The role of fungal taxa and developmental stage of mushrooms in determining the composition of the mycophagous insect community in a Japanese forest

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Abstract. We hypothesize that differences in fungal taxonomic groups may exert a direct influence on the composition of mycophagous insect communities, and that the relative importance of taxonomy compared to other fungal traits may change as the mushrooms decay. We conducted a 3-year field survey and analyzed the species composition of mycophagous insect communities using partial canonical correspondence analysis (partial CCA). We collected 2457 mushrooms belonging to 27 genera, and 4616 insects belonging to 16 families emerged from 439 of the mushrooms. For the whole insect community, fungal genera explained 10–19% of the total variance in the family composition of the insect communities of mushrooms at different developmental stages. Only the fungal genus Collybia significantly affected the community composition almost irrespective of developmental stage. In the drosophilid community, which consisted of 844 individuals from 9 species, fungal genera explained 19–34% of the total variance. Some fungal genera, such as Amanita and Collybia, affected the drosophilid community, but not at all developmental stages. The number of fungal genera that significantly affected the insect community composition did not differ among fungal stages both in the whole insect community and in the drosophilid community. Thus, our former hypothesis was supported by the present analysis, whereas the latter was not. However, the percentages of variance explained by fungal genera were rather small. This suggests that the importance of fungal genera is likely to be less significant than that of other selection pressures in determining the species composition of mycophagous insect communities.

INTRODUCTION

Mycophagous insects are generally recognized as polyphagous insects (Hackman & Meinander, 1979; Hanski, 1989), and Hanski (1989) proposed two compatible hypotheses to explain why polyphagy is widely observed in mycophagous insect communities. The quantity hypothesis proposes that polyphagy is due to the low predictability of occurrence of fungal fruiting bodies (Jaenike, 1978), and the quality hypothesis proposes that differences in chemical traits between host species are not a major barrier to wider host use.

Species composition of mycophagous insect communities differ depending on the traits of the fruiting bodies they use; the tough and long-lived fruiting bodies of Aphyllophorales (bracket fungi) versus the fragile and ephemeral ones of Agaricales (mushrooms). Many studies have revealed that insects feeding on bracket fungi are generally mono- or oligophagous beetles (Ashe, 1984; Lawrence, 1989; Komonen, 2001), whereas those feeding on mushrooms are generally polyphagous flies (Hackman & Meinander, 1979; Hanski, 1989). Fruiting bodies of Aphyllophorales are likely to be more predictable than those of Agaricales, and this trait may facilitate monophagy on bracket fungi and polyphagy on mushrooms (Courtney et al., 1990; Jonsell & Nordlander, 2004).

Jonsell & Nordlander (2004) surveyed the mycophagous beetles feeding on bracket fungi and proposed that polyphagous insects use decaying fruiting bodies to avoid the fungal chemical defenses (Kukor & Martin, 1987). Agaric fruiting bodies (mushrooms) contain insecticidal compounds that affect non-mycophagous insects (Jaenike et al., 1983) and the toxicity differs among fungal species (Mier et al., 1996). It is proposed that these fungal insecticides do not affect mycophagous insects that are adapted to them (Jaenike et al., 1983; Hanski, 1989), but these studies did not take into account the state of decay of the mushrooms.

The odour of Coriolus versicolor (Aphyllophorales) change with the age of its fruiting bodies and two species of mycophagous beetles time their attack according to the odour of the fungi (Guevara et al., 2000). The odor of Fomitopsis pinicola (Aphyllophorales) and Fomes fomentarius (Aphyllophorales) also changes with the age of their fruiting bodies and their odour attracts some mycophagous beetles (Fäldt et al., 1999). Although the responses of mycophagous insects to the odor of agaric mushrooms have scarcely been studied, we observed that the amount of sap produced by Lactarius mushrooms, which contain an antifeedant to non-mycophagous beetles (Daniewski et al., 1993), declined as after the mushrooms decayed. This suggests that chemical components other than the odor of agaric fungi may also change with age.

