Evidence in stable isotope ratios for lichen-feeding by Lithosiini moths from a tropical rainforest but not from a temperate forest

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16 **Abstract**

17 Lithosiini (Lepidoptera: Erebidae: Arctiinae) is characteristic in having some species that
18 feed on lichens, whereas the majority of moths, feeds on vascular plants. However, larval
19 diet of most Lithosiini species is poorly known. This study examines if Lithosiini species,
20 collected in a tropical rainforest of Borneo (nine species) and a temperate forest of Japan
21 (eight species), feed on lichens as larvae, based on stable isotope analyses. As a result,
22 the $\delta^{15}N$ values for eight of nine Lithosiini species collected from Borneo were notably
23 lower than those of nine co-occurring herbivorous non-Lithosiini species, and were
24 similar to those of sympatric, lichen-feeding termites; however, $\delta^{13}C$ and $\delta^{15}N$ values of
25 one Lithosiini species (*Adites* sp.) were significantly higher than those of the other moth
26 species and similar to those of humus-feeding termites and predatory insects occurring at
27 the same site. These results have suggested that the Lithosiini in the Southeast Asian
28 tropical rainforests contain some species that feed on lichens as their larval main diet and
29 at least one species whose larvae feed on humus or animal-derived materials. In contrast,
30 the $\delta^{13}C$ and $\delta^{15}N$ values of all examined Lithosiini species (eight species) in the
31 temperate forest have suggested that their larvae fed on plants and not on lichens. Our
32 stable isotope ratio analysis presented quantitative evidence suggesting lichen-feeding by
33 Lithosiini moths in a tropical rainforest without observation of feeding behavior during
34 the larval stages.

35 ***Key words:*** *larval diet, Lepidoptera, Lithosiini, Sarawak, stable C and N isotopes.*

INTRODUCTION

The Lithosiini (Lepidoptera: Erebidae: Arctiinae) contain ca. 3,150 known species and are estimated to contain approximately twice as many unknown species (Conner 2009). This tribe is distinctive in having some lichen-feeding species as larvae (Hampson 1900; Holloway 2001; Pöykkö & Hyvärinen 2003; Wagner *et al.* 2008; Conner 2009), although most lepidopteran species feed on vascular plants at the larval stages (Powell *et al.* 1998; Richardson *et al.* 2010; Table S1). In addition, there are known to be some Lithosiini species in each of which both lichen-feeding larvae and larvae that exclusively feed on non-lichen food resources, such as vascular plants and mosses, coexist within a population (Holloway 2001; Conner 2009).

Presently, however, the diversity and phylogenetic distribution of the lichen-feeders in Lithosiini are poorly known (Anderson *et al.* 2017). The scarcity of the information is partly because a tremendous amount of time, effort and labor power is required to find, collect, rear and observe a sufficient number of larvae (Novotny *et al.* 2002; Bodner *et al.* 2010), taking into account of intraspecific and within-population variations in diets (Novotny *et al.* 2002).

Stable isotope ratio analysis is useful for reconstructing the larval diet of Lithosiini using the trophic relationship between the moths and their food resources. This method is based on the empirical relationship of nitrogen and carbon isotope ratios between animal and their food resources: the nitrogen isotope ratio ($\delta^{15}N$) values of the animals are

56 approximately 3.4‰ higher than those of the food resources, and the carbon isotope ratio
57 ($\delta^{13}C$) values of the animals are approximately the same as those of the food resources
58 (DeNiro & Epstein 1978; Minagawa & Wada 1984). The nitrogen that composes the
59 tissue of lichens is mainly derived from inorganic nitrogen in rainwater (Hietz *et al.* 2002;
60 Ellis *et al.* 2003; Fogel *et al.* 2008), while plants obtain nitrogen mainly by absorbing
61 soluble nitrogen from the soil (Högberg 1997). The $\delta^{15}N$ in those lichens thus tends to be
62 lower than the $\delta^{15}N$ in plants (Högberg 1997). Assuming that this empirical rule is the
63 case, moths that feed mainly on lichens can be distinguished from those that feed mainly
64 on plants by measuring the $\delta^{15}N$ of the body tissue of the moths (Adams *et al.* 2016; Shin
65 *et al.* 2018). A fraction of lichens are known to obtain nitrogen through nitrogen fixation
66 by symbiotic cyanobacteria (Lücking *et al.* 2009). Because nitrogen in such nitrogen-
67 fixing lichens tends to be close to the $\delta^{15}N$ value of atmospheric nitrogen (0‰) (Hietz *et*
68 *al.* 2002), the $\delta^{15}N$ values in Lithosiini moths feeding on nitrogen-fixing lichens should
69 be different from those in plant-feeding moths. However, the difference is not always
70 distinct, because the $\delta^{15}N$ values of plants are empirically known to be sometimes close
71 to 0‰ as those of nitrogen-fixing lichens in tropical areas (Hietz *et al.* 2002).

72 To date, five Lithosiini species in the European temperate zone and two Lithosiini
73 species in the Southeast Asia have been examined by the stable isotope ratio analysis,
74 suggesting that only one of the five examined species (*Lithosia quadra*) fed on lichens
75 (Adams *et al.* 2016; Shin *et al.* 2018). Although the previous studies supported a view

that there are some Lithosiini species which do not use lichens as the primary food, the number of investigated species and study sites are not enough for concluding so. It is therefore necessary to examine whether larvae feed on lichens, for sufficient number of Lithosiini species, in various climate regions, particularly in tropical regions, where the species richness of Lithosiini is considered to be notably high (Holloway 2001).

In this study, we assess the larval diet of several Lithosiini species in a tropical rainforest and in a temperate forest, with special reference to the lichen-feeding. We thus measure and analyze the $\delta^{13}C$ and $\delta^{15}N$ of their tissues and those of co-occurring moth species. This study adds new information on the phylogenetic distribution of lichen-feeding species in Lithosiini.

MATERIALS AND METHODS

Study site

We conducted our study in the following two sites: Lambir Hills National Park (hereafter, 'Lambir'), located at 4°12′ N and 114°02′ E (100–250 m a.s.l.) in tropical rainforest climate areas in Sarawak, Malaysia on Borneo; and Kamigamo Experimental Station, Kyoto University (hereafter, 'Kamigamo'), located at 35°04′04″ N and 135°45′38″ E (224 m a.s.l.) in temperate and humid climate areas on the main island of Japan.

The main type of vegetation at Lambir is a primary lowland mixed dipterocarp forest (Ashton & Hall 1992). The mean annual temperature and rainfall are 27°C and 2,600 mm,

95 respectively, with no clear dry season (see Kumagai *et al*. 2009 for the details of
96 meteorological conditions in Lambir). Construction facilities at this study site include two
97 observation towers, ladders attached to trunks of several emergent trees, and aerial
98 walkways suspended between emergent trees at approximately 20 m above the ground,
99 which allow access to the branches and leaves in the forest canopy ranging from the
100 ground to approximately 60 m above the ground (Inoue *et al.* 1994; Yumoto &
101 Nakashizuka 2005).

102 The vegetation at Kamigamo is mainly composed of secondary evergreen coniferous
103 forests dominated by *Pinus densiflora* and *Chamaecyparis obtusa*, and secondary broad-
104 leaved forests dominated by *Quercus serrata* (Osada *et al.* 2003). The mean annual
105 temperature and rainfall are 14.7℃ and 1,578 mm, respectively (Field Science Education
106 and Research Center, Kyoto University 2016).

107 **Moth sampling**

108 In Lambir, adult moths were sampled with a light trap set at the forest floor in a plot
109 located in the primary mixed dipterocarp forest at approximately 250 m above sea level,
110 three times on August 27, 2017, March 19, 2019, and November 22, 2019. On each
111 sampling, light trapping was started immediately after dusk. The light trap was equipped
112 with six 4-W ultraviolet tubes (2-way black light, MBL-LB, MAXER DENKI Co.) and a
113 200 cm wide and 180 cm high white cloth, which was suspended from a height of 170 cm

114 above the ground. All moths attracted and approached to the light trap were collected with
115 insect nets for three hours after sunset, and they were then killed in a bottle containing
116 ethyl acetate.

