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Carbon to nitrogen excretion ratio in lepidopteran larvae: relative importance of ecological stoichiometry and metabolic scaling

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The importance of consumers in regulating ecosystem processes has been increasingly recognized. Although insect herbivores have significant impacts on nutrient cycling through excretion in terrestrial systems, few studies have explored how insect species differ in this ecosystem process. Using 130 lepidopteran species, we tested two hypotheses based on ecological stoichiometry and metabolic scaling, respectively, both of which provide a mechanistic framework for consumer-driven nutrient recycling. Our results highlighted that host plant C:N ratio is the most important determinant of interspecific variation in frass C:N ratio. Insect body mass also partially contributed to the variation in frass C:N ratio. These findings indicate that insect herbivores would play an important role in nutrient recycling with the characteristics of ecological stoichiometry in terrestrial systems.

It has been increasingly recognized that consumers impact nutrient cycling through excretion, a process termed consumer-driven nutrient recycling (Elser and Urabe 1999, Sterner and Elser 2002, Bardgett and Wardle 2010). Theories of ecological stoichiometry and metabolic scaling provide a mechanistic framework for how consumer species differ in nutrient recycling (Vanni et al. 2002, Torres and Vanni 2007, Alves et al. 2010). For example in recycling of carbon (C) and nitrogen (N), stoichiometric theory assumes that animals can maintain a constant body C:N ratio (Sterner and Elser 2002, Kagata and Ohgushi 2007). Therefore, it is hypothesized that C:N ratio in animal excrement should be positively correlated with their diet C:N ratio and negatively correlated with body C:N ratio in order to maintain a constant body C:N ratio (Elser and Urabe 1999, Sterner and Elser 2002, Anderson et al. 2005). Metabolic scaling is a term expressing the fact that the metabolic rate per unit body mass declines with body mass (West et al. 1997, Schaus et al. 1997, Glazier 2005). A decrease in the metabolic rate would result in a decrease in respiration rate, and therefore the amount of C emitted through respiration would be decreased, and conversely C in excrement would be increased. Hence, it is hypothesized that the C:N ratio in animal excrement is positively correlated with body mass.

Consumer-driven nutrient recycling has been documented mostly in aquatic systems (Elser and Urabe 1999, Vanni et al. 2002), because of the relatively high consumption rate (50–80%) of primary production in aquatic systems (Cyr and Pace 1993, Cebrian and Lartigue 2004). In terrestrial systems, herbivorous insects are important in determining consumer diversity (Gullan and Cranston 2010). It is generally thought that insect excrement (i.e. frass and honeydew) represents a minor fraction of energy and nutrient inputs for the decomposition process in terrestrial systems because of the low herbivory rate, i.e. less than 20% (Cyr and Pace 1993, Cebrian and Lartigue 2004). However, various insect herbivores sometimes show outbreaks and reach extremely high density (Schowalter 2000, Kamata 2002), whereupon the amount of insect excrement reaches a critical level of energy and nutrient input, which affects the decomposition process (Hunter 2001, Lovett et al. 2002, Clark et al. 2010). For example, since insect frass contains higher concentrations of N and labile 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). Nevertheless, few studies have explored how terrestrial insect species differ in nutrient recycling.

Here we tested the following two hypotheses based respectively on ecological stoichiometry and metabolic scaling as determinants of interspecific variation in the frass C:N ratio of 130 lepidopteran species collected from 60 plant species; 1) frass C:N ratio is positively correlated to host plant C:N ratio, but negatively correlated to body C:N ratio, based on ecological stoichiometry, and 2) frass C:N ratio is positively correlated to body mass, based on metabolic scaling.

Material and methods

Insect collection and rearing

From July to October 2009 and from April to October 2010, we collected lepidopteran larvae from their host plants in and around an experimental field of the Center for Ecological Research (35°N, 136°E), Kyoto University, in Shiga prefecture, central Japan. The collected larvae were reared in different-sized plastic containers (250, 500, 1000 or 3000 ml), depending on larval size. The rearing containers were placed in an environmental chamber at 25°C with a 16L:8D light cycle. The larvae were provided with leaves that were taken from the plant species on which the larvae had been found, and the leaves were replaced with new ones every day. To remove the effects of larval ontogeny on frass quality, frass was collected from the final instar larvae for each species. Leaves of the larval food plant were also collected to measure C and N concentrations. The frass and leaves were oven-dried at 60°C for two weeks. After pupation, the pupae were also oven-dried at 60°C for two weeks, and their dry weight was measured. The dried frass, leaves, and pupae were stored at −20°C until C and N analyses. We used the parameters in the pupal stage as index of insect body mass and C:N ratio in order to remove the effects of larval ontogeny and gut contents on these parameters. However, using the pupal parameters instead of larval ones may, to some extent, distort outputs of the analysis.

