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Home-field advantage in decomposition of leaf litter and insect frass

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Abstract Home-field advantage (HFA) hypothesis regarding litter decomposition states that litter is decomposed more rapidly in the habitat from which it is derived (i.e., home) than in other habitat (i.e., away) due to local adaptation of soil decomposers. We tested the HFA hypothesis regarding decomposition of leaf litter, insect frass, and their mixtures, using laboratory incubation of leaf litter from an evergreen (*Pinus densiflora*) and a deciduous (*Quercus acutissima*) tree species, frass excreted by two insect herbivores (*Dendrolimus spectabilis* and *Lymantria dispar*) fed on one of the two trees, and soil collected underneath the two trees. We found evidence that decomposers in each soil were specialized to decompose the litter derived from the tree species above them, indicating that the HFA occurred in litter decomposition. In contrast, the HFA was not detected in the decomposition of insect frass or litter-frass mixtures. Mixing with *D. spectabilis* frass non-additively decelerated, while mixing with *L. dispar* frass non-additively accelerated, decomposition of the mixtures, independent of soil and litter types. These indicate that the presence of insect herbivores may make it difficult to form and maintain a decomposer community specialized to a certain leaf litter, and that it may consequently cancel or weaken HFA in litter decomposition.

Keywords Insect outbreaks · Insect-plant interaction · Non-additive effect · Soil-litter interaction

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Introduction

Leaf litter inputs are major sources of energy and nutrients for the decomposition process in forests (Cebrian 1999; Wardle et al. 2002). Leaf litter from different tree species generally differs in physical and chemical characteristics, which can determine the community structure of soil decomposers and litter decomposition rate (Negrete-Yankelevich et al. 2008; St. John et al. 2011). One can expect that soil decomposers may be specialized to decompose leaf litter derived from trees above them (Ayres et al. 2009). Hence, it has been suggested that leaf litter may be decomposed faster in the habitat from which it is derived (i.e., home) than in other habitat (i.e., away), which is called the home-field advantage (HFA) hypothesis for litter decomposition (Gholz et al. 2000). Several studies have tested this hypothesis using litter-bag experiments with litter transplantation between home and away environments, and found that litter was decomposed faster in its home than in away environments (e.g., Negrete-Yankelevich et al. 2008; Vivanco and Austin 2008, but see St. John et al. 2011). Moreover, Ayres et al. (2009) conducted a meta-analysis to test the HFA hypothesis based on published data of litter decomposition in forests. They showed that HFA commonly occurs in forest ecosystems, and that the litter decomposition rate was approximately 8% greater in home than in away environments.

In addition to leaf litter, excrements of insect herbivores (i.e., frass and honeydew) are also important as energy and nutrient sources for the decomposition process in forests when insects occur at high density (Hunter 2001). It is generally thought that insect excrement represents a minor fraction of energy and nutrients in terrestrial ecosystems because of the low herbivory rate, i.e., less than 20 % (Cyr and Pace 1993; Cebrian and Lartigue 2004). However, a

wide range of insect herbivores in forests sometimes show outbreaks and reach to extremely high density (Schowalter 2000; Kamata 2002), at which the amount of insect excrement can reach a critical level of energy and nutrient inputs affecting the decomposition process (Hunter 2001; Lovett et al. 2002; Clark et al. 2010). There is increasing appreciation that frass of insect herbivores has significant impacts on decomposition and soil nutrient availability (Hunter 2001; Lovett et al. 2002). Insect frass contains higher concentrations of nitrogen (N) and labile carbon (C) than does leaf litter (Lovett and Ruesink 1995; Madritch et al. 2007). It can enhance microbial growth (Frost and Hunter 2004), which in turn accelerates the decomposition rate (Zimmer and Topp 2002), N mineralization, and N immobilization (Lovett and Ruesink 1995; Frost and Hunter 2007). The chemical characteristics of insect frass, such as C:N ratio and tannins, are largely dependent on those of the host plant leaves (Madritch et al. 2007; Kagata and Ohgushi 2011), and influence the decomposition process of the frass (Madritch et al. 2007; Kagata and Ohgushi 2012a). Therefore, similarly to leaf litter decomposition, insect frass may also be decomposed faster underneath the tree species on which the insect fed than underneath other tree species. However, to our knowledge there have been no studies exploring whether the HFA hypothesis is applicable to insect frass decomposition. Elucidating the decomposition features of insect frass should contribute importantly to further understanding how insect outbreaks influence litter decomposition and nutrient cycling in terrestrial ecosystems.