117 In addition, we conducted another type of light-trapping from the sunsets on the 28th
118 of June and the 30th of August to the following mornings in 2019. At each of the dates,
119 we set up light traps that were different from the above-mentioned light-trapping, at five
120 locations. The light trap was designed to collect moths without human operations and
121 each trap was equipped with an ultraviolet LED light (375 THREE, Association of
122 Wildlife Research (http://www.npo-wildlife.com/)), a board for intercepting light-
123 attracted flying moths, a funnel, and a vessel to collect the fallen moths. Flying moths
124 were attracted to the trap by ultraviolet light, hit the board, and fell into a vessel filled
125 with volatilized ethyl acetate. All moths trapped in the vessel were collected the following
126 morning.

127 In Kamigamo, light-trapping was conducted at a plot near the summit of the highest
128 hill at an elevation of approximately 224 m on May 25, June 22, July 16, August 20, and
129 September 17, 2020, in the same way as conducted three times (the former method) in
130 Lambir. Similar to the Lambir survey, we captured all individual moths that flew onto the
131 white cloth for approximately three hours after sunset.

132 The moths were pinned and then dried in an oven at 60°C for 48 h. Among the
133 collected moths, only the species of Lithosiini, as well as the species whose larvae have

been confirmed to feed on plants by previous studies using more than three individuals, were analyzed. In Lambir, nine species (27 individuals) of Lithosiini, and nine species (27 individuals) of non-Lithosiini moths that had been confirmed to feed on plants based on the rearing or observation by Holloway (1983, 1987, 1993, 1998, 2001, 2005) were analyzed for their isotopic compositions (Table S2). In Kamigamo, the isotopic signatures were measured for eight species (24 individuals) of Lithosiini, and 37 species (111 individuals) of non-Lithosiini moths that had been confirmed to be herbivores by Kishida (2011a; 2011b, 2020), Hirowatari *et al.* (2013), and Nasu *et al.* (2013) on the basis of rearing and observations (Table S3).

Leaf litter sampling

Leaf litter was collected from 20 plots near the site where moths were sampled in Kamigamo on June 22, 2020. Ten fallen leaves were collected from the ground litter in a plot of approximately 30 cm^2; each plot was set at least 10 m away from each other. Each sample of the collected leaf litter was gathered in a paper bag, dried up in an oven at 60°C for 48 h, and grinded using a ball mill.

Stable isotopic measurements

The moth legs and powdered samples of leaf litter materials were weighed on a micro-balance and placed in Sn capsules. The $\delta^{15}N$ and $\delta^{13}C$ values were measured using a mass spectrometer (Delta V Advantage; Thermo Fisher Scientific, Waltham, MA, USA)

153 coupled with an elemental analyzer. These isotope ratios are expressed in standard δ-unit
154 notation, defined as $\delta^{15}N$ or $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$, where, R is either the
155 $^{15}N/^{14}N$ ratio for nitrogen or the $^{13}C/^{12}C$ ratio for carbon. The standards were atmospheric
156 nitrogen and Vienna Pee Dee belemnite for nitrogen and carbon, respectively. The
157 analytical precision was better than 0.2‰ for $\delta^{15}N$ and $\delta^{13}C$ values.

158 **Data analysis**

159 We performed a one-way analysis of variance (ANOVA) to compare the values of $\delta^{15}N$
160 and $\delta^{13}C$ of Lithosiini moths with those of non-Lithosiini moths collected from the two
161 sites. Tukey-Kramer HSD post hoc tests were performed for multiple comparisons of the
162 ANOVA results. All analyses were conducted using RStudio Desktop version 3.5.2 (R
163 Development Core Team 2018).

164 Hyodo *et al.* (2011) measured the $\delta^{13}C$ and $\delta^{15}N$ values of leaf litter at the same
165 tropical study site as ours in Lambir. By incorporating these values into the empirical
166 rules for the increment of the values at higher trophic levels (DeNiro & Epstein 1978;
167 Minagawa & Wada 1984, see Appendix S1), the ranges of $\delta^{13}C$ and $\delta^{15}N$ values of
168 herbivores at the locality were estimated (Fig. 1). The $\delta^{13}C$ and $\delta^{15}N$ values of each target
169 moth species were assessed by comparing with the estimated ranges of herbivores.
170 Similarly, based on the $\delta^{13}C$ and $\delta^{15}N$ values of the litter sampled at Kamigamo, we
171 estimated the ranges of $\delta^{13}C$ and $\delta^{15}N$ values that most herbivores present there were

172 expected to show (Fig. 2).

173 **RESULTS**

174 **Stable isotope ratios of moths in the tropical rainforest**

175 The $\delta^{15}N$ values significantly varied among the moth species (ANOVA, $F_{17, 36} = 18.85$, P
176 < 0.0001, Fig. 3). Eight Lithosiini species had significantly lower $\delta^{15}N$ values than four
177 non-Lithosiini species (*Eupterote* sp., *Hyposidra talaca*, *Phalera javana*, and *Biston*
178 *insularis*). Four Lithosiini species (Lithosiini sp. 2, sp. 3, *Barsine crustata*, and *Teulisna*
179 sp.) had significantly lower $\delta^{15}N$ values than all nine non-Lithosiini species. One
180 Lithosiini species (*Schistophleps* sp.) had significantly lower $\delta^{15}N$ values than all the non-
181 Lithosiini species (Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 3). Among eight
182 Lithosiini species, there was no significant difference in the $\delta^{15}N$ values (Tukey-Kramer
183 HSD post-hoc test, $P > 0.05$, Fig. 3).

184 The $\delta^{13}C$ and $\delta^{15}N$ values of nine non-Lithosiini moths were within, or were
185 considerably close to, the estimated ranges of $\delta^{13}C$ and $\delta^{15}N$ values for herbivores at the
186 study site, whereas the $\delta^{15}N$ values of eight (other than *Adites* sp.) of nine Lithosiini
187 species were markedly out of the ranges (Fig. 1).

188 The remaining one Lithosiini species, *Adites* sp., was considerably different from
189 the other above-mentioned Lithosiini species in the $\delta^{15}N$ value, which was significantly
190 higher than in the other Lithosiini species and higher among four of non-Lithosiini species

191 (*Hypochrosis binexata*, *Daphnusa ocellaris*, *Petelia medardaria*, and *Hamodes propitia*).
192 There were no significant differences in $\delta^{15}N$ values between *Adites* sp. and the other five
193 non-Lithosiini species (*Lyssa zampa*, *Eupterote* sp., *Hyposidra talaca*, *Phalera javana*,
194 and *Biston insularis*) (Tukey-Kramer HSD post-hoc test, $P > 0.05$, Fig. 3).

195 The $\delta^{13}C$ value was significantly different among all moth species (ANOVA, $F_{17, 36}$
196 $= 8.43$, $P < 0.0001$, Fig. 4). *Adites* sp. had the highest and significantly higher $\delta^{13}C$ values
197 than most of the other moth species studied, except for the three non-Lithosiini species
198 (*Hypochrosis binexata*, *Hamodes propitia*, and *Hyposidra talaca*). The non-Lithosiini
199 species, *Phalera javana*, had the lowest and significantly lower $\delta^{13}C$ values than the three
200 Lithosiini species (*Trischalis stomata*, *Asura* sp., and *Adites* sp.) and five non-Lithosiini
201 species (*Lyssa zampa*, *Petelia medardaria*, *Hypochrosis binexata*, *Hamodes propitia*, and
202 *Hyposidra talaca*) (Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 4). There were no
203 significant differences in $\delta^{13}C$ values among the six Lithosiini species (*Teulisna* sp.,
204 Lithosiini spp. 1–3, *Barsine crustata,* and *Schistophleps* sp.) and three non-Lithosiini
205 species (*Biston insularis*, *Daphnusa ocellaris*, and *Eupterote* sp.) (Tukey-Kramer HSD
206 post-hoc test, $P > 0.05$, Fig. 4). Thus, based on the $\delta^{13}C$ values, the eight Lithosiini species
207 that showed lower $\delta^{15}N$ values than those of the non-Lithosiini species (Fig. 3), were not
208 discriminated as a group from the non-Lithosiini species (Fig. 4).

