, litter species, home or away, and the three-factor interactions among litter species, home or away, and the other factors. Using the main effects and interactions of environmental factors, soil properties, and litter traits, we estimated $\beta_{F|p}$ for each factor. Also, P_p , L_p and LP_{lp} were estimated using litter species, home or away, and their interaction. Finally, the intercept of the model was used for estimation of α . Before constructing the model, we used the scale function of R to standardize the continuous explanatory variables to have mean = 0 and SD = 1 to facilitate comparisons of the relative strengths of the effects of the explanatory variables on HFA.

Because preliminary backward model selection using Akaike's information criterion (AIC) showed weak support for the model with the best predictive ability (the difference in AIC between the best and second-best models = 0.06), we adopted a model-averaging approach (Burnham and Anderson 2002) to control uncertainty in the model formulation. First, we created candidate models using the dredge function in the 'MuMIn' package in R (Bartoń 2023). Because dredge can create a model set for all possible combinations of a maximum of 31 explanatory variables, while we had 32 explanatory variables including interactions, we created eight candidate model sets: each set excluded one soil property or litter trait and its interactions with the litter species and with home or away. The leaf litter species was retained in all candidate models in all model sets. After constructing the model sets, we eliminated duplicate models and obtained a model set with 1 620 385 models. We then averaged the top 3765 models with the lowest values of AIC_c (the small-sample version of AIC) and for which AIC_c differed between the focal model and the best model (ΔAIC_c) by less than 10, weighted by the Akaike weights of each model (Burnham and Anderson 2002). The models with ΔAIC_c greater than 10 can be considered 'sufficiently poorer' than the best model (Burnham and Anderson 2002, Symonds and Moussalli 2011). Note that because we used a full model averaging approach, which assigns zero to estimates for explanatory variables not included in a model during averaging, the averaged estimates of explanatory variables which tend to be omitted from the top 3765 models became close to zero.

Using the averaged model (Supporting information) and the equations described above, we conducted a sensitivity analysis which investigated the dependence of HFAI on each explanatory variable for *A. mariesii* and *F. crenata* in the home and away plots. We first estimated the dependence of percent mass loss on each explanatory variable using the averaged model and Eq. 7 for the four conditions: 1) *A. mariesii* litter decomposed at home plots, 2) *A. mariesii* litter decomposed at away plots, 3) *F. crenata* litter decomposed at home plots and 4) *F. crenata* litter decomposed at away plots. Values of the explanatory variables other than the focal ones were fixed at their means (i.e. zero, because we standardized the explanatory variables) when calculating the dependences. Then, by applying Eq. 2–3 for the resultant dependences of mass loss, we calculated the two-dimensional dependence of HFAI on each explanatory variable in both *A. mariesii* and *F. crenata* plots or *A. mariesii* and *F. crenata* litters.

All statistical analyses were performed in R ver. 4.1.1 software (www.r-project.org).

Results

Climatic parameters, leaf litter traits and soil properties along the elevation gradient

The MAT, which was calculated from temperatures recorded at hourly intervals in each plot, generally decreased with increasing elevation in the *A. mariesii* plots, but the pattern

varied in the *F. crenata* plots (Supporting information). The length of the growing season, which we defined as the season without snow cover, also varied with elevation (Supporting information). The mean soil temperature during the growing season (MTG) decreased with increasing elevation for both species. The variation in MAT can be explained by variations in the duration of snow cover.

Leaf litter N showed a significant increase with elevation for both species with no difference between the two species (Fig. 2b). Leaf litter total phenolics and condensed tannins were significantly higher in *A. mariesii* litter than in *F. crenata*

litter (Fig. 2d–e). Leaf litter lignin showed the opposite trend and was about 12 percentage points higher in *F. crenata* litter than in *A. mariesii* litter (Fig. 2f). Leaf litter C and C/N showed no trend with elevation and no differences between the species (Fig. 2a, c). We found no significant species $\times$ elevation interaction for any leaf litter traits.

Soil C decreased significantly with increasing elevation, but the slope was marginally steeper for the *F. crenata* plots with lower soil C (Fig. 3c). Soil N decreased significantly with increasing elevation for both species plots with no difference between the two species plots (Fig. 3d). Soil C/N