Here, we tested the HFA hypothesis for decomposition of leaf litter, insect frass, and their mixtures, using laboratory incubation of leaf litter from an evergreen and a deciduous tree species, frass excreted by two insect herbivores fed on one of the two trees, and soil collected underneath the two trees.

Materials and methods

Collection of soil, leaf litter, and insect frass

Soil, leaf litter, and insect herbivores were collected in and around an experimental field of the Center for Ecological Research (forest of CER; 34°97′N, 135°96′E), Kyoto University, in Shiga prefecture, central Japan. The secondary forest includes more than 50 tree species occurring naturally and artificially. We selected two tree species for the present study: Japanese red pine, *Pinus densiflora* Siebold. & Zucca. (Pinaceae) and sawtooth oak, *Quercus acutissima* Carruth. (Fagaceae). *Pinus densiflora* and *Q. acutissima* are evergreen coniferous and deciduous broad-leaved trees, respectively. They are commonly co-occur in temperate forests in Japan. The soil was collected underneath (<5 cm in depth) five *P. densiflora* and five *Q. acutissima* trees in late November 2010. It was air-dried for 1 month and passed though a 2 mm sieve. Although the soil was used as the source of microbial decomposers in the present study, we noted that the microbial communities may have been, to some extent, affected by the drying. After samples were isolated from the soil for CN analysis, the remaining soil was pooled for each tree species. They were stored at 5 °C until the incubation experiment or CN analysis. We also collected leaf litter underneath 10 trees of each tree species in late November 2010. Similarly to the soil, the litter was air-dried for 1 month, and stored at 5 °C.

The pine caterpillar, *Dendrolimus spectabilis* Bulter (Lepidoptera: Lasiocampidae), and gypsy moth, *Lymantria dispar* (Linnaeus) (Lepidoptera: Lymantriidae), are important insect pests for coniferous and broad-leaved forests, respectively, and several outbreaks of these two insects have been recorded in Japan (Kamata 2002). *Dendrolimus spectabilis* is generally univoltine, but partly bivoltine, in central Japan, and overwinters as larvae. Overwintered larvae start to feed on the host plants in March and pupate in June to July in this area, although there is a large phenological variation among individuals (Habu 1969). Larvae of *D. spectabilis* exclusively feed on Pinaceae species (Kamata 2002). We collected 3rd- to 5th-instar larvae from several *P. densiflora* trees in November 2009. The larvae were placed in 3-l plastic containers with *P. densiflora* leaves in dark and temperature-uncontrolled (i.e., without heater) rooms until the end of March 2010. Approximately 50 individuals of *D. spectabilis* successfully overwintered. In April, the overwintered larvae were transferred to 3-l containers, with a maximum of five individuals per container, in an environmental chamber at 25 °C with a LD 16:8 h cycle. One-year leaves of *P. densiflora* collected from ten randomly selected trees were provided as food and replaced with new ones every day. When the larvae reached the final instar (mostly 8th-instar larvae), 15 larvae were randomly transferred individually to a 500-ml plastic cup with leaves of *P. densiflora*. The frass was collected for 3 days. Thereafter, the larvae were kept for 24 h without food to allow them to excrete the frass in their gut. These frass and larvae were used for CN analysis. The one-year leaves of *P. densiflora* from the ten trees were also collected for CN analysis. The frass, larvae, and leaves were oven-dried at 60 °C for 1 week, and stored at 5 °C until CN analysis. The remaining larvae (more than 30 individuals) continued to be reared in the 3-l containers, and the frass was collected every day until pupation for the incubation experiment. Collected frass was pooled, oven-dried, and stored at 5 °C until the experiment.