Insect species were identified by the morphology of final instar larvae, but sex was not distinguished. When the species identification was difficult, a few pupae were reared until adult eclosion. In total, we obtained the frass and pupae of 426 individuals belonging to 130 species (1–10 individuals per species) in 16 families (3–19 species per family) from 60 plant species in 33 families (Appendix 1 Table A1). The higher-level classification (i.e. family) followed Jinbo (2008) with recent reconstruction of lepidopteran classification by molecular-based phylogenetic relationships (Kristensen et al. 2007). Because the monophyly of Noctuidae has not been supported by molecular-based phylogenetic trees (Mutanen et al. 2010), Noctuidae was divided into two groups in the present study, according to Mutanen et al. (2010) (Appendix 1 Table A1). All lepidopteran species in the present study were external leaf chewers at least during the final instar stage.

Carbon and nitrogen analysis

Prior to the analysis, all samples (plant leaves, larval frass, and pupae) were ground to a fine powder. Total C and N contents were determined using an elemental analyzer. For several species, pupal and/or frass mass of individuals was insufficient to measure C and N. Therefore, the pooled samples of several individuals were used for C and N analysis in those species.

Statistical analyses

The means for species were used for all analyses in which there were multiple measurements per species. Differences between host plant C:N ratio and pupal C:N ratio and between host plant C:N ratio and frass C:N ratio were examined by paired t tests. Differences in % N were also examined by paired t-tests. Pupal mass, host plant C:N ratio, pupal C:N ratio and frass C:N ratio were compared among insect families using ANOVAs. All data were log-transformed, except for % N data that were arcsin-square-root transformed, prior to the analyses, which met the equal variances and normal distribution. However, comparisons of C:N ratio and % N between legume and non-legume plants were examined by Mann-Whitney U-test because they markedly differed in sample size. To test whether frass C:N ratio of lepidopteran larvae can be explained by ecological stoichiometry (host plant and pupal C:N ratio) and metabolic scaling (pupal mass), we constructed linear models with the ordinary least squares method (OLS). To examine the relative importance of the independent variables, partial regression analyses were conducted. We also tested the effects of ecological stoichiometry and metabolic scaling on frass C:N ratio by a phylogenetically generalized least squares method (PGLS) that modifies the linear models by incorporating phylogenetic relationships into the error structure to evaluate the effects of phylogeny on the models (Martins and Hansen 1997). A phylogenetic hypothesis for the present study species was constructed in the base of a molecular-based phylogenetic tree for lepidoptera (Mutanen et al. 2010). The phylogenetic tree of Mutanen et al. (2010) was resolved at the subfamily level. When there was a subfamily that was not included in the phylogenetic tree, polytomy within the family was assumed. In addition, we placed the genera as branches within subfamilies and species as branches within genera, where there were multiple species within a subfamily. All branch lengths were assumed to be equal. The phylogenetic distance was estimated by assuming a Brownian motion model of evolution of the trait variables (Martins and Hansen 1997), and was incorporated into the error term in the PGLS. Models for all possible combinations of the independent variables (i.e. pupal mass and C:N ratio of host plants and pupae) were constructed. We used Akaike's information criterion (AIC) to evaluate the fit of the models. In addition, we also constructed linear models in OLS and PGLS without legume-feeders (16 species), since legume plants that have much lower C:N ratio than other plants may mask the effects of the other independent variables. To explore potential relationships between the independent variables (i.e. multicollinearity), we calculated Pearson's correlation coefficients. All analyses were conducted using JMP ver. 6 (SAS Inst.), except for the PGLS, which was analyzed using the packages *ape* and *geiger* in R (<www.R-project.org>).

Results

Pupal mass and C:N ratio of plants, pupae and frass

There was a large interspecific variation in pupal mass, which ranged from 5.5 to 1485.5 mg, but the pupal mass of most (90%) species was <500 mg (Fig. 1a). The coefficient of variance (CV) of pupal mass was 133.3, which was the