Stable isotope ratios of moths in the temperate forest

The $\delta^{15}N$ value was significantly different among the moth species ($F_{53, 105} = 6.45$, $P < 0.0001$, multiple comparisons by Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 5). A non-Lithosiini species, *Comostola subtiliaria nympha,* showed the lowest $\delta^{15}N$ value, which was significantly lower than those of 17 species, including one Lithosiini species, *Cyana hamata hamata* (Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 5). Another non-Lithosiini species, *Athetis stellata*, showed the highest $\delta^{15}N$ value, which was not significantly different from those of 29 species, including all Lithosiini species (Tukey-Kramer HSD post-hoc tests, $P < 0.05$, Fig. 5). Thus, the distribution of the $\delta^{15}N$ values for all Lithosiini species overlapped with that of all non-Lithosiini species (Fig. 5).

The $\delta^{13}C$ value was significantly different among the moth species ($F_{53, 105} = 5.34$, $P < 0.0001$, Fig. 6). A non-Lithosiini species, *Herpetogramma luctuosale zelleri*, showed the lowest $\delta^{13}C$ value, which was significantly lower than those of 13 species, including the two Lithosiini species, *Eilema japonica japonica* and *Miltochrista miniata* (Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 6). Another non-Lithosiini species, *Paragona cleorides*, showed the highest $\delta^{13}C$ value, which was significantly higher than those of 23 species, including the three Lithosiini species, *Cyana hamata hamata*, *Eilema aegrota*, and *Eilema deplana pavescens* (Tukey-Kramer HSD post-hoc test, $P < 0.05$, Fig. 6). Thus, similar to the distribution of the $\delta^{15}N$ values, the distribution of the $\delta^{13}C$ values in all Lithosiini species overlapped with that of all non-Lithosiini species (Fig. 6).

229 The $\delta^{13}C$ and $\delta^{15}N$ values of the eight Lithosiini species overlapped considerably
230 with the range of 37 non-Lithosiini species, and with the range of expected values that
231 was estimated based on the values of litter, for herbivores in the study site (Fig. 2).

232 **DISCUSSION**

233 The remarkable overlap between the ranges of $\delta^{13}C$ and $\delta^{15}N$ values expected for
234 herbivores in the tropical rainforest (Lambir) and those of the nine non-Lithosiini moth
235 species targeted the expected ranges of $\delta^{13}C$ and $\delta^{15}N$ values for herbivores can be
236 inferred from the $\delta^{13}C$ and $\delta^{15}N$ values measured for leaf litters in the same habitat, as
237 mentioned above (DeNiro & Epstein 1978; Minagawa & Wada 1984). The overlap
238 between the expected ranges and the ranges of the values measured for moths in a habitat
239 suggests that the moths are herbivores. The remarkable overlap between them in the
240 tropical rainforest (Lambir) in this study (Fig. 1) strengthens the suggestions of Holloway
241 (1983, 1987, 1993, 1998, 2001, 2005) with quantitative evidence that these nine moth
242 species are plant-feeders. On the other hand, there was a difference in $\delta^{15}N$ values
243 between eight (other than *Adites* sp.) of the nine Lithosiini species collected from Lambir
244 and the above-mentioned plant-feeding moth species (Fig. 3). Furthermore, the ranges of
245 $\delta^{13}C$ and $\delta^{15}N$ values of the eight Lithosiini species deviated remarkably from those
246 estimated for herbivores at the study site (Fig. 1). These results suggest that the eight
247 Lithosiini species feed mainly on lichens during their larval stages at the study site. The

248 similarity between the $\delta^{13}C$ and $\delta^{15}N$ values of these eight Lithosiini species and the
249 values measured by Hyodo *et al*. (2011) for a lichen-feeding termite species,
250 *Hospitalitermes hospitalis* (Fig. 7), at the same study site also strongly supports this
251 suggestion.

252 Adams *et al.* (2016) and Shin *et al.* (2018) used methods similar to those used in this
253 study and examined whether Lithosiini were lichen feeders by measuring the $\delta^{13}C$ and
254 $\delta^{15}N$ values of the moths and lichens in the European temperate zone and the Southeast
255 Asian subtropical zone, respectively. Their results demonstrated that the majority of their
256 target Lithosiini species were not lichen feeders. In addition, these results seem to be
257 consistent with our results of stable isotope ratio analysis of Lithosiini moths collected
258 from Kamigamo, suggesting that the majority of Lithosiini moths do not feed on lichens
259 in the temperate region (Figs. 5, 6). Thus, the results of stable isotope analysis of
260 Lithosiini moths inhabiting non-tropical forests are inconsistent with those of Lithosiini
261 moths inhabiting tropical rainforests.

262 The great difference in $\delta^{13}C$ and $\delta^{15}N$ values between Lithosiini moths in the tropical
263 rainforest and those in temperate forests could be explained by the following hypothetical
264 scenario. The food habits of the majority of Lithosiini moth species differ between
265 tropical and non-tropical zones; a majority of Lithosiini species do not feed on lichens in
266 the temperate zone, or in sub-tropical and temperate zones, whereas a majority feed on

267 lichens in tropical rainforests. Some differences in environmental conditions between
268 tropical and non-tropical zones may affect the differences in food habits. However, there
269 is another explanation. The difference could be a randomly derived result due to
270 unintended selection biases: the sample size (the number of target species) and the number
271 of study sites were limited. Although the food resources during larval stages have been
272 clarified for most Lithosiini species in a particular region (*e.g.,* European temperate zone,
273 Table S1), they have not been sufficiently investigated for the majority of described
274 Lithosiini species. For example, this has been investigated at most for 38% and 6% of
275 Lithosiini species recorded from Japan (East Asian temperate zone) and Borneo (the
276 Southeast Asian tropics), respectively (Table S1). To explore these possibilities, or to
277 determine whether there are any significant differences in the percentage of lichen-
278 feeding species in Lithosiini species between non-tropical and tropical zones, the stable
279 isotope ratios of nitrogen and carbon should be analyzed for a larger number of Lithosiini
280 species in both climatic zones at much broader spatial scales.

281 In Lambir, the $\delta^{13}C$ and $\delta^{15}N$ values of *Adites* sp. were remarkably different not only
282 from those of the other eight Lithosiini species, which are suggested to be lichen feeders
283 as mentioned above, but also from those of the plant-feeding non-Lithosiini moth species
284 (Fig. 1), as well as those measured by Hyodo *et al*. (2010) for eight species of herbivorous
285 insects at the same study site (Fig. 7). On the other hand, the values were similar to those
286 of animals that feed on matter derived from animal bodies, such as predatory and

287 detritivorous insects (e.g., Carabidae spp. inhabiting the same site, Hyodo *et al*. 2010),
288 and those of animals that feed on soil organic matter, including humus or litter of dead
289 plant tissues, such as soil-feeding termites (e.g., *Prohamitermes mirabilis* inhabiting the
290 same site, Hyodo *et al*. 2011) (Fig. 7). These similarities suggest that *Adites* sp. possibly
291 feeds on animal-derived matter or soil organic matter during the larval stages. Although
292 no Lithosiini species has been found to feed on animal-derived matter or humus during
293 larval stages, several species of the tribe Arctiini and Syntomini, which belong to the
294 subfamily Arctiinae together with the tribe Lithosiini, have been found to feed on animal-
295 derived matter or humus (Krasnoff & Roelofs 1989; Pierce 1995; Conner 2009). This fact
296 supports the possibility of animal-derived matter or humus feeding in *Adites* sp.

297 Larvae of three Lithosiini species have been suggested to feed on lichens in the
298 tropical rainforest zone of Southeast Asia (Holloway 2001). However, to the best of our
299 knowledge, food habits remain to be clarified with robust evidence, such as records of
300 larval rearing, for almost all of the 300 described Lithosiini species in this zone (Holloway
301 2001), except for the eight Lithosiini species that have been suggested to feed on lichens
302 in this study. To understand the diversity, evolution, and ecology of Lithosiini, it is
303 necessary to identify food resources for many Lithosiini species whose larval food
304 preferences are not yet known. This may require finding or collecting a sufficient number
305 of larvae for observation to determine their dietary habits under a wide range of
306 environmental conditions or under well-controlled laboratory conditions in captivity.