Lymantria dispar is univoltine and overwinters as eggs. Larvae generally hatch in March to April and pupate in

June in central Japan. They are highly polyphagous and can feed on over 500 plant species, including many deciduous broad-leaved trees such as Betulaceae, Fagaceae, Salicaceae, and Tiliaceae (Barbosa and Krischik 1987; Liebhold et al. 1995). We collected egg masses of *L. dispar* from several tree species in the forest of CER in March 2010. Each egg mass was placed in a petri dish (9 cm in diameter) in a temperature-uncontrolled room. When the larvae hatched, they were transferred to 3-l containers in an environmental chamber at 25 °C with a LD 16:8 h cycle with newly flushed leaves of *Q. acutissima*. Larval rearing and frass collection for *L. dispar* were done in a similar manner to that for *P. densiflora*. The frass of *P. densiflora* and *L. dispar* was collected in the same period, i.e., from late May to early June.

Incubation experiment

Decomposition of leaf litter and insect frass was examined by an incubation experiment in a laboratory microcosm. Before the experiment, leaf litter and insect frass were each roughly ground and mixed well to obtain homogeneous quality. Soil, litter, and/or frass (1.5 g in total, see Table 1) was placed in a 50-ml glass vial (35 mm in diameter and 65 mm in height) with 2 ml of distilled water, which brought the samples to 60–70 % of the water capacity of the substrates. These substrates made an approximately 5-mm layer at the bottom of the vial. We established 18 treatments consisting of various combinations of soil, litter, and frass, including home and away environments (Table 1). Soil:litter and soil:frass mass ratios of 1:1 (i.e., 750:750 mg) were arbitrarily used. Litter : frass ratio in the treatments of soil + litter + frass mixtures was also set as 1:1 (i.e., 375:375 mg), which is roughly equal to the observed ratio during a gypsy moth outbreak in a northeastern US forest reported by Clark et al. (2010). Note that our experimental design for incubation of the litter and frass mixtures would not simulate the natural condition; decomposition of litter and frass was examined simultaneously in the present study, while the insect frass and the leaf litter are loaded to the soil in spring and autumn, respectively, in natural ecosystem. This difference may, to some extent, distort outputs of the incubation experiment. The glass vials with plastic lids were placed in the dark at 25 °C in an environmental chamber for 2 months. Although we did not supply additional water, the surface of the substrate remained wet during the incubation. After the incubation, the test materials were oven-dried at 60 °C for 2 weeks in order to measure dry weight. Dry weight was measured as total weight of soil, litter and/or frass in a vial, because isolation of these compounds was not possible. Fifteen replications were conducted for each treatment. The

Table 1 Treatments for incubation experiments

Treatment code	Substrates in the vial			H/A
	Soil	Leaf litter	Insect frass	
PS	PS (1500 mg)	–	–	–
QS	QS (1500 mg)	–	–	–
PS + PL	PS (750 mg)	PL (750 mg)	–	H
PS + QL	PS (750 mg)	QL (750 mg)	–	A
QS + PL	QS (750 mg)	PL (750 mg)	–	A
QS + QL	QS (750 mg)	QL (750 mg)	–	H
PS + PF	PS (750 mg)	–	PF (750 mg)	H
PS + QF	PS (750 mg)	–	QF (750 mg)	A
QS + PF	QS (750 mg)	–	PF (750 mg)	A
QS + QF	QS (750 mg)	–	QF (750 mg)	H
PS + PL + PF	PS (750 mg)	PL (375 mg)	PF (375 mg)	H
PS + PL + QF	PS (750 mg)	PL (375 mg)	QF (375 mg)	A
PS + QL + PF	PS (750 mg)	QL (375 mg)	PF (375 mg)	A
PS + QL + QF	PS (750 mg)	QL (375 mg)	QF (375 mg)	A
QS + PL + PF	QS (750 mg)	PL (375 mg)	PF (375 mg)	A
QS + PL + QF	QS (750 mg)	PL (375 mg)	QF (375 mg)	A
QS + QL + PF	QS (750 mg)	QL (375 mg)	PF (375 mg)	A
QS + QL + QF	QS (750 mg)	QL (375 mg)	QF (375 mg)	H