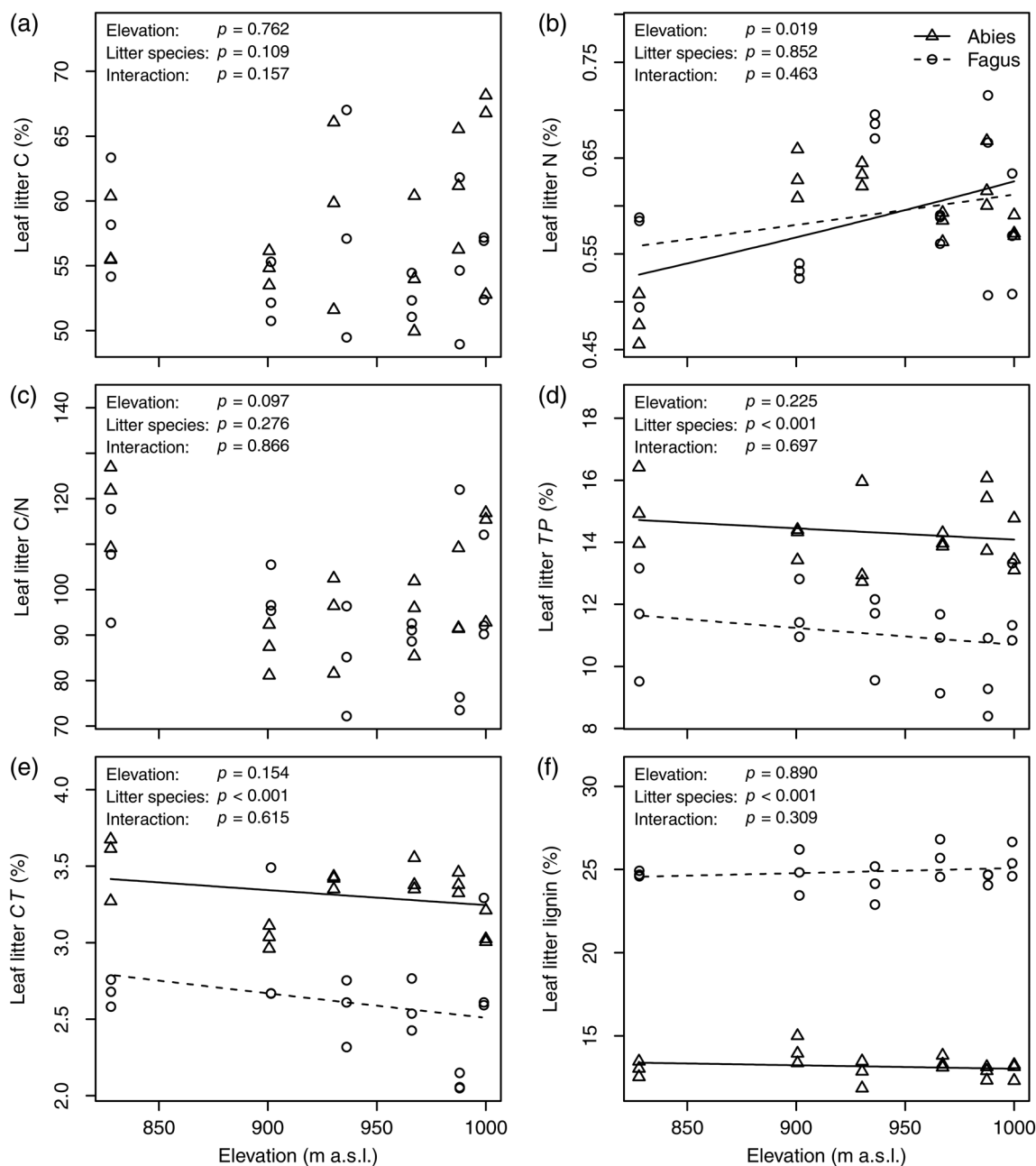


Figure 2. The effect of elevation, leaf litter species (*A. mariesii* and *F. crenata*), and their interaction on leaf litter (a) carbon, (b) nitrogen, (c) C/N ratio, (d) total phenolics (TP), (e) condensed tannins (CT), and (f) lignin. The significances and regression lines were obtained using generalized linear models.

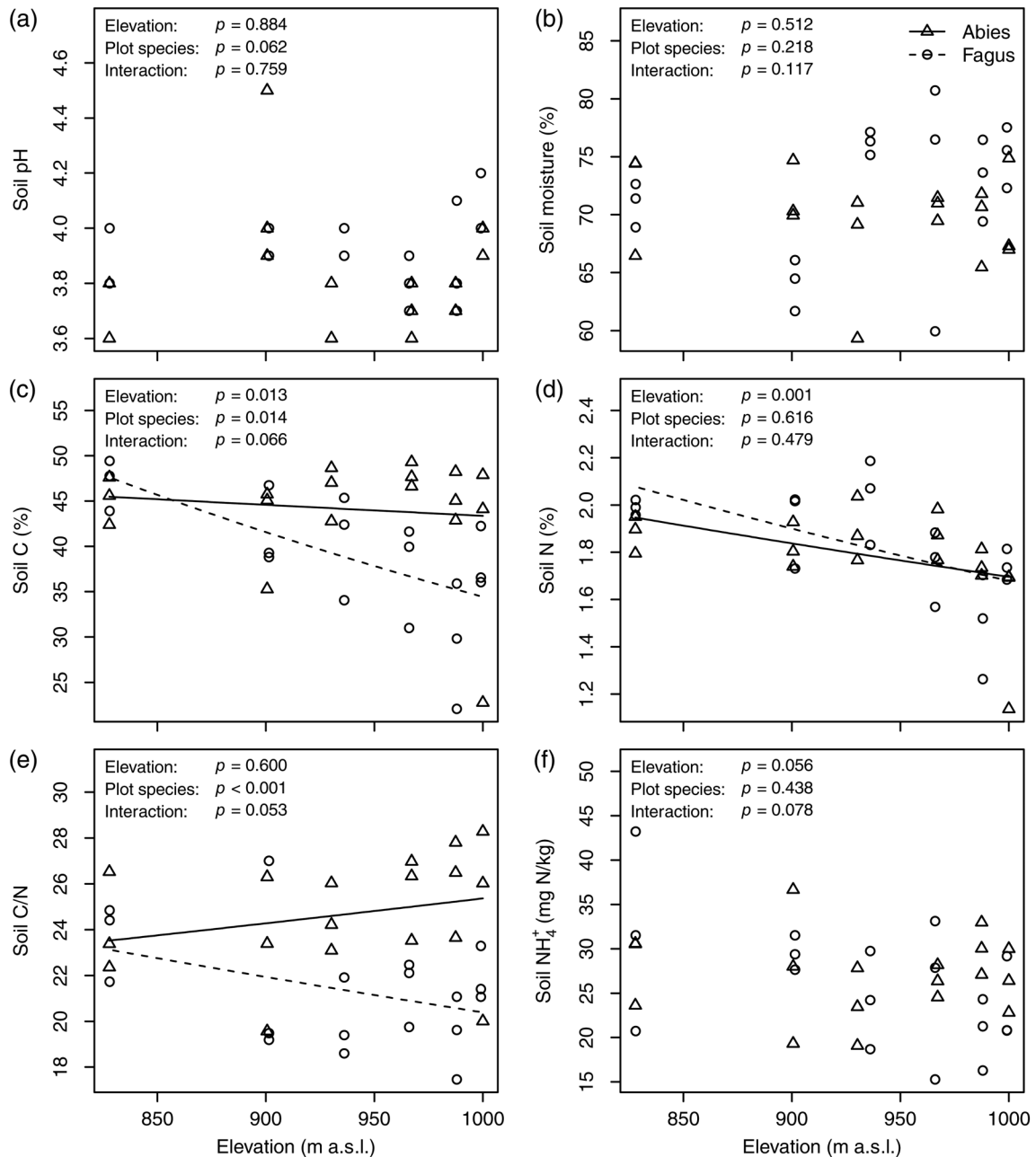


Figure 3. Effects of elevation, dominant species in the plot (*A. mariesii* or *F. crenata*), and their interaction on soil (a) pH, (b) moisture content, (c) total C, (d) total N, (e) C to N ratio (C/N), and (f) ammonium (NH_4^+). The solid and dashed regression lines for the two species were obtained using generalized linear models.

increased with increasing elevation for *A. mariesii* plots, while it decreased for *F. crenata* plots (Fig. 3e). Soil pH, moisture and NH_4^+ showed no trends with elevation and no differences between the *F. crenata* and *A. mariesii* plots (Fig. 3a, b, f).