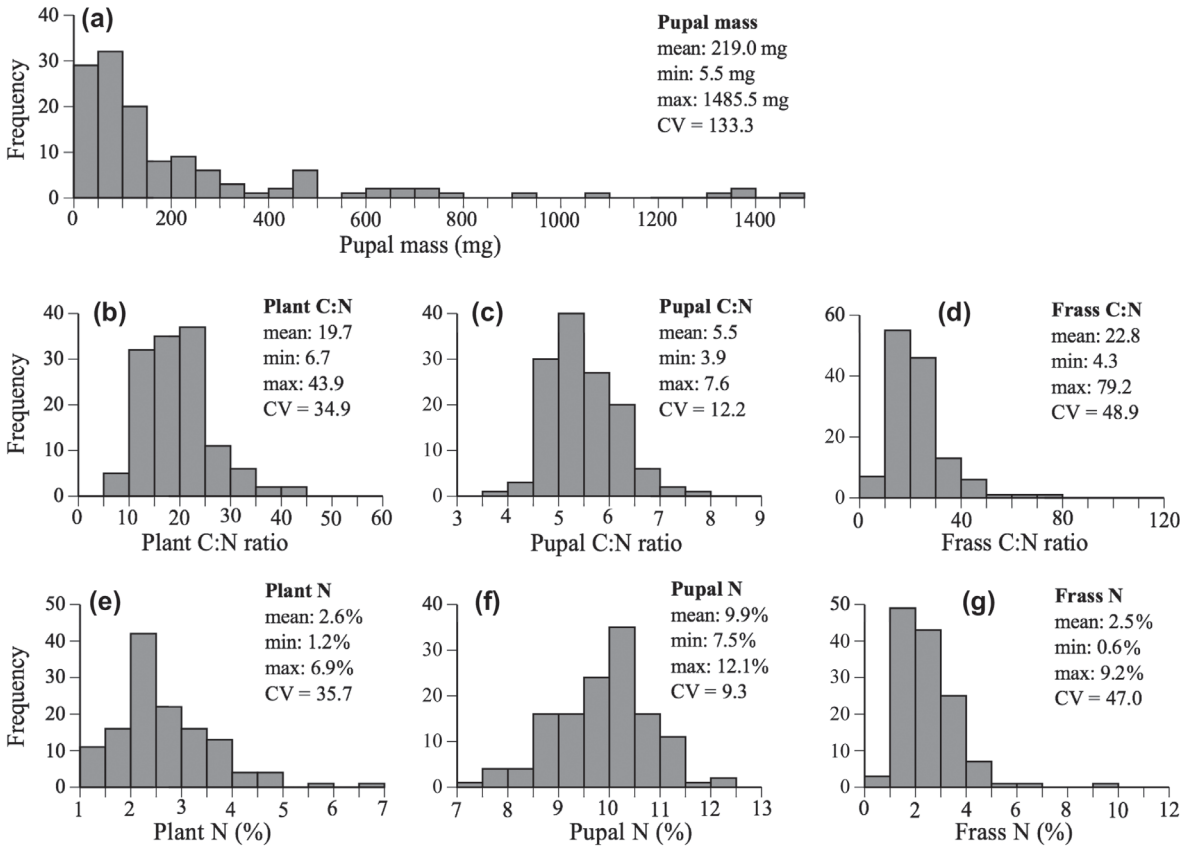

Figure 1. Frequency of (a) pupal mass, (b) host plant C:N ratio, (c) pupal C:N ratio, (d) frass C:N ratio, (e) host plant N, (f) pupal N, and (g) frass N of 130 lepidopteran species.

largest among the CVs of the measured parameters. Pupal mass differed significantly among lepidopteran families (ANOVA: DF = 16,113, F = 10.9, $p < 0.0001$, Fig. 2a).

The C:N ratio also varied from 6.7 to 43.9 for host plant leaves (Fig. 1b), from 3.9 to 7.6 for pupae (Fig. 1c), and from 4.3 to 79.2 for larval frass (Fig. 1d). The interspecific variation of the pupal C:N ratio was smaller (CV = 12.2) than that of the plant C:N ratio (CV = 34.9) and frass C:N ratio (CV = 48.9). Pupal C:N ratio differed significantly among lepidopteran families (ANOVA: DF = 16,113, F = 2.27, $p = 0.0067$, Fig. 2c), while there was a neither significant difference among lepidopteran families in plant C:N ratio (ANOVA: DF = 16,113, F = 1.55, $p = 0.09$, Fig. 2b) nor in frass C:N ratio (ANOVA: DF = 16,113, F = 1.23, $p = 0.26$, Fig. 2d). Pupal C:N ratio was significantly smaller than plant C:N ratio (paired t-test: $t = -23.9$, $p < 0.0001$). Frass C:N ratio was significantly larger than plant C:N ratio (paired t-test: $t = 5.84$, $p < 0.0001$). N concentration varied from 1.2 to 6.9 % for host plant leaves (Fig. 1e), from 7.5 to 12.1% for pupae (Fig. 1f), and from 0.6 to 9.2% for frass (Fig. 1g). Pupal N was significantly higher than plant N (paired t-test: $t = 48.0$, $p < 0.0001$). Frass N was significantly lower than plant N (paired t-test: $t = -5.38$, $p < 0.0001$). Legume plants had significantly lower C:N ratio and higher N than non-legume plants (median = 12.2 and 20.1 for C:N ratio in legumes and non-legumes, respectively, Mann-Whitney U-test: $p < 0.0001$; median = 3.6 and 2.3 for % N in legumes and non-legumes, respectively. Mann-Whitney U-test: $p < 0.0001$).