PS, soil collected underneath *P. densiflora*; QS, soil collected underneath *Q. acutissima*; PL, leaf litter of *P. densiflora*; QL, leaf litter of *Q. acutissima*; PF, frass excreted by *D. spectabilis* larvae fed on *P. densiflora* leaves; QF, frass excreted by *L. dispar* larvae fed on *Q. acutissima* leaves; H, home-field environment; A, away-field environment

decomposition of litter and frass was assessed by the reduction in dry mass during the incubation, because reduction of soil mass was negligibly small (see "Results").

Carbon and nitrogen analysis

Before the analysis, all samples (soil, fresh leaves, leaf litter, insect frass, and larvae) were ground to fine powder. Total C and N contents were determined using an elemental analyzer (JM 1000CN: J-Science Co., LTD, Kyoto, Japan).

Statistical analyses

Differences in the N concentration and C:N ratio of the soil, fresh leaves, leaf litter, insect body, and frass were compared using one-way ANOVAs, The differences in dry mass loss after incubation were separately compared for soil, soil + litter mixture, soil + frass mixture, and soil + litter + frass mixture, using one-way, two-way, two-way, and three-way ANOVAs, respectively. The differences among all treatments were also compared by a Tukey–Kramer HSD multiple comparison ($P < 0.05$).

Presence of HFA was determined using the ANOVA and HFA index (HFAI) (Ayres et al. 2009). Significant soil-by-litter (or frass) interaction and soil-by-litter-by frass interaction could indicate that HFA occurred in decomposition of litter (or frass) and of litter + frass mixture, respectively. HFA was also evaluated quantitatively using HFAI. The relative mass loss of substrate (RML), for example, in litter decomposition at home environments for *Pinus* system was calculated as:

$$\mathrm{RML}_{(\mathrm{PS+PL})} = \frac{\mathrm{ML}_{(\mathrm{PS+PL})}}{\mathrm{ML}_{(\mathrm{PS+PL})} + \mathrm{ML}_{(\mathrm{PS+QL})}} \times 100$$

where ML represents mean mass loss of each treatment (see Table 1 for treatment code). RMLs in other treatments were also calculated as same manner. Then, HFAI for decomposition of litter was calculated as:

$$\mathrm{HFAI}_{(\mathrm{litter})} = \left[\frac{\mathrm{RML}_{(\mathrm{PS+PL})} + \mathrm{RML}_{(\mathrm{QS+QL})}}{2} \Big/ \frac{\mathrm{RML}_{(\mathrm{PS+QL})} + \mathrm{RML}_{(\mathrm{QS+PL})}}{2} \right] \times 100 - 100$$

where HFAI shows the percent faster mass loss of litter when it decomposed at home versus away environments (Ayres et al. 2009). HFAIs for decomposition of frass and litter + frass mixture were also calculated as a same manner.

We also examined whether mixing of leaf litter and insect frass non-additively accelerates their decomposition by a protocol following Kagata and Ohgushi (2012b) (see also Wardle et al. 1997; Ball et al. 2008). The expected mass loss in the soil + litter + frass mixture ($\mathrm{MIX_E}$) was calculated as:

$$\mathrm{MIX_E} = \frac{\mathrm{Litter_O} + \mathrm{Frass_O}}{2}$$

where $\mathrm{Litter_O}$ and $\mathrm{Frass_O}$ are the mean observed values of mass loss in the incubation of soil + litter mixture and soil + frass mixture, respectively. Then, the log response ratio (LRR) was calculated as:

$$\mathrm{LRR} = \ln\left(\mathrm{MIX_O} / \mathrm{MIX_E}\right)$$

where $\mathrm{MIX_O}$ is the observed value of mass loss found experimentally in the incubation of soil + litter + frass mixture. LRR was calculated for each soil + litter + frass mixture, and the average with 95 % confidence limit was determined for each mixture. When the 95 % confidence limit does not cross 0, the effects is non-additive, and when the average LRR is >0 or <0, the effects are synergistic or antagonistic, respectively. The differences in the LRR among soil + litter + frass mixture treatments were also compared by a Tukey–Kramer HSD multiple comparison ($P < 0.05$). All analyses were conducted using JMP version 8 (SAS Institute Japan, Tokyo, Japan).

Results

Nitrogen and C:N ratio

Nitrogen concentration and C:N ratio clearly differed between the *Pinus* system (i.e., soil collected underneath *P. densiflora* trees, leaves and litter of *P. densiflora*, larvae of *D. spectabilis* fed on *P. densiflora*, and their frass) and the *Quercus* system (soil collected underneath *Q. acutissima* trees, leaves and litter of *Q. acutissima*, and larvae of *L. dispar* fed on *Q. acutissima*, and their frass) (Table 2). Overall, the *Quercus* system had higher N and lower C:N ratio than the *Pinus* system, except for soil C:N ratio.

Incubation experiment

Reduction of substrate mass (soil, litter, and/or frass) after a 2-month incubation differed significantly among the treatments (Fig. 1). The mass decreased by less than 1 mg in the soil alone treatments, and there was no significant difference between soil types (Table 3).

The mass loss in the soil + litter mixtures differed significantly among the treatments (Fig. 1; Table 3). Soil type and soil-by-litter interaction significantly influenced the mass reduction, but litter type did not (Table 3). Both *P. densiflora* litter and *Q. acutissima* litter were more rapidly decomposed in the soil collected underneath *Q. acutissima* than in the soil collected underneath

Table 2 Comparisons between *Pinus* and *Quercus* systems in nitrogen concentration and C:N ratio

	Nitrogen (%)		C:N ratio	
	Pinus	*Quercus*	*Pinus*	*Quercus*
Soil	0.13 ± 0.01	0.37 ± 0.01*	7.7 ± 0.2	11.2 ± 0.1*
Leaves	1.17 ± 0.03	3.24 ± 0.07*	44.2 ± 1.0	14.7 ± 0.3*
Leaf litter	0.54 ± 0.01	0.83 ± 0.01*	95.5 ± 0.7	59.4 ± 0.5*
Insect body	7.46 ± 0.09	8.98 ± 0.10*	7.3 ± 0.1	5.5 ± 0.1*
Insect frass	0.64 ± 0.02	2.61 ± 0.05*	80.7 ± 2.9	17.4 ± 0.4*

The *Pinus* system consists of soil collected underneath *P. densiflora* trees, leaves and litter of *P. densiflora*, larvae of *D. spectabilis* fed on *P. densiflora* leaves, and their frass, and the *Quercus* system consists of soil collected underneath *Q. acutissima* trees, leaves and litter of *Q. acutissima*, and larvae of *L. dispar* fed on *Q. acutissima* leaves, and their frass. Mean ± SE are presented