Leaf litter decomposition of *A. mariesii* and *F. crenata* along the elevation gradient

The leaf litter decomposition rates were significantly affected by the interactions among the three explanatory variables (litter species, plot species, elevation), although the significance

was $p = 0.048$ (Table 1). As such our results indicated that the effect of litter species on decomposition rates differed between the plot species, and the difference was influenced by elevation. In general, the leaf litter of both species decomposed faster in their home plots than in the away plots (Fig. 4); thus, both species often experienced a positive HFA. Overall, the decomposition rates of *A. mariesii* litter were higher than those of *F. crenata* litter (Fig. 4), with *A. mariesii* litter in *A. mariesii* plots having the highest decomposition rate and *F. crenata* litter in *A. mariesii* plots having the lowest rate. *A. mariesii* litter and *F. crenata* litter in the *F. crenata* plots had decomposition rates that converged at lower elevations.

Table 1. Effects of elevation, litter species, the dominant species in the plot (plot species), and their interactions on the leaf litter decomposition rate k . Results of the likelihood-ratio test are shown. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Explanatory variables	χ^2	df	p
Elevation	0.03	1	0.870
Litter species	208.30	1	<0.001***
Plot species	2.19	1	0.139
Elevation $\times$ Litter species	6.94	1	0.008**
Elevation $\times$ Plot species	1.69	1	0.194
Litter $\times$ Plot species	8.01	1	0.005**
Elevation $\times$ Litter species $\times$ Plot species	3.89	1	0.048*

Factors affecting leaf litter decomposition of *A. mariesii* and *F. crenata*

The estimated effects of litter traits and environmental factors in the averaged model on the leaf litter decomposition rates are shown in Supporting information and visualized in Fig. 5. The averaged model suggested that the decomposition rate was largely influenced by the differences in litter species and between home and away, and then by the environmental factors and leaf litter traits shown in the Supporting information, including some of their interactions with 'Litter species' or 'Home or away', or the three-way interactions among them. Among the factors, MAT, soil moisture and NH_4 had relatively weaker influences on the decomposition rates (their main estimates were one or two digits smaller than the others as shown in the Supporting information). Soil pH and soil C had opposite influences on the decomposition rate between the two species (see estimates for Soil pH $\times$ Litter species and Soil C $\times$ Litter species in the Supporting information). As soil pH or soil C increased, the decomposition rates of *A. mariesii* litter decreased in both home and away plots, while the decomposition rates of *F. crenata* litter increased in both home and away plots (Fig. 5b, e).

The magnitude of the HFA between the two species and the controlling factors

HFAI calculated using the observed decomposition rate k in the transplants between *F. crenata* and *A. mariesii* varied from -3.89 to 28.3% (Table 2). Furthermore, Fig. 6 shows the predicted relationships between modeled HFAI and the factors investigated in the averaged model for decomposition rate (Fig. 5, Supporting information). The modeled HFAI possibly varies from ca -5 to 25% depending on the variation of explanatory factors (shown as the variation of HFAI indicated as contour in the unshaded area of each panel in Fig. 6) when it is assumed that a focal explanatory factor switched in all possible combinations between the *F. crenata* subplots and *A. mariesii* subplots (between the *F. crenata* plots and *A. mariesii* plots in case of MAT) while other factors remained unchanged. For example, HFAI could vary from ca -1 to 15% when soil pH changed within the range observed in each of the *F. crenata* subplots and *A. mariesii* subplots, while it could vary ca 7 – 10% when leaf litter N changed within the range observed in each of the *F. crenata* subplots and *A. mariesii* subplots.

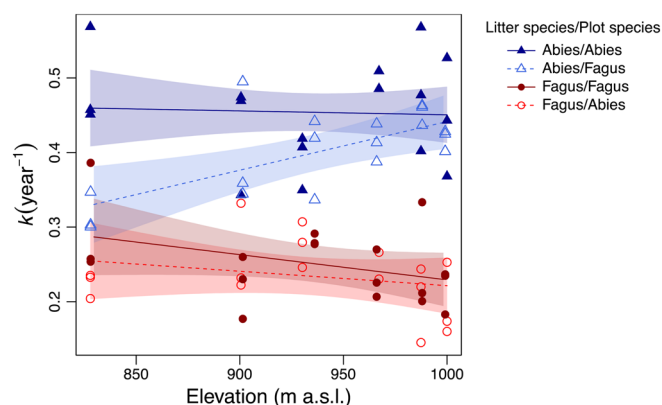


Figure 4. Decay rate constants for litter mass (k) as a function of elevation for the four treatment groups. The shaded areas represent 95% confidence intervals for the relationships. For the significance of the factors and their interactions, see Table 1. The plot was made using the 'partial.plot' (Oguro 2021) and 'emmeans' (Lenth 2016) packages.

In the HFAI model based on the decomposition model, for a factor to affect HFAI, the factor must affect the difference in decomposition rate between home and away. This effect was represented by the interactions between factor $\times$ 'Home or away' and factor $\times$ 'Home or away' $\times$ 'Litter species' in the GLM (Fig. 7, Supporting information). A larger estimated value of an interaction term indicates that a given factor has a stronger effect on HFAI. Among the examined factors, soil pH and leaf litter N had stronger effects on HFAI (Fig. 7). HFAI decreased from ca 9.5 – 6% (arrow A in Fig. 6b) and from ca 10 – 7.3% (arrow A in Fig. 6f) with increasing soil pH and leaf litter N content, respectively, shown as changes in HFAI along the dashed diagonal line in each panel, when it was hypothesized that there were no differences in the explanatory factors between the *F. crenata* plots and *A. mariesii* plots. Variations in the other factors changed HFAI less than 1% (Fig. 6a, c, d, e, g, h).