Under the conditions in which larval food resources vary plastically in response to changes in environmental conditions, it is extremely difficult to identify the larval food resources of Lithosiini only by direct observation of the feeding behavior of larvae. Therefore, the stable isotope ratio analysis performed in this study, which can provide evidence supporting food resources during larval stages without observation of feeding behavior, would be useful for future studies attempting to determine phylogenetic distribution of lichen-feeding in and around the lineage of Lithosiini for better inference of the origin(s) of lichen feeding in moths.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Appendix S1. A method for estimating the range of $\delta^{13}C$ and $\delta^{15}N$ values that herbivores in a site are expected to exhibit, based on the $\delta^{13}C$ and $\delta^{15}N$ values of litter in that site.

Table S1. The numbers of Lithosiini species whose larval food resources have been confirmed to be lichens, both lichens and non-lichens, and non-lichens in the European temperate zone, Japan, and Borneo. The percentages among all of the recorded Lithosiini species from each region are provided in the parentheses.

Table S2. The $\delta^{13}C$ and $\delta^{15}N$ values of moths in Lambir Hills National Park. The sample size (the number of individuals examined in this study) was three for each species.

Table S3. The $\delta^{13}C$ and $\delta^{15}N$ values of moths in Kamigamo Experimental Station, Kyoto University. The sample size (the number of individuals examined in this study) was three for each species.

448 **Figure legends**

449 Fig. 1 Scatter plot of $\delta^{13}C$ and $\delta^{15}N$ values of Lithosiini, non-Lithosiini, and litter in a
450 tropical rainforest (Lambir). The plots and bars indicate their mean values and
451 standard deviations. The rectangle area enclosed by the red broken line
452 indicates the predicted ranges of $\delta^{13}C$ and $\delta^{15}N$ values estimated for plant-
453 feeding insects based on the empirical rules for the increase of their values
454 through an elevation of trophic level from the values of litter, which were
455 obtained from Hyodo *et al*. (2011).

456 Fig. 2 Scatter plot of $\delta^{13}C$ and $\delta^{15}N$ values of Lithosiini, non-Lithosiini, and litter in a
457 temperate forest (Kamigamo). The plots and bars indicate their mean values
458 and standard deviations. The rectangle area enclosed by the red broken line
459 indicates the predicted ranges of $\delta^{13}C$ and $\delta^{15}N$ values estimated for plant-
460 feeding insects based on the empirical rules for the increase of their values
461 through an elevation of trophic level from the values of litter.

462 Fig. 3 $\delta^{15}N$ values of Lithosiini (solid circles) and non-Lithosiini (open circles) moths
463 in a tropical rainforest (Lambir). A plot and horizontal bar indicate the mean
464 and standard deviation, respectively, for each moth species. The sample size
465 was three for each moth species and 15 for litter. The same letters indicate no
466 significant difference in the value between the compared species (Tukey-
467 Kramer post hoc test, $P > 0.05$).

468 Fig. 4 $\delta^{13}C$ values of Lithosiini (solid circles) and non-Lithosiini (open circles) moths
469 in a tropical rainforest (Lambir). A plot and horizontal bar indicate the mean
470 and standard deviation, respectively, for each moth species. The sample size
471 was three for each moth species and 15 for litter. The same letters indicate no

significant difference in the value between the compared species (Tukey-Kramer post hoc test, $P > 0.05$).

Fig. 5 $\delta^{15}N$ values of Lithosiini (solid circles) and non-Lithosiini (open circles) moths in a temperate forest (Kamigamo). A plot and horizontal bar indicate the mean and standard deviation, respectively, for each moth species. The sample size was three for each moth species and 20 for litter. The same letters indicate no significant difference in the value between the compared species (Tukey-Kramer post hoc test, $P > 0.05$).

Fig. 6 $\delta^{13}C$ values of Lithosiini (solid circles) and non-Lithosiini (open circles) moths in a temperate forest (Kamigamo). A plot and horizontal bar indicate the mean and standard deviation, respectively, for each moth species. The sample size was three for each moth species and 20 for litter. The same letters indicate no significant difference in the value between the compared species (Tukey-Kramer post hoc test, $P > 0.05$).

Fig. 7 Scatter plot of $\delta^{13}C$ and $\delta^{15}N$ values of Lithosiini, lichen-feeding termite, soil-feeding termites, herbivorous insects, predatory insects, and litter in a tropical rainforest (Lambir). The plots and bars indicate their mean values and standard deviations. The rectangle area enclosed by the red broken line indicates the predicted ranges of $\delta^{13}C$ and $\delta^{15}N$ values estimated for plant-feeding insects based on the empirical rules for the increase of their values through an elevation of trophic level from the values of litter, which was obtained by Hyodo *et al*. (2011). The values for lichen-feeding termite, soil-feeding termites, herbivorous insects, and predatory insects were obtained from Hyodo *et al*. (2010, 2011).

Appendix S1. A method for estimating the range of $\delta^{13}C$ and $\delta^{15}N$ values that herbivores in a site are expected to exhibit, based on the $\delta^{13}C$ and $\delta^{15}N$ values of litter in that site.

Many previous studies have shown that the $\delta^{15}N$ and $\delta^{13}C$ values of herbivores in a site can be estimated from the $\delta^{15}N$ and $\delta^{13}C$ values of leaf litter in that site, respectively, from the empirical rule expressed by the following equations (DeNiro & Epstein 1978; Minagawa & Wada 1984):

$$\delta^{15}N_{herb} = \delta^{15}N_{litt} + \Delta^{15}N,$$

$$\delta^{13}C_{herb} = \delta^{13}C_{litt} + \Delta^{13}C,$$

where, $\delta^{15}N_{herb}$, ,$\delta^{15}N_{litt}$, and $\Delta^{15}N$ are the $\delta^{15}N$ values for herbivores, leaf litter, and the trophic enrichment, respectively, and $\delta^{13}C_{herb,}$ $\delta^{13}C_{litt}$, and $\Delta^{13}C$ are the $\delta^{13}C$ values for herbivores, leaf litter, and the trophic enrichment, respectively. In general, the $\Delta^{15}N$ is estimated to be 3.4 ± 1.1‰ (mean ± SD) (Minagawa & Wada 1984), and the $\Delta^{13}C$ is estimated to be 0.8 ± 1.1‰ (DeNiro & Epstein 1978).

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Table S1 The numbers of Lithosiini species whose larval food resources have been confirmed to be lichens, both lichens and non-lichens, and non-lichens in European temperate zone, Japan, and Borneo, respectively. The percentages among all of the recorded Lithosiini species from each region are provided in the parentheses. Among the larval food resources of Lithosiini used in this study, five species were lichen, one species was both lichen and non-lichen and two species were unknown in Japan (Kishida 2020), and all species were unknown in Borneo (Holloway 2001).

Region	Food resource(s)	No. of species (%)	References
European temperate zone			Paolo *et al.* (1999), Leraut (2006)
	Lichen	26 (59.1)	
	Both lichen and non-lichen	8 (18.2)	
	Non-lichen	5 (11.4)	
	(Food resources detected)	39 (88.6)	
	(Unknown)	5 (11.4)	
	(Total: All recorded species)	44 (100)	
Japan			Kishida (2020)
	Lichen	13 (19.4)	
	Both lichen and non-lichen	7 (10.4)	
	Non-lichen	5 (7.5)	
	(Food resources detected)	25 (37.3)	
	(Unknown)	42 (62.7)	
	(Total: All recorded species)	67 (100)	
Borneo			Holloway (2001)
	Lichen	3 (1.0)	
	Both lichen and non-lichen	0 (0.0)	
	Non-lichen	13 (4.4)	
	(Food resources detected)	16 (5.4)	
	(Unknown)	281 (94.6)	
	(Total: All recorded species)	297 (100)	

Table S2 The $\delta^{13}C$ and $\delta^{15}N$ values of moths in Lambir Hills National Park.
The sample size (the number of individuals examined) was three for each species.