* $P < 0.0001$

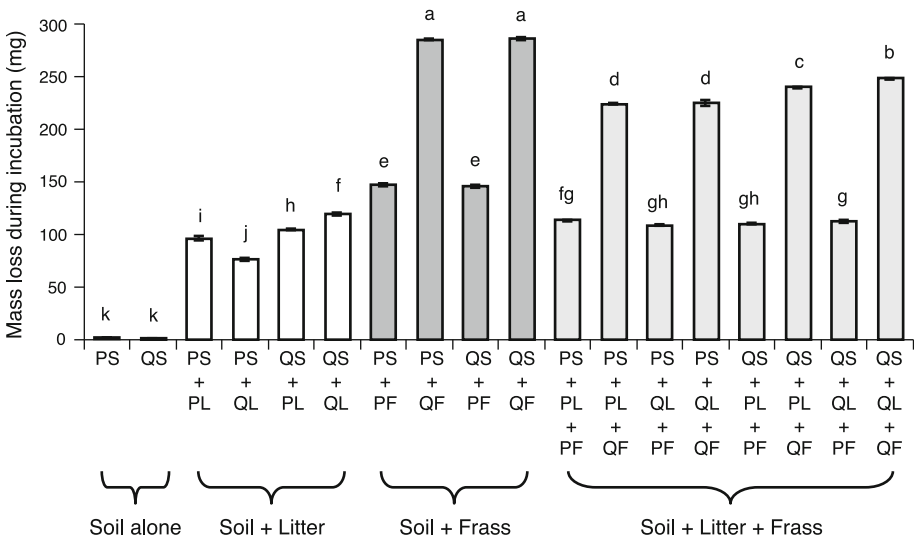

Fig. 1 Mass loss of soil, leaf litter and/or frass during incubation. Mean ± SE are presented. *Different letters* indicate significant difference ($P < 0.05$). See Table 1 for treatment codes

P. densiflora. On the other hand, *P. densiflora* litter was more rapidly decomposed than *Q. acutissima* litter in the soil collected underneath *P. densiflora* trees (Fig. 1). Similarly, *Q. acutissima* litter was more rapidly decomposed than *P. densiflora* litter in the soil collected underneath *Q. acutissima* trees. HFAI for litter decomposition was 20.6. Coupled with the result of ANOVA, HFA occurred in litter decomposition.

The mass loss in soil + frass mixtures also differed among the treatments, but only frass type had a significant effect on the mass loss (Fig. 1; Table 3). Frass of *L. dispar* was more rapidly decomposed than frass of *D. spectabilis*, independent of soil type. HFAI for frass decomposition was 0.4, indicating that there is no HFA in frass decomposition. Furthermore, frass was more rapidly decomposed than litter, independent of soil, litter, and frass type (Fig. 1).

For the incubation of soil + litter + frass mixtures, mass loss was greater in the mixtures with *L. dispar* frass than in the mixtures with *D. spectabilis* frass (Fig. 1). Soil type, frass type, and interactive effects of soil-by-litter, soil-by-frass, and litter-by-frass significantly influenced mass loss, but neither litter type nor soil-by-litter-by-frass interaction influenced it (Table 3). HFAI for decomposition of litter + frass mixtures was 5.0. LRR (i.e., difference between observed and expected values) of mass loss was significantly different from 0 in all soil + litter + frass mixture treatments (Fig. 2). The addition of *L. dispar* frass (+QF) to soil + litter mixtures non-additively accelerated decomposition (i.e., LRR >0), irrespective of the soil-litter combination (Fig. 2). In contrast, the addition of *D. spectabilis* frass (+PF) to soil + litter mixtures non-additively decelerated decomposition (i.e., LRR <0), irrespective of the soil-litter combination. The non-additive acceleration of decomposition was not particularly greater in the home environments (i.e., PS + PL + PF and QS + QL + QF treatments) than in the away environments. These results show that there is no HFA in decomposition of litter + frass mixtures.

Table 3 ANOVA tables for effects of soil, litter, frass, and their interactions on reduction of dry mass after 2-month incubation

	df	*F* value	*P* value
One factor (soil)			
Soil	1,28	2.72	0.11
Two factors (soil and litter)			
Soil	1,56	351.66	<0.0001
Litter	1,56	2.87	0.0958
Soil × litter	1,56	169.83	<0.0001
Two factors (soil and frass)			
Soil	1,56	0.003	0.9561
Frass	1,56	14807.83	<0.0001
Soil × frass	1,56	0.54	0.4644
Three factors (soil, litter, and frass)			
Soil	1,112	100.27	<0.0001
Litter	1,112	3.56	0.0619
Frass	1,112	16580.00	<0.0001
Soil × litter	1,112	13.36	0.0004
Soil × frass	1,112	104.65	<0.0001
Litter × frass	1,112	9.14	0.0031
Soil × litter × frass	1,112	0.001	0.9708