We then focused on the effects of differences in the explanatory factors between the *F. crenata* plots and the *A. mariesii* plots at the same elevations and found that differences in soil pH and soil C between the *F. crenata* plots and the *A. mariesii* plots had relatively large influences on the magnitude of HFAI (Fig. 6b, e). Soil pH was generally higher in the *F. crenata* plots than in the *A. mariesii* plots (shown as points in each panel), which increased HFAI up to ca 3% (arrow B in Fig. 6b). Soil C was generally higher in the *A. mariesii* plots than in the *F. crenata* plots, which decreased HFAI up to ca 10% (arrow B in Fig. 6e).

Discussion

The HFA for decomposition between *A. mariesii* and *F. crenata* litter

We found that the leaf litter decomposition rates were often higher at home than away for both species (Fig. 4, Table 1), resulting in the range of -3.89 to 28.30% in HFAI between the two species calculated using the observed decomposition rate (Table 2). The modeled HFAI between the two species

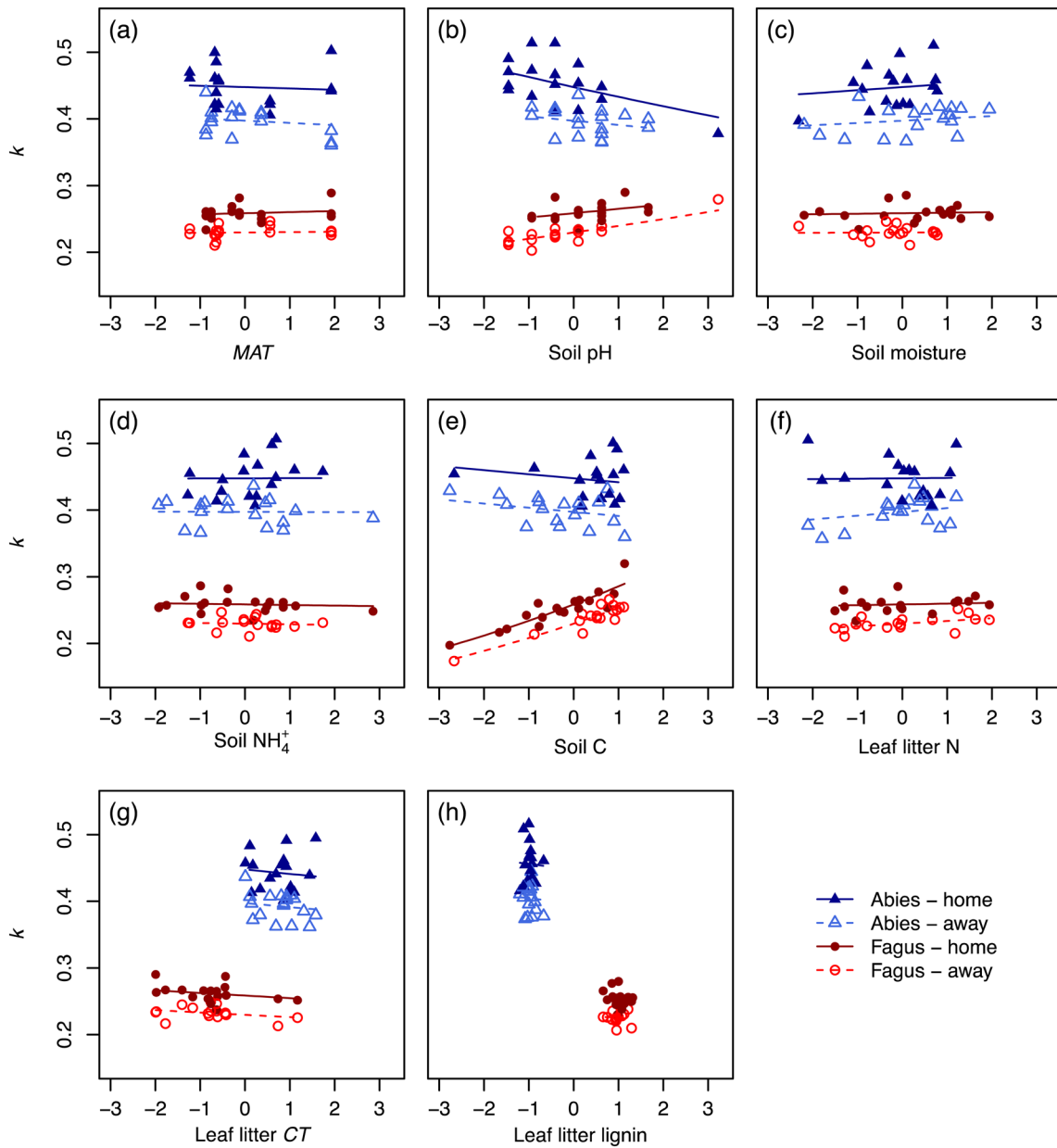


Figure 5. The predicted relationships of standardized (i.e. scaled to have mean = 0 and standard deviation = 1) (a) mean annual temperature (MAT), (b) soil pH, (c) soil moisture, (d) soil ammonium (NH_4^+), (e) soil carbon (C), (f) leaf litter nitrogen (N) content, (g) leaf litter condensed tannins content (CT), and (h) leaf litter lignin content, to the litter decay rate constant (k) for *A. mariesii* and *F. crenata* in home and away conditions. Lines represent predicted relationships for each condition and points represent partial residuals of k for each subplot. Values of explanatory variables other than the one on the x-axis were fixed at zero.

possibly varies from ca -5 to 25%, depending on changes in the explanatory factors and the differences in the factors between the two species plots (Fig. 6), which was comparable to the range of the observed HFAI. These observed and modeled variations in HFAI were comparable to the variation found in the meta-analysis with 35 reciprocal leaf litter transplants among a variety of tree species (Ayres et al. 2009b). Thus, even in a reciprocal leaf litter transplant between two species, the magnitude of the HFA could vary widely depending on the examined factors and their differences between home and away.