Determinants of frass C:N ratio

The best fit model in OLS was estimated to be 'Frass C:N = $-0.260 + 0.041 \times$ Mass $+ 1.173 \times$ Plant C:N', indicating that frass C:N ratio was positively correlated to pupal mass and host plant C:N ratio (Table 1). The second fit model ($\Delta AIC < 2$) was estimated to be 'Frass C:N = $-0.217 + 0.041 \times$ Mass $+ 1.178 \times$ Plant CN $- 0.065 \times$ Pupal CN (Table 1). Host plant C:N ratio was the most important determinant of frass C:N ratio, and explained 78% of the variance in frass C:N ratio (Fig. 3a). Pupal mass explained 5% of, and pupal C:N ratio explained little of the variance (Fig. 3b–c). The best fit model in PGLS was estimated to be 'Frass C:N = $-0.210 + 1.182 \times$ Plant C:N', indicating that frass C:N ratio was explained by host plant C:N ratio alone (Table 1). Analyses without legume plants did not change the results (statistical parameters are not shown).

There was a significant, positive, but weak correlation between plant and pupal C:N ratio ($r = 0.20$, $p = 0.02$), indicating that there was a weak multicollinearity. There was neither a significant correlation between plant C:N ratio and pupal mass ($r < 0.01$, $p = 0.99$), nor between pupal mass and pupal C:N ratio ($r = -0.05$, $p = 0.55$).

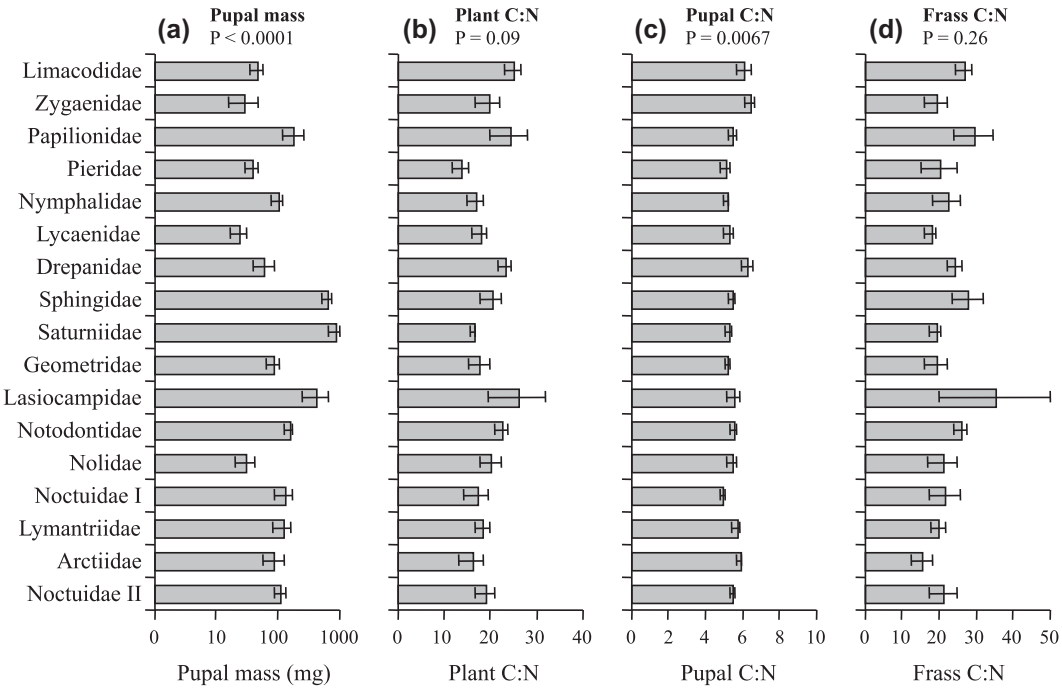

Figure 2. Mean values at lepidopteran family level of (a) pupal mass, (b) host plant C:N ratio, (c) pupal C:N ratio, and (d) frass C:N ratio. Error bars show SE. Noctuidae was divided into two groups in the present study (Appendix 1), because the monophyly of Noctuidae has not been supported by molecular-based phylogenetic trees (Mutanen et al. 2010).