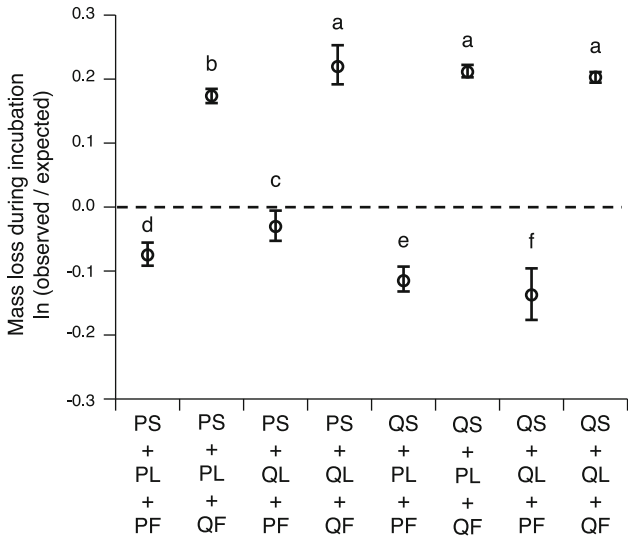

Fig. 2 Non-additive effects of litter and frass mixtures on their decomposition. Means of log-response ratio (LRR) ± 95 % confidence limits are presented. When the 95 % confidence limit does not cross 0, the effects are considered non-additive, and when the average LRR is >0 or <0, the effects are considered to be synergistic or antagonistic, respectively. See text for details. *Different letters* indicate significant difference among treatments ($P < 0.05$). See Table 1 for treatment codes

Discussion

Our incubation experiment clearly supported HFA hypothesis for litter decomposition, indicating that decomposers in soils would have been specialized to decompose the leaf litter derived from the trees above them. We obtained two different results regarding litter decomposition: (1) both *P. densiflora* and *Q. acutissima* litter were decomposed faster in soil underneath *Q. acutissima* trees than in soil underneath *P. densiflora* trees. (2) *P. densiflora* litter was decomposed faster than *Q. acutissima* litter in soil underneath *P. densiflora* trees, and vice versa. The first result shows that the soil (and/or decomposers) underneath *Q. acutissima* trees could have inherently higher ability to decompose leaf litter because of biological, chemical, and/or physical properties of the soil (Hobbie and Gough 2004). The HFAI is useful to evaluate HFA without such an inherent effect (Ayres et al. 2009). Ayres et al. (2009) quantitatively evaluated HFA regarding litter decomposition using the HFAIs; the mean value of HFAI is 8.0 (approximately ranged from −9 to 29) for 35 reciprocal leaf litter transplanting studies in forests. HFAI for litter decomposition in the present study was 20.6 that was relatively large value. Coupled with a significant soil-by-litter interactive effect in ANOVA, they indicate relatively strong HFA for litter decomposition of our experimental system.

In contrast to the leaf litter decomposition, insect frass decomposition did not show of an HFA, which indicates that there was no specialization of decomposers to a particular frass. There are two possible, not mutually exclusive, reasons why HFA might not be present in frass decomposition. One would be due to high quality of frass. Several researchers have suggested that HFA and decomposer specialization should occur in decomposition of low-quality litter, and that high-quality litter would be decomposed by almost all decomposers (Hunt et al. 1988; Ayres et al. 2009; Strickland et al. 2009). Actually, both *D. spectabilis* and *L. dispar* frass had higher quality in context of N and C:N ratio than, and were decomposed faster than, leaf litter. The other possible reason for a lack of HFA would be due to an unstable supply of insect frass to decomposers. The population size of insect herbivores, and consequently the amount of frass excreted, tends to fluctuate largely over time (Schowalter 2000). For example, Clark et al. (2010) showed that the amount of frass was negligibly small at low density of insect herbivores, but was comparable to the amount of leaf litter during an insect outbreaks. Moreover, outbreaks of insect herbivores in forests are often terminated within 2–3 years (e.g., Higashiura and Kamijo 1978). These population dynamics of insect herbivores may make it difficult to maintain a decomposer community specialized for a certain insect frass. In the forest of CER, outbreaks of *D. spectabilis* and *L. dispar* have not been observed for at least 10 years, although larvae of these insects have emerged at low density every year (H. Kagata, personal observation). This