Factors that influence the magnitude of HFA

The influences of soil pH and leaf litter N on HFAI were larger than the other factors, including MAT, on the magnitude of HFA (Fig. 7). The HFA was higher in more acidic soils and for less-decomposable litter (Fig. 6b, f). These observations partly support our hypothesis that HFA is higher in soils that are unfavorable for decomposition and induced by less-decomposable litter traits (Aerts 1997, Ayres et al. 2009b, Freschet et al. 2012, Veen et al. 2015b). The effects were caused by the fact that the relationship between soil pH

Table 2. HFAI calculated for each plot pair at each elevation using observed values of k . The six pairs of plots along an elevation gradient are numbered with A (dominated by *A. mariesii*) and F (dominated by *F. crenata*) as shown in Fig. 1b. The number in the parentheses indicate elevation in meter above sea level.

Plot pair	HFAI % calculated with measured k
1A (828)-1F (828)	28.30
2A (901)-2F (901)	-3.89
3A (930)-3F (936)	0.02
4A (967)-4F (966)	3.30
5A (987)-5F (988)	9.68
6A (1000)-6F (999)	6.18

or leaf litter N and the decomposition rate differed between the home and away plots for both species (Fig. 5b, f, 7). The decomposition rate of *F. crenata* litter decreased as soil acidity increased, whereas that of *A. mariesii* increased (Fig. 5b), even though soil acidity generally reduces microbial activity. This may be due to soil decomposers in acidic soils being more able to adapt and decompose *A. mariesii* leaf litter in nature. As a coniferous tree, *A. mariesii* has a higher content of soluble phenolics (total phenolics and condensed tannins) in its leaves (Fig. 2d–e) than *F. crenata*, which could make the soils under *A. mariesii* trees more acidic. The decomposition rate increased more as soil acidity increased in the home plots compared to the away plots for *A. mariesii*. In contrast, the decomposition rate decreased more as soil acidity increased in the away plots than in the home plots for *F. crenata* (Fig. 5b). Thus, the differences in the decomposition rate between the home and away plots became greater in more acidic soil for both species, which eventually increased the HFA of the two species as soil acidity increased (Fig. 6b). On the other hand, the leaf litter decomposition of each species decreased as leaf litter N concentrations decreased in the away plots, although leaf litter N had relatively small effects on decomposition of both species in the home plots (Fig. 5f), resulting in a greater HFAI between the two species at lower concentrations of leaf litter N (Fig. 6f–7).

The concentration of condensed tannins and lignin in the leaf litter scarcely affected HFAI (Fig. 6g–h), although both are known to slow decomposition (Cornwell et al. 2008, Chomel et al. 2016, Supporting information). This is because they did not affect differences in decomposition between the home and away plots for either species (Fig. 7). The variation in lignin concentration for each species, along the elevation gradient, was very small in this study (Fig. 2f).

We also found that the dissimilarity in plot properties, especially soil pH and soil C, between the *F. crenata* and *A. mariesii* plots at a given elevation influenced HFAI (Fig. 6b, e). This partly supported previous findings that the magnitude of HFA increases when the plot or soil properties become more different between the home and away plots (Ayres et al. 2009b, Freschet et al. 2012), although differences in soil C between home and away plots decreased HFAI. Earlier studies suggested that such dissimilarity was a better predictor of the magnitude of the HFA than changes in the factors themselves (Veen et al. 2015a). However, in our study, the influence of the dissimilarity varied depending

on the types of factors. For example, the effect of the dissimilarity between soil pH in the *F. crenata* and *A. mariesii* plots at the same elevation (ca 3% change) was comparable to the effect of soil pH itself (ca 3.5% change) on HFAI (Fig. 6b). On the other hand, HFAI was only slightly influenced by the soil C content itself, because the responses of the decomposition rate to the soil C content were similar in the home and away plots for both species (Fig. 5e, Supporting information). However, the dissimilarity in soil C content between the *F. crenata* and *A. mariesii* plots greatly affected HFAI (ca 10% change) (Fig. 6e). This is in part because the change of the decomposition rate of *F. crenata* litter with soil C content (i.e. the slope in Fig. 5e) was the largest among the relationships between the examined factors and the decomposition rate. Thus, the difference in the decomposition rate of *F. crenata* litter was sensitive to differences in the soil C content between the home and away plots, which could greatly affect the magnitude of the HFA between the two species, presumably through the HFA for *F. crenata*. Soil C content can be an indicator of microbial biomass (Wardle 1998), and *F. crenata* leaf litter (with a higher lignin concentration) may need more or specific soil microbes to promote decomposition. Moreover, if the transplants were conducted between the *F. crenata* and *A. mariesii* plots in all possible combinations across elevations (although the actual transplants were only conducted between the two species at the same elevation), HFAI could vary greatly within a range of 30% (Fig. 6e). Thus, differences in soil microbes (e.g. fungi and bacteria) could be very important factors influencing the magnitude of the HFA. Further study is needed to investigate the relationship between the HFA and soil microbial composition and activities (Keiser et al. 2014).

In summary, changes in factors, which had relatively large (soil pH) or small (leaf litter N) effects on the decomposition rate of each species in their home soil, influenced the magnitude of HFA. In addition, like the case of soil C, differences between home and away could have a large influence on the magnitude of the HFA, even though changes in the factors do not.

Response of the decomposition rate to future climate change

Our study demonstrates that factors that do or do not directly affect the decomposition rate could indirectly affect the decomposition rate via the HFA. This result is different from what Veen et al. (2015b) found in their reciprocal decomposition experiment conducted in subarctic tundra. They transplanted leaf litter decomposition among three types of vegetation (heath-, meadow-, and *Salix*-dominated) along an elevation gradient, and observed that the occurrence of the HFA was limited and factors that drive litter decomposition did not play major roles in determining the magnitude of the HFA (Veen et al. 2015b). The reasons for the lack of HFA between the vegetation types in Veen et al. (2015a, b), as the authors discussed, may be that their studied litter consisted of a mixture of several coexisting plant species with contrasting