Discussion

Carbon to nitrogen excretion ratio in lepidopteran larvae

In the present study, we tested the following hypotheses; 1) frass C:N ratio is positively correlated to diet C:N ratio, but negatively correlated to body C:N ratio, based on stoichiometric theory, and 2) frass C:N ratio is positively correlated to body mass, based on metabolic scaling.

In accord with the finding of Madritch et al. (2007) of a positive correlation between host plant and frass C:N ratio in two lepidopteran species, we found that the frass C:N ratio of 130 lepidopteran species was strongly, positively correlated with the host plant C:N ratio, independent of the use of OLS or PGLS methods, and of the presence or absence of legumes. Regression coefficients of the host plant C:N ratio against frass C:N ratio were >1 in all fit models. This indicates that the larvae use N more efficiently when fed on a N-poor diet. The dependence of N use efficiency on diet N has been detected in several insect species as an intraspecific physiological-level response to various quality of diet (Slansky and Feeny 1977). Our finding expands this pattern to the interspecific level in response to the diet quality. In contrast, the insect body C:N ratio could not explain the frass C:N ratio, although it was included in the second fit model in OLS. This is probably because the insect body C:N ratio was positively correlated with host plant C:N ratio, which may mask the effect of body C:N ratio. This positive correlation was not due to gut contents, because we measured the C:N ratio of pupae without gut contents. It may be an adaptation of insect herbivores that utilize low nutrient plants as food resources (Markow et al. 1999, Fagan et al. 2002). Furthermore, interspecific variation in insect body C:N ratio may be too small, compared to host plant C:N ratio, to detect significant effects of the body C:N ratio on the frass C:N ratio.

The metabolic scaling hypothesis was supported by the best fit model in the OLS, i.e., the frass C:N ratio was positively correlated to body mass. However, the body mass was less important than host plant C:N ratio as a determinant of the frass C:N ratio. This may also be due to the small variation in insect body mass, whereas metabolic scaling has been examined across more orders of magnitude (Lind and Barbosa 2010). Furthermore, the metabolic scaling hypothesis was not supported by the PGLS taking

Table 1. Relative fit of hypothesized models to the frass C:N ratio of lepidopteran larvae in ordinary least squares (OLS) and phylogenetically generalized least squares (PGLS) methods. AIC = Akaike's information criterion. Data were log-transformed prior to the analyses.

	OLS		PGLS	
Model	AIC	ΔAIC	AIC	ΔAIC
Mass + Plant C:N + Pupal C:N	−611.04[2]	1.84	−181.84	9.47
Mass + Plant C:N	−612.88[1]	0	−185.31	6.00
Mass + Pupal C:N	−417.15	195.73	12.10	203.52
Plant C:N + Pupal C:N	−606.29	6.59	−188.04	3.27
Mass	−415.61	197.27	11.89	203.20
Plant C:N	−608.00	4.88	−191.31[3]	0
Pupal C:N	−417.37	195.51	6.18	197.49

[1]best fit model in OLS: (Frass C:N) = −0.260 + 0.041 × (Mass) + 1.173 × (Plant C:N).
[2]second fit model in OLS: (Frass C:N) = −0.217 + 0.041 × (Mass) + 1.178 × (Plant C:N) − 0.065 × (Pupal C:N).
[3]best fit model in PGLS: (Frass C:N) = −0.210 + 1.182 × (Plant C:N).

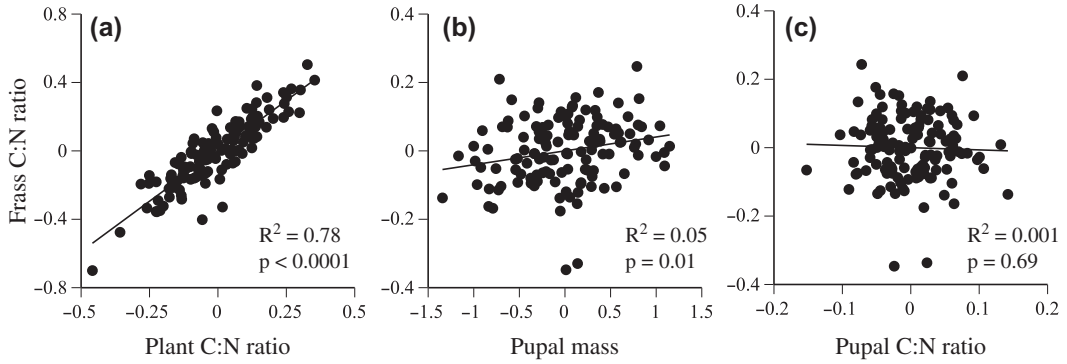

Figure 3. Partial regression plots of frass C:N ratio against (a) host plant C:N ratio, (b) pupal mass, and (c) pupal C:N ratio. Y-axis shows residuals from regressing frass C:N ratio against all the independent variables except for the target variable. X-axis shows residuals from regressing the target variable against the remaining independent variables. Data were log-transformed prior to the analyses.

account of phylogenetic relationships. Therefore, the effects of body mass on frass C:N ratio would be constrained by phylogeny in lepidopteran species.