Taxa	$\delta^{13}C$ (‰) (mean ± SE)	$\delta^{15}N$ (‰) (mean ± SE)
Eupterotidae		
Eupterotinae		
Eupterote sp.	-30.7 ± 0.1	3.8 ± 1.1
Sphingidae		
Smerinthinae		
Daphnusa ocellaris	-31.7 ± 0.9	1.1 ± 1.7
Uraniidae		
Uraniinae		
Lyssa zampa	-29.3 ± 1.6	2.7 ± 0.8
Geometridae		
Ennominae		
Biston insularis	-32.0 ± 2.3	5.3 ± 1.9
Hypochrosis binexata	-27.7 ± 1.1	-0.4 ± 0.4
Hyposidra talaca	-26.4 ± 0.7	4.1 ± 0.4
Petelia medardaria	-28.0 ± 0.6	1.2 ± 0.9
Notodontidae		
Phalera javana	-35.2 ± 1.5	4.2 ± 1.8
Erebidae		
Arctiinae		
Lithosiini		
Adites sp.	-23.1 ± 0.9	6.4 ± 1.1
Asura sp.	-27.9 ± 1.1	-3.8 ± 1.3
Barsine crustata	-30.9 ± 0.3	-2.3 ± 1.9
Schistophleps sp.	-29.7 ± 0.3	-5.5 ± 1.6
Teulisna sp.	-32.7 ± 1.1	-1.0 ± 0.6
Trischalis stomata	-28.8 ± 1.1	-4.2 ± 1.1
Lithosiini sp.1	-29.8 ± 2.2	-5.0 ± 0.2
Lithosiini sp.2	-30.7 ± 0.4	-1.5 ± 2.0
Lithosiini sp.3	-31.4 ± 0.6	-3.5 ± 1.6
Calpinae		
Hamodes propitia	-27.4 ± 0.9	1.7 ± 0.5

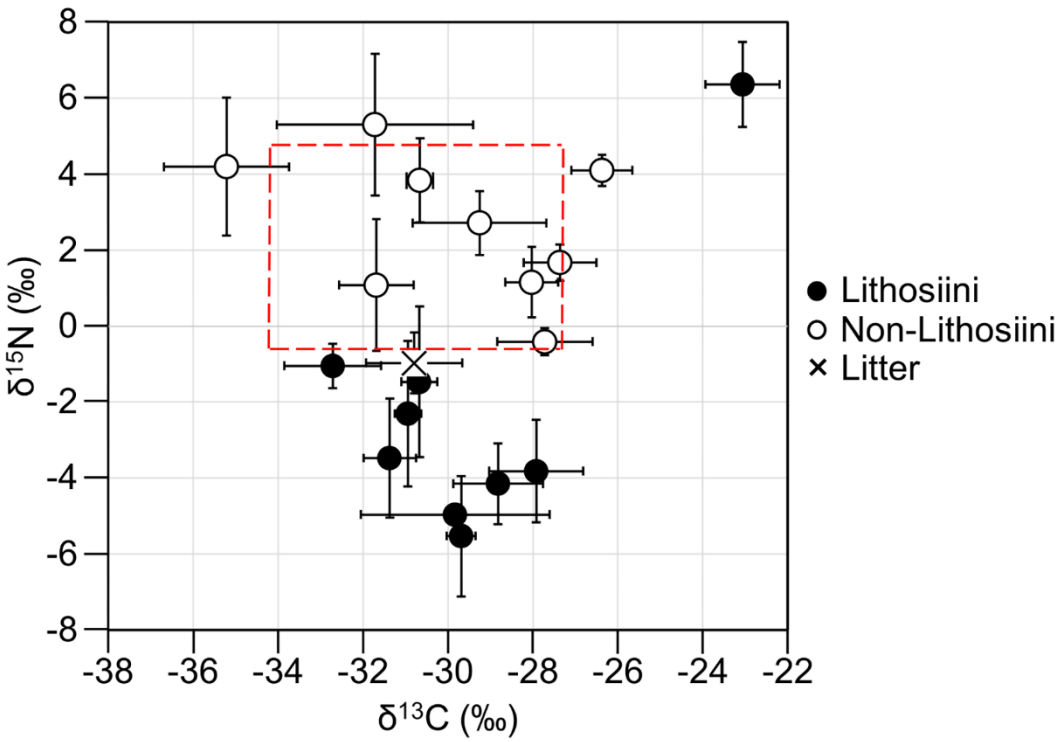
Table S3 The $\delta^{13}C$ and $\delta^{15}N$ values of moths in Kamigamo Experimental Station, Kyoto University. The sample size (the number of individuals examined) was three for each species.

Taxa	$\delta^{13}C$ (‰) (mean ± SE)	$\delta^{15}N$ (‰) (mean ± SE)
Limacodidae		
Limacodinae		
Phrixolepia sericea	-31.6 ± 1.2	2.8 ± 1.2
Zygaenidae		
Chalcosiinae		
Pidorus atratus	-32.7 ± 0.6	-1.3 ± 1.3
Tortricidae		
Tortricinae		
Archips audax	-32.1 ± 2.2	-4.3 ± 1.6
Olethreutinae		
Hystrichoscelus spathanum	-28.5 ± 2.1	1.9 ± 3.0
Rhopobota ilexi	-31.5 ± 0.8	-6.7 ± 1.4
Pyralidae		
Pyralinae		
Hypsopygia regina	-27.3 ± 0.5	0.8 ± 1.5
Phycitinae		
Addyme confusalis	-28.6 ± 1.5	1.9 ± 0.8
Crambidae		
Crambinae		
Chrysoteuchia distinctella	-32.0 ± 0.1	0.4 ± 0.5
Pyraustinae		
Herpetogramma luctuosale zelleri	-33.1 ± 0.8	4.5 ± 3.0
Palpita nigropunctalis	-27.7 ± 1.4	4.1 ± 1.8
Drepanidae		
Drepaninae		
Macrocilix mysticata watsoni	-30.3 ± 0.2	-0.5 ± 0.2
Geometridae		
Ennominae		
Alcis angulifera	-28.4 ± 1.4	0.6 ± 2.3
Euchristophia cumulata cumulata	-29.5 ± 0.9	-2.0 ± 0.3
Garaeus specularis mactans	-29.8 ± 1.9	-2.6 ± 2.0
Nothomiza formosa	-28.8 ± 1.8	-2.7 ± 3.0
Ourapteryx nivea	-30.1 ± 1.7	-3.2 ± 1.4
Ourapteryx obtusicauda	-28.6 ± 1.1	-2.1 ± 0.7
Paradarisa chloauges kurosawai	-27.7 ± 0.8	-1.1 ± 4.0
Plagodis pulveraria japonica	-32.3 ± 1.0	-2.7 ± 2.0
Platycerota incertaria	-27.5 ± 0.7	-5.3 ± 2.5
Plesiomorpha flaviceps	-26.3 ± 0.2	-5.5 ± 2.5
Rhynchobapta cervinaria	-30.4 ± 0.9	-0.3 ± 1.2
Synegia hadassa	-26.2 ± 0.3	-5.3 ± 2.3
Geometrinae		
Comostola subtiliaria nympha	-27.5 ± 0.3	-8.5 ± 0.3

Sterrhinae		
Idaea remissa	-28.4 ± 0.5	-2.0 ± 1.6
Idaea denudaria	-28.0 ± 0.7	3.6 ± 0.6
Scopula epiorrhoe	-26.9 ± 1.8	-0.9 ± 1.8
Larentiinae		
Chloroclystis excisa	-27.6 ± 1.9	-4.2 ± 2.4
Chloroclystis v-ata lucinda	-27.3 ± 1.6	-5.5 ± 1.1
Notodontidae		
Notodontinae		
Cnethodonta grisescens grisescens	-31.1 ± 1.8	2.2 ± 0.2
Noctuidae		
Eriopinae		
Callopistria japonibia	-29.2 ± 1.7	0.9 ± 0.5
Noctuinae		
Sineugraphe oceanica	-28.8 ± 0.7	1.3 ± 3.0
Hadeninae		
Athetis stellata	-29.6 ± 0.5	7.2 ± 1.7
Erebidae		
Lymantriinae		
Kidokuga piperita	-29.4 ± 2.4	2.7 ± 0.1
Herminiinae		
Zanclognatha helva	-28.7 ± 0.8	-3.4 ± 0.2
Arctiinae		
Lithosiini		
Cyana hamata hamata	-31.0 ± 0.1	-0.3 ± 0.9
Eilema aegrota	-30.0 ± 0.9	-2.4 ± 1.8
Eilema deplana pavescens	-29.8 ± 0.9	-1.8 ± 2.2
Eilema japonica japonica	-27.3 ± 0.2	-4.1 ± 1.8
Eilema nankingica	-28.2 ± 0.4	-6.4 ± 0.6
Macrobrochis staudingeri staudingeri	-28.1 ± 0.5	-1.7 ± 0.5
Miltochrista miniata	-26.9 ±0.8	-0.5 ± 0.8
Philenora latifasciata	-28.4 ± 0.2	-1.7 ± 1.3
Calpinae		
Oraesia excavata	-27.7 ± 0.6	2.1 ± 0.5
Erebinae		
Paragona cleorides	-23.3 ± 1.2	0.1 ± 2.6