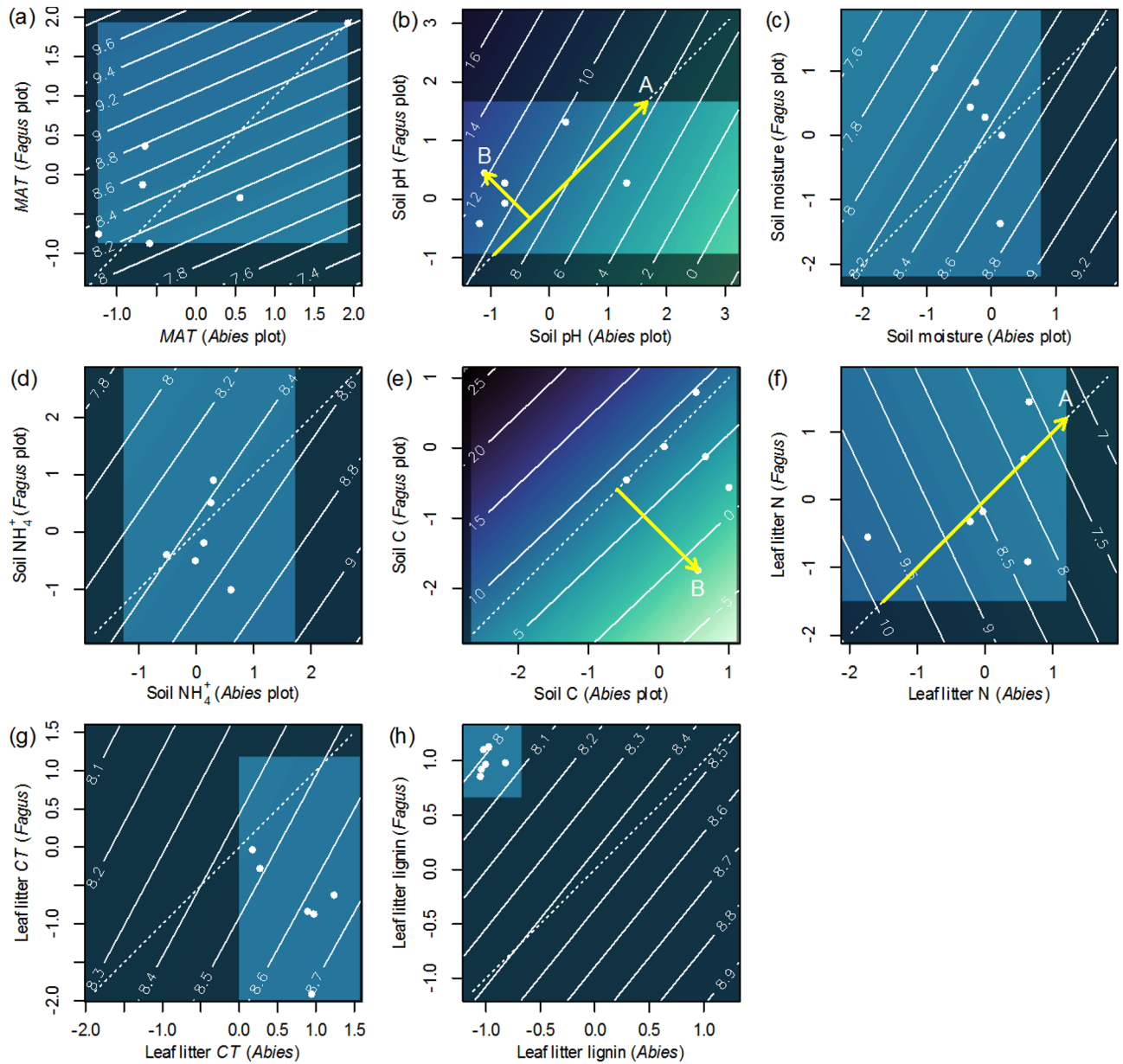


Figure 6. Predicted dependence of the home-field advantage index (HFAI) on the explanatory variables in the *Abies* and *Fagus* plots or of the *Abies* and *Fagus* litters: (a) mean annual temperature (MAT), (b) soil pH, (c) soil moisture, (d) soil ammonium (NH_4^+), (e) soil carbon (C), (f) leaf litter nitrogen content, (g) leaf litter condensed tannins (CT) content, and (h) leaf litter lignin content. The contour and background color of each panel represent estimated values of HFAI. Shaded area represents extrapolation, i.e. outside of the observed range of the explanatory variable for all measurements. The dotted diagonal lines represent $y=x$ and change in contour values along the lines indicate predicted changes in HFAI corresponding to the changes in the explanatory variables assuming no difference in the variables between the *Abies* and *Fagus* plots or *Abies* and *Fagus* litters. For example, a change in standardized soil pH from -1 to 2 (, arrow A) both in *Abies* and *Fagus* plots changes HFAI by ca 3. Points represent mean values of the explanatory variables for each elevation. For MAT and soil properties, changes in contour values between the points and the diagonal lines indicate changes in HFAI due to differences in the explanatory variables between the home and away plots (e.g. arrow B in b and e). Note that values of the explanatory variables other than the focal ones were fixed at their means across the species (i.e. zero) when calculating HFAI. Therefore, absolute values of HFAI can change depending on the values of other explanatory variables.

qualities, each potentially experiencing different home-field effects. This may mask very local-scale HFA effects that occur at the species level because neighboring plants may promote contrasting decomposer communities that are each adapted to break down their own litter (Freschet et al. 2012), or

there may be stimulation interactions among different qualities of litter (Gartner and Cardon 2004, Klotzsch et al. 2011), although such a community-level approach accounts for complex environmental conditions and species interactions that occur in natural ecosystems. On the other hand,

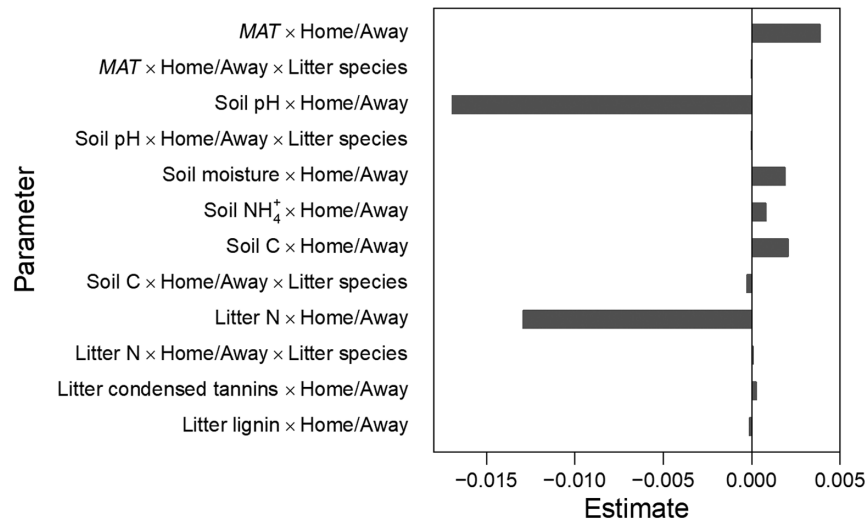


Figure 7. Estimated values of interaction terms including ‘Home or away’ in the averaged model shown in the Supporting information. They indicate the magnitude of influences on HFA between the two species.