Consumer-driven nutrient recycling in terrestrial ecosystems

Our results highlighted that host plant C:N ratio is the most important factor responsible for the interspecific variation in the C to N excretion ratio in lepidopteran larvae. This importance of diet stoichiometry on the consumer-driven nutrient recycling was in accord with the findings of previous studies in aquatic systems (Elser and Urabe 1999, Vanni et al. 2002, Torres and Vanni 2007, Verant et al. 2007, Alves et al. 2010). However, the effects of diet C:N stoichiometry on the nutrient recycling may be more important in terrestrial systems than in aquatic systems, because the variation in C:N ratio of autotrophs, the base of food webs, is larger in terrestrial systems (Elser et al. 2000). For example, Elser et al. (2000) showed that C:N ratio varied more than twice as much in the foliage of terrestrial plants (CV = 64) as in freshwater algae (CV = 29), while terrestrial herbivores (insects: CV = 29) and their freshwater counterparts (zooplankton: CV = 21) had similar variation in body C:N ratio. Thus, terrestrial herbivores use a wide variety of resources with respect to nutrient quality, which causes large interspecies variations in frass quality.

Furthermore, the present study quantitatively determined the relationship between host plant and frass C:N ratio. For example, calculating from the best fit model in PGLS, the threshold in the diet C:N ratio, at which the larvae excrete relatively more N-biased or C-biased frass compared to the diet C:N ratio, was approximately 14, i.e. the larvae excrete relatively more N-biased (or C-biased) frass when they fed on a diet with C:N ratio smaller (or larger) than 14. Although this threshold would, to some extent, be dependent on insect body mass, a C:N ratio of 14 is a small value in terrestrial plants (Elser et al. 2000). Hence, terrestrial insect herbivores would generally excrete relatively C-biased frass compared to host plant C:N ratio. However, plant C:N ratio is largely dependent on environmental factors. For example, N enrichment due to N deposition increases N in plants (Fenn et al. 1996, Throop and Lerdau 2004). If the plant C:N ratio is less than 14, insect herbivores that feed on those plants may excrete relatively N-biased frass (Kagata and Ohgushi 2011). In contrast, elevated atmospheric CO_2 level decreases N in plants (Cotrufo et al. 1998, Lindroth 2010), and therefore insect herbivores may excrete more C-biased frass in such an environmental condition (but see Knepp et al. 2007). These considerations indicate that insect herbivores may promote C or N recycling through frass excretion, depending on the plant nutrient status. Coupled with the fact that most insect herbivores are specialists feeding on species-specific host plants (Schoonhoven et al. 1998), the findings of the present study emphasize that insect herbivores would play an important role in nutrient recycling through the quality of their host plants in terrestrial systems.

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Appendix 1

Table A1. Lepidopteran species and their host plants in the present study. n = number of larvae reared to pupa.