sp. 1

Fig. 1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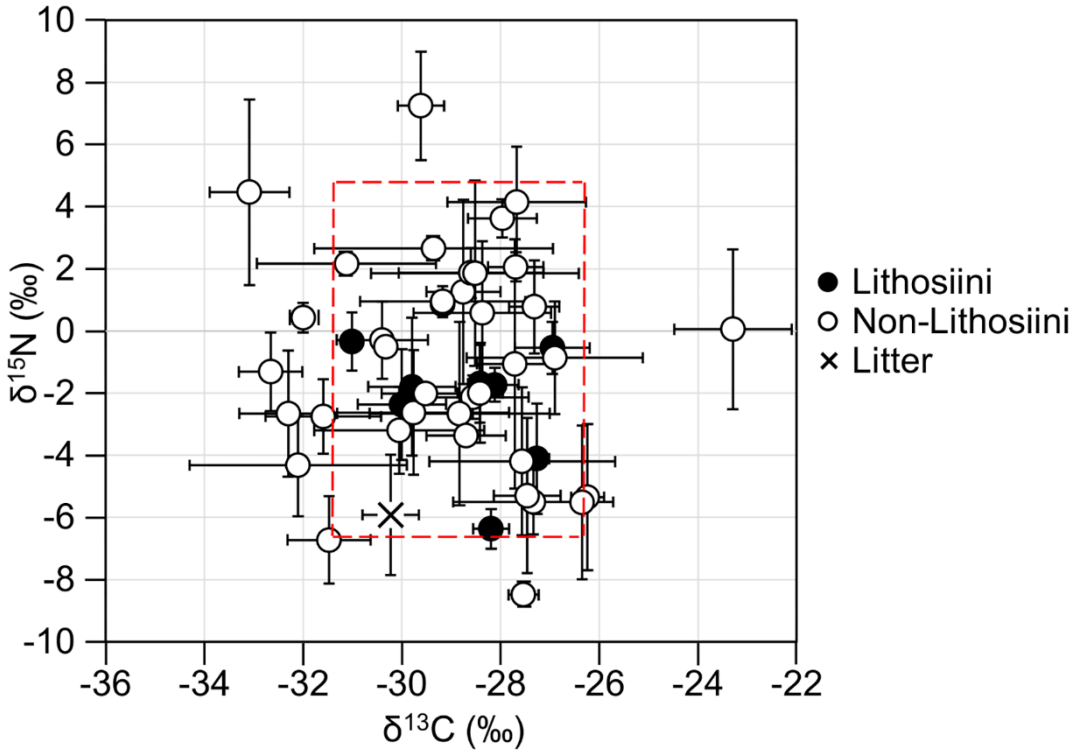
δ13C (‰)
Lithosiini
Non-Lithosiini
Litter

Fig. 2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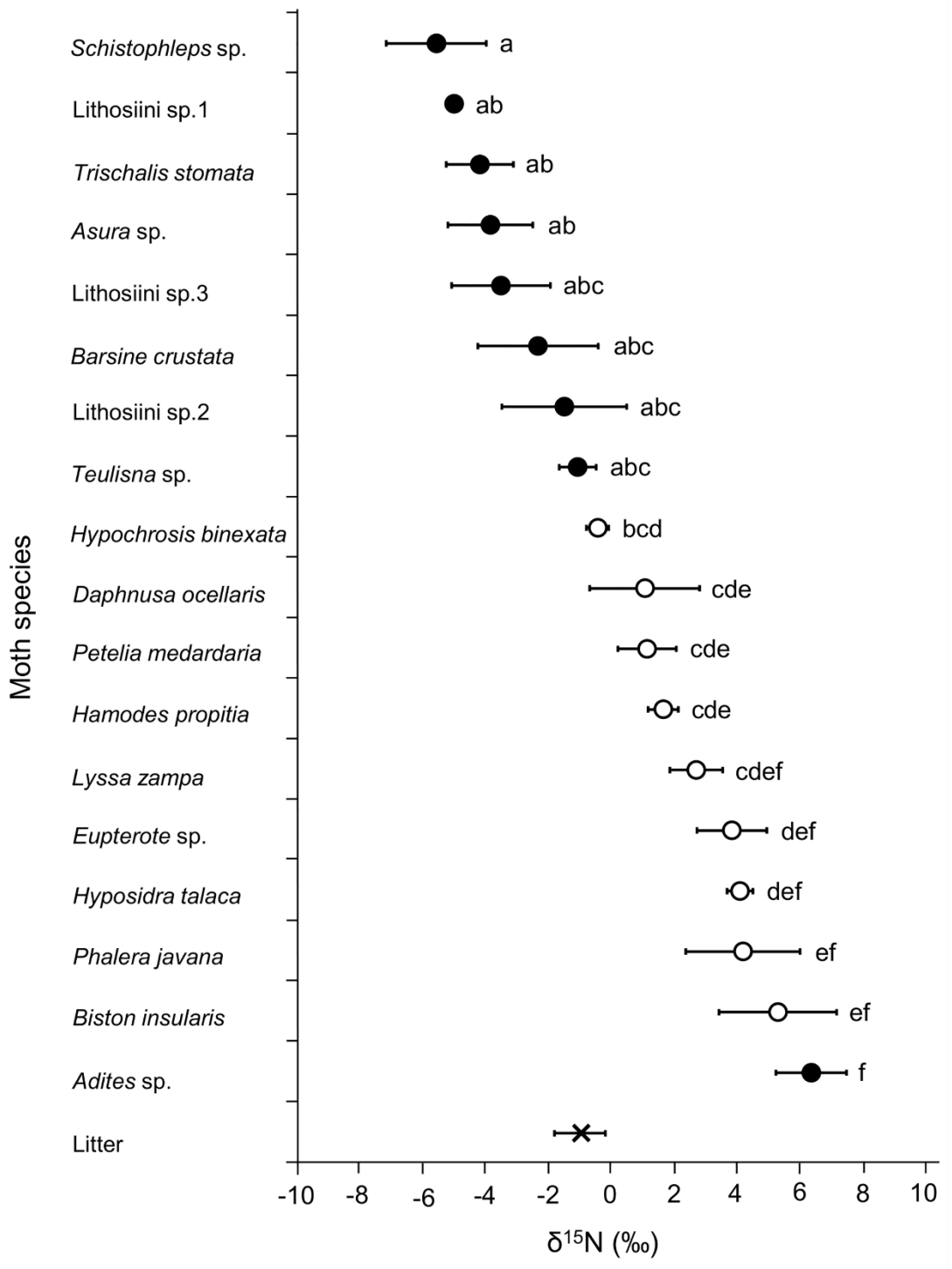
δ13C (‰)
Lithosiini
Non-Lithosiini
Litter