our empirical experiments in natural conditions with modeling for two distinct species can explicitly show how the litter qualities and environmental conditions control the HFA. Both types of studies are needed for better understanding of how compositional changes in plant communities affect material cycles through HFA in changing climates. Moreover, our study suggests that the dissimilarity in some soil properties between home and away could influence the magnitude of the HFA. Thus, if the compositional change in plant community due to climate change decoupled the specific interaction between plants and soil decomposer communities, the response of decomposition to environmental changes might vary not only through the direct effects of vegetation traits but also through indirect effects on the HFA (Keiser and Bradford 2017). In our study area, it is expected that climate change will cause *F. crenata* to shift upward into forests where *A. mariesii* is currently dominant (Matsui et al. 2004). In such situations, consideration of the HFA becomes important for accurately predicting the response of local carbon and nutrient cycles to climate change.

Conclusions

The magnitude of the HFA between *A. mariesii* and *F. crenata* leaf litter decomposition varied widely from -3.89 to 28.3% , even though only two species were compared. Its strength was influenced by both a factor that affected leaf litter decomposition (soil pH) and another that scarcely affected the decomposition (leaf litter N) of each species. Our results suggest that the magnitude of the HFA increased as soil acidity increased (under unfavorable conditions for decomposition), and as the leaf litter N content decreased (for less-decomposable litter) in the expected way. Moreover, differences in soil properties, especially soil C and soil pH, between home and away conditions could have larger influences on the magnitude of

the HFA than the changes of the factors themselves. It will be necessary to expand our study to include factors such as the characteristics of the decomposer communities under a dominant species, which should be an important driver of HFA effects. Further, HFA effects should be tested across a large number of plant species, including reciprocal transplant experiments with three or more species, because the magnitude of the HFA varies greatly among plant species and the HFA should be quantified separately from site effects and litter qualities. Such future studies will be essential for more fully understanding the mechanisms responsible for the effect of the home-field advantage on leaf litter decomposition and improving estimates of future carbon cycles.

Acknowledgements – We thank Kohei Iwai and Keisuke Hashimoto from Tohoku University for helping with the field work. We also thank the staff of the Tohoku University Botanical Garden in Hakkoda and the Forest Dynamics Laboratory, Forestry and Forest Products Research Institute, in Tsukuba, Japan, who made this study possible.

Funding – This study was supported by the Global Environmental Research Fund of Japan’s Ministry of the Environment (no. D-0904), by a research grant from the Mitsui & Co. Ltd. Environment Fund (no. R11-G4-1046), Japan, and by a Japan Society for the Promotion of Science KAKENHI grant (no. 26281049, 17H03835) to TN and HK.

Author contributions

Maya Misha Daumal, Michi Oguro and Hiroko Kurokawa contributed equally to this publication. **Maya Mischa Daumal**: Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Michio Oguro**: Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal).

Miki U. Ueda: Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Sakino Takayanagi:** Investigation (supporting). **Tohru Nakashizuka:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Hiroko Kurokawa:** Conceptualization (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8pk0p2nrs> (Daumal et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. – *Oikos* 79: 439–449.
- Ayres, E., Steltzer, H., Berg, S. and Wall, D. H. 2009a. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. – *J. Ecol.* 97: 901–912.
- Ayres, E., Steltzer, H., Simmons, B. L., Simpson, R. T., Steinweg, J. M., Wallenstein, M. D., Mellor, N., Parton, W. J., Moore, J. C. and Wall, D. H. 2009b. Home-field advantage accelerates leaf litter decomposition in forests. – *Soil Biol. Biochem.* 41: 606–610.
- Ball, B. A., Bradford, M. A., Coleman, D. C. and Hunter, M. D. 2009. Linkages between below and aboveground communities: decomposer responses to simulated tree species loss are largely additive. – *Soil Biol. Biochem.* 41: 1155–1163.
- Bartoň, K. 2023. MuMIn: Multi-Model Inference R package ver. 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Soft.* 67: 1–48.
- Berg, B. and McClaugherty, C. 2014. Plant litter: decomposition, humus formation, carbon sequestration. – Springer.
- Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R. and Wood, S. A. 2016. Understanding the dominant controls on litter decomposition. – *J. Ecol.* 104: 229–238.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Chomel, M., Guittonny-Larchevêque, M., Fernandez, C., Gallet, C., DesRochers, A., Paré, D., Jackson, B. G. and Baldy, V. 2016. Plant secondary metabolites: a key driver of litter decomposition and soil nutrient cycling. – *J. Ecol.* 104: 1527–1541.
- Cornwell, W. K. et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. – *Ecol. Lett.* 11: 1065–1071.
- Daumal, M. M., Oguro, M., Ueda, M. U., Takayanagi, S., Nakashizuka, T. and Kurokawa, H. 2024. Data from: What makes decomposition faster under conspecific trees? The factors controlling the magnitude of home-field advantage. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.8pk0p2nrs>.
- Du, H., Liu, J., Li, M., Büntgen, U., Yang, Y., Wang, L., Wu, Z. and He, H. S. 2018. Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. – *Global Change Biol.* 24: 1256–1266.
- Dullinger, S., Dirnböck, T. and Grabherr, G. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. – *J. Ecol.* 92: 241–252.
- Fox, J. and Weisberg, S. 2011. An R companion to applied regression. – SAGE Publications.
- Freschet, G. T., Aerts, R. and Cornelissen, J. H. C. 2012. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. – *J. Ecol.* 100: 619–630.
- Fukushima, R. S. and Hatfield, R. D. 2001. Extraction and isolation of lignin for utilization as a standard to determine lignin concentration using the acetyl bromide spectrophotometric method. – *J. Agric. Food Chem.* 49: 3133–3139.
- Gartner, T. B. and Cardon, Z. G. 2004. Decomposition dynamics in mixed-species leaf litter. – *Oikos* 104: 230–246.
- Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E. and Parton, W. J. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. – *Global Change Biol.* 6: 751–765.
- Iiyama, K. and Wallis, A. F. A. 1990. Determination of lignin in herbaceous plants by an improved acetyl bromide procedure. – *J. Sci. Food Agric.* 51: 145–161.
- Johansson, M.-B., Berg, B. and Meentemeyer, V. 1995. Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests. Long-term decomposition in a Scots pine forest. IX. – *Can. J. Bot.* 73: 1509–1521.
- Julkunen-Tiitto, R. 1985. Phenolic constituents in the leaves of northern willows: methods for the analysis of certain phenolics. – *J. Agric. Food Chem.* 33: 213–217.
- Kagata, H. and Ohgushi, T. 2013. Home-field advantage in decomposition of leaf litter and insect frass. – *Popul. Ecol.* 55: 69–76.
- Keiser, A. D. and Bradford, M. A. 2017. Climate masks decomposer influence in a cross-site litter decomposition study. – *Soil Biol. Biochem.* 107: 180–187.
- Keiser, A. D., Keiser, D. A., Strickland, M. S. and Bradford, M. A. 2014. Disentangling the mechanisms underlying functional differences among decomposer communities. – *J. Ecol.* 102: 603–609.
- Klotzbücher, T., Filley, T. R., Kaiser, K. and Kalbitz, K. 2011. A study of lignin degradation in leaf and needle litter using ¹³C-labelled tetramethylammonium hydroxide (TMAH) thermochemolysis: comparison with CuO oxidation and van Soest methods. – *Organic Geochem.* 42: 1271–1278.
- Kuzyakov, Y. 2010. Priming effects: interactions between living and dead organic matter. – *Soil Biol. Biochem.* 42: 1363–1371.
- Lenth, R. V. 2016. Least-squares means: the R package lsmeans. – *J. Stat. Soft.* 69: 1–3.
- Matsui, T., Yagihashi, T., Nakaya, T., Taoda, H., Yoshinaga, S., Daimaru, H. and Tanaka, N. 2004. Probability distributions, vulnerability and sensitivity in *Fagus crenata* forests following predicted climate changes in Japan. – *J. Veg. Sci.* 15: 605–614.
- Milcu, A. and Manning, P. 2011. All size classes of soil fauna and litter quality control the acceleration of litter decay in its home environment. – *Oikos* 120: 1366–1370.