Family/Species	Host plant	Plant family	n
Limacodidae			
Austrapoda dentata	*Castanea crenata*	Fagaceae	3
Microleon longipalpis	*Salix integra*	Salicaceae	4
Monema flavescens	*Salix gilgiana*	Salicaceae	9
Parasa consocia	*Salix gilgiana*	Salicaceae	10
Parasa lepida lepida	*Salix integra*	Salicaceae	5
Parasa sinica	*Salix gilgiana*	Salicaceae	4
Phrixolepia sericea	*Wisteria floribunda*	Leguminosae	4
Scopelodes contracta	*Zelkova serrata*	Ulmaceae	2
Zygaenidae			
Artona martini	*Phyllostachys nigra*	Poaceae	8
Illiberis rotundata	*Prunus jamasakura*	Rosaceae	3
Elcysma westwoodii westwoodii	*Prunus* x *yedoensis*	Rosaceae	2
Papilionidae			
Sericinus japonica	*Aristolochia debilis*	Aristolochiaceae	2
Atrophaneura alcinous alcinous	*Aristolochia debilis*	Aristolochiaceae	3
Graphium sarpedon	*Cinnamomum camphora*	Lauraceae	2
Papilio helenus	*Zanthoxylum ailanthoides*	Rutaceae	3
Papilio xuthus	*Zanthoxylum piperitum*	Rutaceae	3
Pieridae			
Colias erate poliographus	*Trifolium repens*	Leguminosae	4
Eurema mandarina	*Lespedeza juncea*	Leguminosae	6
Pieris rapae	*Brassica juncea*	Cruciferae	5
Nymphalidae			
Lethe diana diana	*Pleioblastus argenteostriatus*	Poaceae	4
Lethe sicelis	*Pleioblastus argenteostriatus*	Poaceae	1
Apatura metis substituta	*Salix gilgiana*	Salicaceae	2
Argyreus hyperbius	*Viola betonicifolia*	Violaceae	3
Neptis sappho	*Pueraria lobata*	Leguminosae	1
Lycaenidae			
Curetis acuta paracuta	*Wisteria floribunda*	Leguminosae	3
Favonius taxila	*Quercus serrata*	Fagaceae	2
Japonica lutea lutea	*Quercus acutissima*	Fagaceae	1
Narathura japonica	*Quercus glauca*	Fagaceae	3
Lycaena phlaeas daimio	*Rumex acetosa*	Polygonaceae	7
Celastrina argiolus ladonides	*Lespedeza juncea*	Leguminosae	3
Zizeeria maha argia	*Oxalis dillenii*	Oxalidaceae	2
Drepanidae			
Callidrepana patrana	*Rhus javanica*	Anacardiaceae	2
Macrauzata maxima maxima	*Quercus acutissima*	Fagaceae	3
Oreta pulchripes	*Viburnum sieboldii*	Caprifoliaceae	5
Tridrepana crocea	*Quercus acutissima*	Fagaceae	1
Sphingidae			
Macroglossum pyrrhosticta	*Paederia scandes*	Rubiaceae	3
Neogurelca himachala sangaica	*Paederia scandes*	Rubiaceae	3
Theretra japonica	*Ampelopsis brevipedunculata*	Vitaceae	1
Theretra oldenlandiae oldenlandiae	*Cayratia japonica*	Vitaceae	1
Callambulyx tatarinovii gabyae	*Zelkova serrata*	Ulmaceae	2
Clanis bilineata tsingtauica	*Pueraria lobata*	Leguminosae	3
Marumba sperchius sperchius	*Quercus acutissima*	Fagaceae	3
Smerinthus planus	*Salix gilgiana*	Salicaceae	2
Smerinthus tokyonis	*Vaccinium oldhamii*	Ericaceae	3
Acherontia lachesis	*Solanum melongena*	Solanaceae	1
Agrius convolvuli	*Calystegia hederaceae*	Convolvulaceae	4
Psilogramma incretum	*Syringa vulgaris*	Oleaceae	1
Sphinx caliginea caliginea	*Pinus desiflora*	Pinaceae	2
Saturniidae			
Aglia japonica microtau	*Alnus sieboldiana*	Betulaceae	2
Actias gnoma gnoma	*Alnus sieboldiana*	Betulaceae	6
Antheraea yamamai yamamai	*Quercus glauca*	Fagaceae	4
Rhodinia fugax fugax	*Castanea crenata*	Fagaceae	4

(Continued)

Table A1. (Continued)