Fig. 3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Asura sp.
Lithosiini sp.3
Barsine crustata
Lithosiini sp.2
Teulisna sp.
Hypochrosis binexata
Daphnusa ocellaris
Petelia medardaria
Hamodes propitia
Lyssa zampa
Eupterote sp.
Hyposidra talaca
Phalera javana
Biston insularis
Adites sp.
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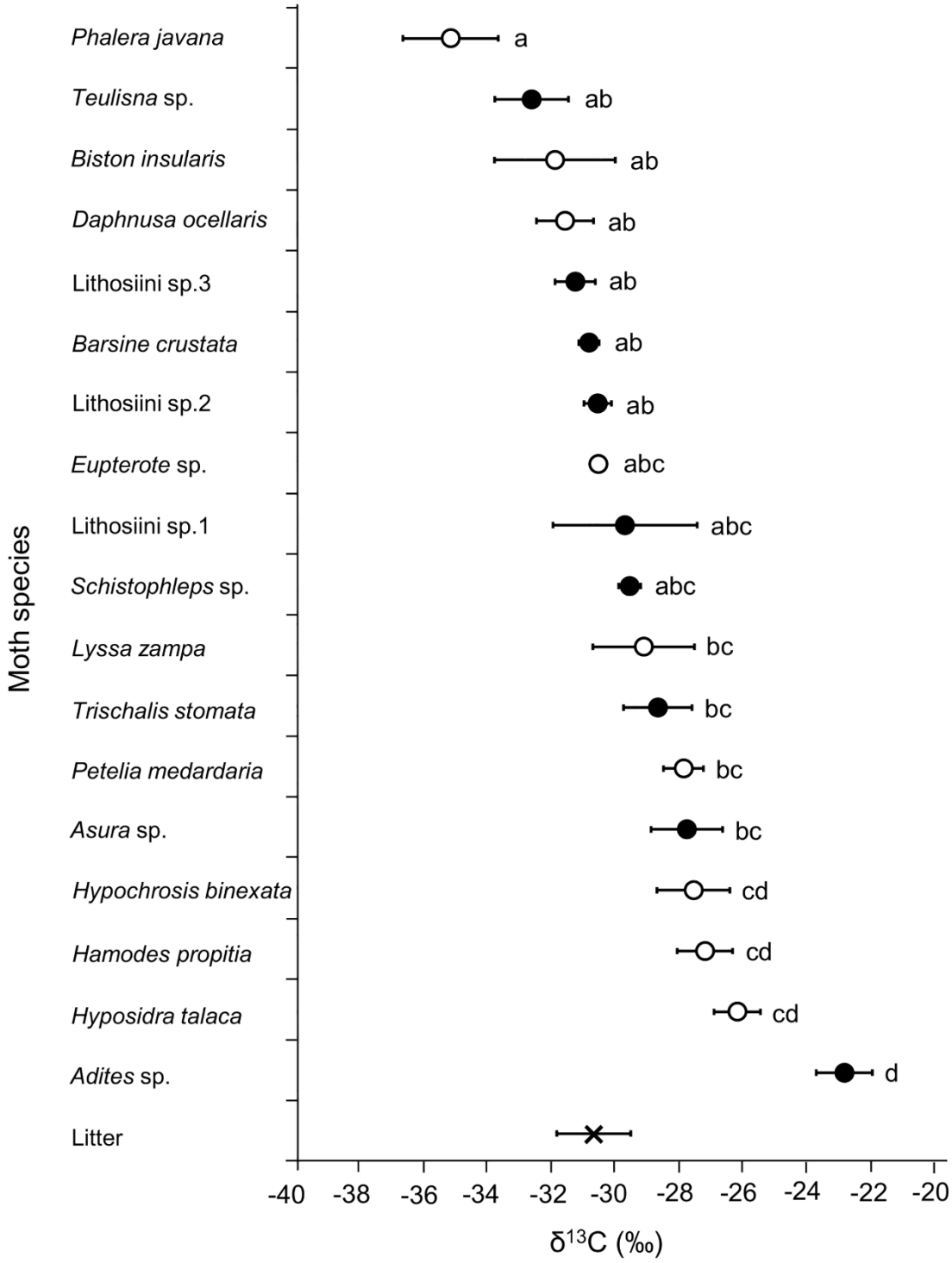
δ15N (‰)

Fig. 4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Biston insularis
Daphnusa ocellaris
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Barsine crustata
Lithosiini sp.2
Eupterote sp.
Lithosiini sp.1
Schistophleps sp.
Lyssa zampa
Trischalis stomata
Petelia medardaria
Asura sp.
Hypochrosis binexata
Hamodes propitia
Hyposidra talaca
Adites sp.
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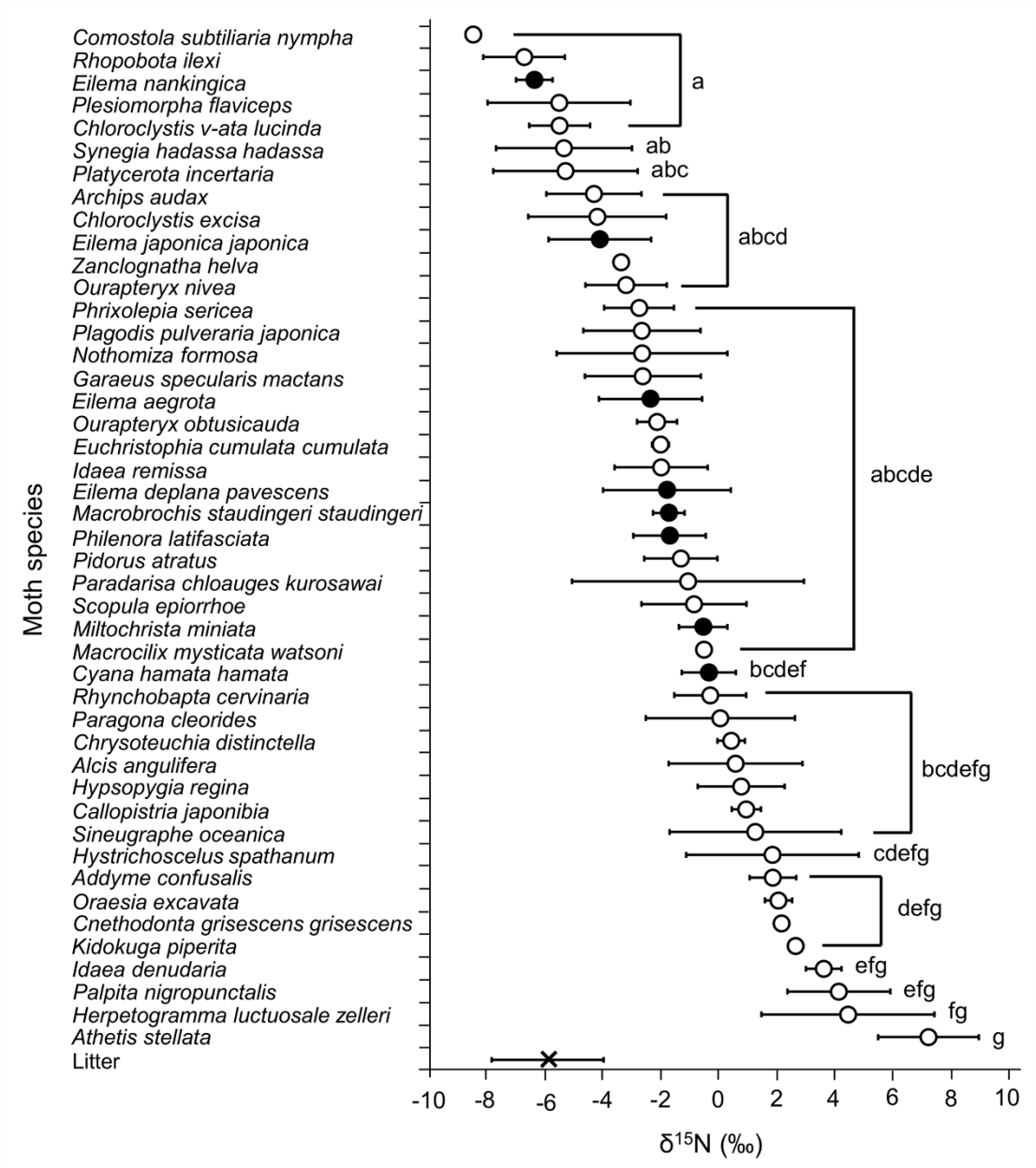
δ13C (‰)