indicates that the soil decomposer community in the forest of CER had not been under the strong influence of the insect frass, and therefore, the soil decomposers would have not specialized to the insect frass.

Furthermore, we did not detect HFA and decomposer specialization in the decomposition of the litter-frass mixtures. On the other hand, we found that the presence of frass of *D. spectabilis* in mixtures non-additively decelerated decomposition, while the presence of frass of *L. dispar* non-additively accelerated decomposition, independent of soil and litter type. Several hypotheses have been proposed to explain non-additive effects on the decomposition of leaf litter mixtures (Gartner and Cardon 2004; Hättenschwiler et al. 2005). In the case of non-additive synergistic effects, for example, the translocation of nutrients from nutrient-rich litter to nutrient-poor litter can facilitate decomposition of low-decomposability litter. In the case of antagonistic effects, secondary metabolites, such as tannins, in the low-decomposability litter may reduce the activity of microbial decomposers, resulting in reduced decomposition of high-decomposability litter. Similar mechanisms would operate in non-additive synergistic or antagonistic effects on the decomposition of the litter-frass mixtures. Actually, *L. dispar* frass had markedly higher quality than leaf litter, and nutrient transfer from this frass to litter may have accelerated litter decomposition. However, we have no data about whether *D. spectabilis* frass contains compounds that inhibit decomposition of the mixtures. Thus, we still need to identify the traits that explain the non-additive effects of litter and frass mixtures on their decomposition.

Mixing of leaf litter and insect frass commonly occurs on the forest floor in temperate forests, where leaf litter accumulates due to the relatively slow rate of litter decomposition (Barbour et al. 1998). Although some studies have shown that mixing of leaf litter and insect frass had no effects on, or non-additively accelerated, decomposition of the mixtures (Reynolds and Hunter 2001; Frost and Hunter 2008; Koukol et al. 2008; Kagata and Ohgushi 2012b), effects of insect frass on decomposition of leaf litter have been poorly explored. Our results highlighted that (1) there was no HFA in the decomposition of frass and litter-frass mixtures, despite the presence of HFA in the decomposition of litter, and (2) mixing of litter and frass synergistically or antagonistically influenced their decomposition, depending on the frass type, but independently of soil and litter type. Since our results were obtained from laboratory microcosm experiment that may differ from outputs of field experiments (Salamanca et al. 1997), complemental field survey and/or experiments are needed to confirm the effects of insect frass on litter decomposition. Nevertheless, our findings indicate that the presence of (out-breaking) insect herbivores may make it difficult to form and maintain a decomposer community specialized to a certain litter, and that it may consequently cancel or weaken HFA in litter decomposition. The litter-decomposer specialization often results in a specialized, exclusive relationship between plant and soil (Ehrenfeld et al. 2005), which may inhibit coexistence of plants (Miki et al. 2010). On the other hand, the weakened specialization of decomposers due to the effects of insect frass may maintain diverse decomposers and may facilitate coexistence of plants (Miki et al. 2010). Interactions between plant and soil critically influence community and ecosystem level properties, such as plant diversity and nutrient cycling (Binkley and Giardina 1998; Kulmatiski et al. 2008). However, the impact of aboveground herbivores on the interactions has tended to be neglected. The present study shows an additional mechanism that determines the relationship between plants and soil (or decomposers) through aboveground insect herbivores in forest ecosystems.

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