Family/Species	Host plant	Plant family	n
Geometridae			
Operophtera brunnea	*Quercus serrata*	Fagaceae	2
Geometra dieckmanni	*Quercus acutissima*	Fagaceae	3
Ascotis selenaria cretacea	*Solidago altissima*	Compositae	3
Biston robustus robustus	*Quercus serrata*	Fagaceae	3
Colotois pennaria ussuriensis	*Quercus serrata*	Fagaceae	2
Erannis golda	*Quercus serrata*	Fagaceae	1
Pachyligia dolosa	*Salix subfragilis*	Salicaceae	1
Paradarisa chloauges kurosawai	*Salix gilgiana*	Salicaceae	1
Phigalia verecundaria	*Quercus acutissima*	Fagaceae	2
Phthonandria atrilineata atrilineata	*Morus australis*	Moraceae	3
Rikiosatoa grisea grisea	*Pinus desiflora*	Pinaceae	3
Wilemania nitobei	*Fagus crenata*	Fagaceae	2
Inurois fletcheri	*Quercus serrata*	Fagaceae	1
Lasiocampidae			
Dendrolimus spectabilis	*Pinus desiflora*	Pinaceae	5
Euthrix albomaculata directa	*Miscanthus sinensis*	Poaceae	1
Gastropacha populifolia angustipennis	*Salix gilgiana*	Salicaceae	10
Malacosoma neustrium testaceum	*Rosa multiflora*	Rosaceae	6
Notodontidae			
Stauropus fagi persimilis	*Salix eriocarpa*	Salicaceae	2
Clostera anachoreta	*Salix eriocarpa*	Salicaceae	6
Clostera anastomosis	*Salix gilgiana*	Salicaceae	10
Drymonia dodonides	*Quercus serrata*	Fagaceae	3
Fentonia ocypete	*Quercus acutissima*	Fagaceae	3
Furcula furcula sangaica	*Salix gilgiana*	Salicaceae	9
Gonoclostera timoniorum	*Salix gilgiana*	Salicaceae	4
Harpyia umbrosa	*Castanea crenata*	Fagaceae	2
Mimopydna pallida	*Pleioblastus argenteostriatus*	Poaceae	5
Peridea gigantea	*Quercus acutissima*	Fagaceae	2
Peridea oberthueri	*Alnus sieboldiana*	Betulaceae	1
Phalera assimilis	*Quercus serrata*	Fagaceae	6
Phalera flavescens	*Prunus jamasakura*	Rosaceae	5
Phalera takasagoensis	*Quercus serrata*	Fagaceae	5
Phalerodonta manleyi manleyi	*Quercus serrata*	Fagaceae	4
Pterostoma gigantinum	*Wisteria floribunda*	Leguminosae	1
Rabtala cristata	*Quercus serrata*	Fagaceae	3
Spatalia doerriesi	*Quercus crispula*	Fagaceae	3
Wilemanus bidentatus bidentatus	*Prunus jamasakura*	Rosaceae	3
Nolidae			
Evonima mandschuriana	*Prunus jamasakura*	Rosaceae	1
Meganola fumosa	*Quercus serrata*	Fagaceae	3
Earias pudicana	*Salix serissaefolia*	Salicaceae	3
Camptoloma interioratum	*Quercus serrata*	Fagaceae	5
Blenina senex	*Diospyros kaki*	Evenaceae	1
Risoba prominens	*Myrica rubra*	Myricaceae	2
Gadirtha impingens	*Sapium sebiferum*	Euphorbiaceae	3
Negritothripa hampsoni	*Quercus serrata*	Fagaceae	4
Lymantriidae			
Artaxa subflava	*Alnus sieboldiana*	Betulaceae	3
Calliteara lunulata	*Quercus acutissima*	Fagaceae	2
Calliteara pseudabietis	*Wisteria floribunda*	Leguminosae	3
Cifuna locuples confusa	*Salix gilgiana*	Salicaceae	4
Lymantria dispar japonica	*Quercus acutissima*	Fagaceae	7
Lymantria mathura aurora	*Quercus serrata*	Fagaceae	3
Orgyia thyellina	*Pueraria lobata*	Leguminosae	1
Sphrageidus similis	*Salix gilgiana*	Salicaceae	7
Arctiidae			
Chionarctia nivea	*Rumex obtusifolius*	Polygonaceae	2
Hyphantria cunea	*Salix chaenomeloides*	Salicaceae	8
Lemyra flammeola	*Viburnum sieboldii*	Caprifoliaceae	1
Lemyra imparilis	*Vicia angustifolia*	Leguminosae	2
Spilarctia seriatopunctata seriatopunctata	*Phaseolus lunatus*	Leguminosae	3
Spilosoma lubricipedum sangaicum	*Salix gilgiana*	Salicaceae	4

(Continued)

Table A1. (Continued)

Family/Species	Host plant	Plant family	n
Noctuidae I			
Eudocima tyrannus	*Akebia quinata*	Lardizabalaceae	2
Gonitis mesogona	*Rubus sieboldii*	Rosaceae	5
Oraesia emarginata	*Cocculus trilobus*	Menispermaceae	5
Arcte coerula	*Boehmeria platanifolia*	Urticaceae	5
Dinumma deponens	*Albizia julibrissun*	Leguminosae	2
Hypopyra vespertilio	*Albizia julibrissun*	Leguminosae	3
Mocis undata	*Pueraria lobata*	Leguminosae	1
Hypena amica	*Boehmeria platanifolia*	Urticaceae	3
Noctuidae II			
Cucullia fraterna	*Sonchus oleraceus*	Compositae	6
Lophoruza pulcherrima	*Smilax china*	Liliaceae	2
Thysanoplusia intermixta	*Plantago asiatica*	Plantaginaceae	1
Acronicta major	*Salix integra*	Salicaceae	1
Moma alpium	*Quercus serrata*	Fagaceae	4
Viminia rumicis	*Rumex obtusifolius*	Polygonaceae	3
Amphipyra monolitha surnia	*Quercus serrata*	Fagaceae	2
Mamestra brassicae	*Ricinus communis*	Euphorbiaceae	6
Orthosia evanida	*Picris hieracioides*	Compositae	1
Orthosia odiosa	*Salix serissaefolia*	Salicaceae	1
Sarcopolia illoba	*Rumex obtusifolius*	Polygonaceae	1