Fig. 5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Platycerota incertaria
Archips audax
Chloroclystis excisa
Eilema japonica japonica
Zanclognatha helva
Ourapteryx nivea
Phrixolepia sericea
Plagodis pulveraria japonica
Nothomiza formosa
Garaeus specularis mactans
Eilema aegrota
Ourapteryx obtusicauda
Euchristophia cumulata cumulata
Idaea remissa
Eilema deplana pavescens
Macrobrochis staudingeri staudingeri
Philenora latifasciata
Pidorus atratus
Paradarisa chloauges kurosawai
Scopula epiorrhoe
Miltochrista miniata
Macrocilix mysticata watsoni
Cyana hamata hamata
Rhynchobapta cervinaria
Paragona cleorides
Chrysoteuchia distinctella
Alcis angulifera
Hypsopygia regina
Callopistria japonibia
Sineugraphe oceanica
Hystrichoscelus spathanum
Addyme confusalis
Oraesia excavata
Cnethodonta grisescens grisescens
Kidokuga piperita
Idaea denudaria
Palpita nigropunctalis
Herpetogramma luctuosale zelleri
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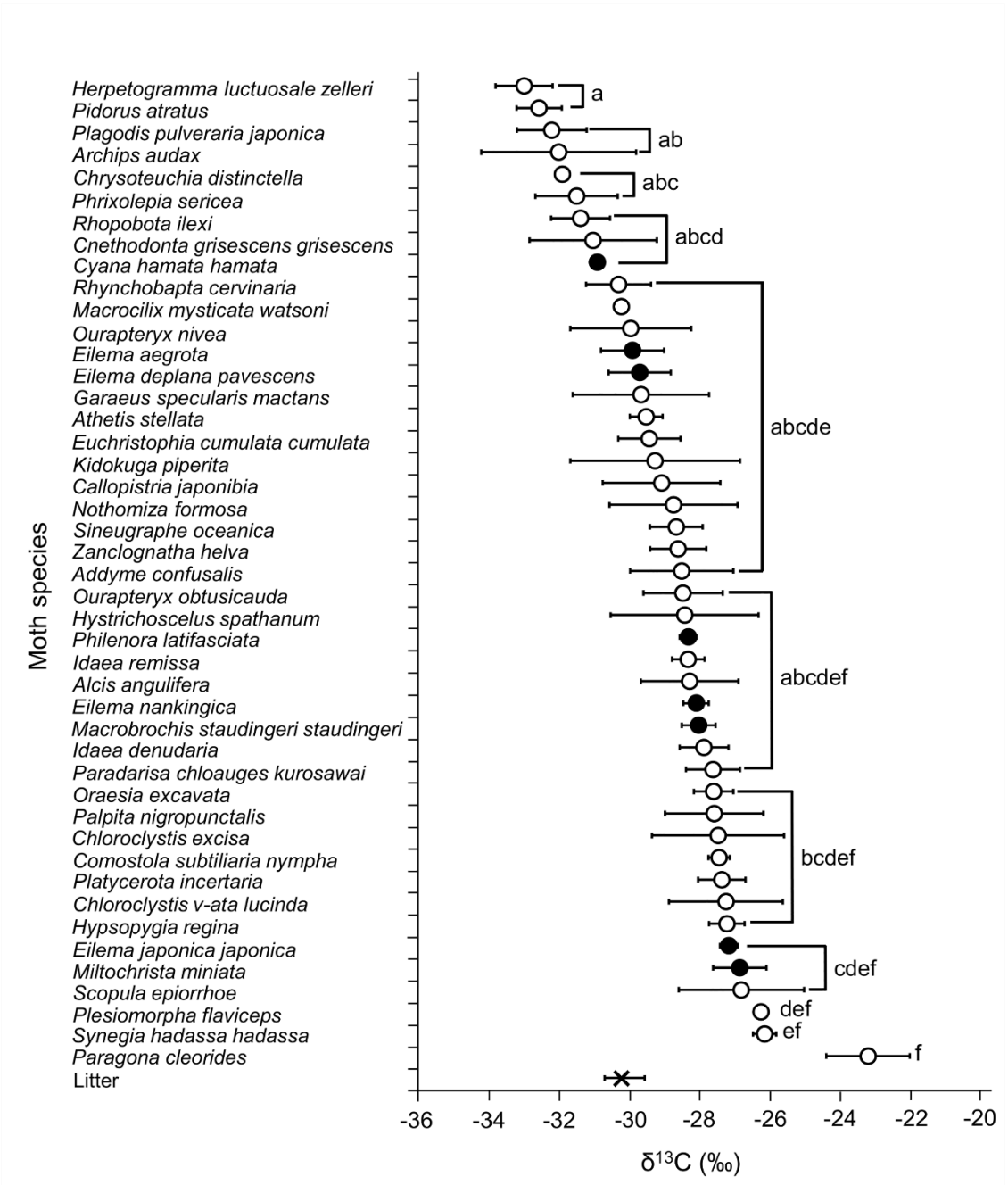
δ15N (‰)

Fig. 6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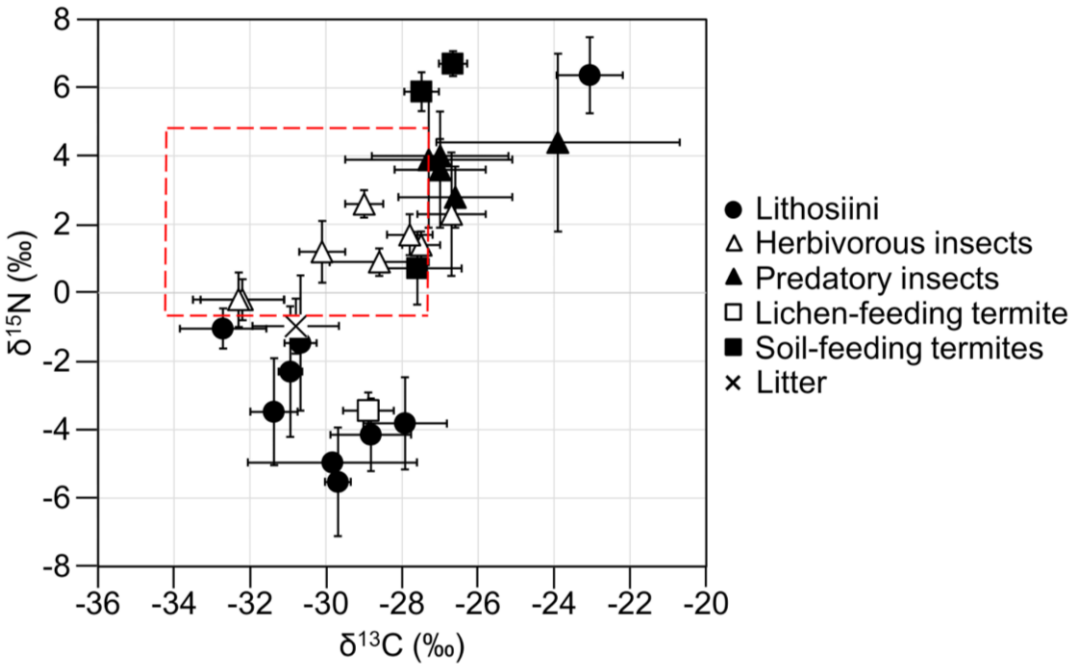
Plagodis pulveraria japonica
Archips audax
Chrysoteuchia distinctella
Phrixolepia sericea
Rhopobota ilexi
Cnethodonta grisescens grisescens
Cyana hamata hamata
Rhynchobapta cervinaria
Macrocilix mysticata watsoni
Ourapteryx nivea
Eilema aegrota
Eilema deplana pavescens
Garaeus specularis mactans
Athetis stellata
Euchristophia cumulata cumulata
Kidokuga piperita
Callopistria japonibia
Nothomiza formosa
Sineugraphe oceanica
Zanclognatha helva
Addyme confusalis
Ourapteryx obtusicauda
Hystrichoscelus spathanum
Philenora latifasciata
Idaea remissa
Alcis angulifera
Eilema nankingica
Macrobrochis staudingeri staudingeri
Idaea denudaria
Paradarisa chloauges kurosawai
Oraesia excavata
Palpita nigropunctalis
Chloroclystis excisa
Comostola subtiliaria nympha
Platycerota incertaria
Chloroclystis v-ata lucinda
Hypsopygia regina
Eilema japonica japonica
Miltochrista miniata
Scopula epiorrhoe
Plesiomorpha flaviceps
Synegia hadassa hadassa
Paragona cleorides
Litter
a
ab
abc
abcd
abcde
abcdef
bcdef
cdef
def
ef
f
-36
-34
-32
-30
-28
-26
-24
-22
-20
δ13C (‰)

Fig. 7


8
6
4
2
0
-2
-4
-6
-8
-36
-34
-32
-30
-28
-26
-24
-22
-20
δ15N (‰)
δ13C (‰)
Lithosiini
Herbivorous insects
Predatory insects
Lichen-feeding termite
Soil-feeding termites
Litter