- Oguro, M. 2021. partial.plot: partial dependence plot for statistical/machine learning models. – R package ver. 0.2.4, <https://github.com/Marchen/partial.plot>.
- Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. – *Ecology* 44: 322–331.
- Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., King, J. Y., Adair, E. C., Brandt, L. A., Hart, S. C. and Fath, B. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. – *Science* 315: 361–364.
- Perez, G., Aubert, M., Decaëns, T., Trap, J. and Chauvat, M. 2013. Home-field advantage: a matter of interaction between litter biochemistry and decomposer biota. – *Soil Biol. Biochem.* 67: 245–254.
- Salinas, N., Malhi, Y., Meir, P., Silman, M., Roman Cuesta, R., Huaman, J., Salinas, D., Huaman, V., Gibaja, A., Mamani, M. and Farfan, F. 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. – *New Phytol.* 189: 967–977.
- Shimazaki, M., Sasaki, T., Hikosaka, K. and Nakashizuka, T. 2011. Environmental dependence of population dynamics and height growth of a subalpine conifer across its vertical distribution: an approach using high-resolution aerial photographs. – *Global Change Biol.* 17: 3431–3438.
- St. John, M. G., Orwin, K. H. and Dickie, I. A. 2011. No ‘home’ versus ‘away’ effects of decomposition found in a grassland–forest reciprocal litter transplant study. – *Soil Biol. Biochem.* 43: 1482–1489.
- Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. – Univ. of California Press.
- Symonds, M. R. E. and Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. – *Behav. Ecol. Sociobiol.* 65: 13–21.
- Ueda, M. U., Kachina, P., Marod, D., Nakashizuka, T. and Kurokawa, H. 2017. Soil properties and gross nitrogen dynamics in old growth and secondary forest in four types of tropical forest in Thailand. – *For. Ecol. Manage.* 398: 130–139.
- Van Der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van De Voorde, T. F. J. and Wardle, D. A. 2013. Plant–soil feedbacks: the past, the present and future challenges. – *J. Ecol.* 101: 265–276.
- Veen, G. F. (Ciska), Freschet, G. T., Ordonez, A. and Wardle, D. A. 2015a. Litter quality and environmental controls of home-field advantage effects on litter decomposition. – *Oikos* 124: 187–195.
- Veen, G. F. (Ciska), Sundqvist, M. K. and Wardle, D. A. 2015b. Environmental factors and traits that drive plant litter decomposition do not determine home-field advantage effects. – *Funct. Ecol.* 29: 981–991.
- Veen, G. F. (Ciska), Keiser, A. D., Van der Putten, W. H. and Wardle, D. A. 2018. Variation in home-field advantage and ability in leaf litter decomposition across successional gradients. – *Funct. Ecol.* 32: 1563–1574.
- Wang, Q., Zhong, M. and He, T. 2013. Home-field advantage of litter decomposition and nitrogen release in forest ecosystems. – *Biol. Fertil. Soils* 49: 427–434.
- Wardle, D. A. 1998. Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. – *Soil Biol. Biochem.* 30: 1627–1637.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H. and Wall, D. H. 2004. Ecological linkages between aboveground and belowground biota. – *Science* 304: 1629–1633.
- Waterman, P. G. and Mole, S. 1994. Analysis of phenolic plant metabolites. – Blackwell Scientific.
- Zhou, Y., Clark, M., Su, J. and Xiao, C. 2015. Litter decomposition and soil microbial community composition in three Korean pine (*Pinus koraiensis*) forests along an altitudinal gradient. – *Plant Soil* 386: 171–183.