Although differences in chemical compounds might play an important role in determining insect community structure, it is difficult to follow the qualitative and quantitative changes in the chemical compounds in mush-
rooms in relation to the community structure of myco-
phagous insects. Thus, in this study the effect of fungal
taxonomic group, which may indicate a difference in
chemical compounds, on the composition of myco-
phagous insect communities was evaluated. We hypothe-
sized that a difference in fungal taxonomic groups may
exert a direct influence on the composition of myco-
phagous insect communities, and that the relative impor-
tance of fungal taxonomic group compared to other
fungal traits may change as the mushrooms decay. We
conducted a 3-year field survey and analyzed the emer-
gence patterns of insects from mushrooms of different
genera and developmental stages.

MATERIAL AND METHODS

Study site
Samples were collected in a mixed stand dominated by Japa-
nese red pine (Pinus densiflora Sieb. et Zucc.), with a few Cha-
maecyparis obtusa (Sieb. et Zucc.) Endl. and Lindera triloba
(Sieb. et Zucc.) Blume. The study site is situated within the
Experimental Forest of Nagoya University, at Inabu in central
Japan (35°11′N, 137°33′E; ca. 1000 m a.s.l.). Three 10 × 10 m
plots were established at the study site, separated by 2–40 m.
Two of the three plots were close to one another, but supported
different types of vegetation: one was dominated only by Japa-
nese red pine, and the other by a mixture of Larix kaempferi,
Betula ermanii and other broad-leaved trees (Yamashita & Hiji,
2006). Each plot was divided into 100 quadrats, each 1 m
square.

Collection of mushrooms and emerging insects
Mushrooms were collected from 1 July 1999 to 24 July 2002
at about 2-week (between 12 and 17 days) intervals, except
during the winter season (January to April). Heavy rain pre-
vented one survey on 14 September 2000. The genera and
developmental stages of all the fruiting bodies of Agaricales
(mushrooms) that were present in the plots on each sampling
occasion were recorded. Identification to species of small mush-
rrooms, such as those of the genera Marasmius and Mycena,
which contain a large number of unknown species, as well as of
decayed mushroom’s is very difficult. Thus, only some of the
mushrooms (that appeared mainly in 1999) were identified to
the species level, all others were identified to genus (Yamashita
Four developmental stages were distinguished: immature, soon
after appearance (stage 1); fresh, with pileus slightly expanded
(stage 2); intermediate, with pileus fully expanded (stage 3); and
entirely decayed or dried out (stage 4). Up to five individuals
belonging to the same genus at each developmental stage were
collected from each quadrat. Large numbers of mushrooms
appeared on 27 September 2000 and 28 September 2001, and as
many mushrooms as possible were collected on these dates.

Each sample was placed on a piece of damp filter paper in a
polyethylene container or paper bag in the field and brought to
the laboratory. Each mushroom was weighed on a microbalance
and then placed on a piece of filter paper on moistened sand in a
polyethylene container with a lid (80-, 200-, 550-, and 4000 ml
volume, according to the size of the mushroom). The containers
were kept in the laboratory under natural light conditions at
25°C and misted when necessary to prevent drying. For 3
months each container was inspected every 3 or 4 days to check
for the emergence of adult insects. All insects were identified to
family level and counted. For drosophilids, all the individuals
were identified to species because they dominated the insect
community and their taxonomy and ecological role is well
known.

Statistical analysis
To reveal the effects of fungal genera on the community com-
position of mycophagous insects, we used canonical ordination
(Jongman et al., 1995). Detrended correspondence analysis
(DCA) was used to check the length of ordination axes
(Jongman et al., 1995): if the length was smaller than 2 s.d.,
redundancy analysis was chosen, because the response curve
could be monotonic: if the length was larger than 4 s.d.,
canonical correspondence analysis (CCA) was chosen, because
the response curve could be unimodal: and if the length falls
between 2 and 4, a unimodal model was chosen. After the DCA,
we found that the lengths of the ordination axes for all the data-
sets except one were larger than 2, and thus CCA was chosen.
These analyses were performed using Canoco 4.5 software (ter
Braak & Šmilauer, 2002), in which the relationships between a
set of environmental variables (fungal genera) and an ordination
score were plotted on ordination diagrams. In the diagrams, cen-
troids for nominal variables depict the direction and magnitude
of the relationships among explanatory variables and insect
communities.

Because we aimed to reveal the effect of fungal quality, indi-
cated by fungal genera, and developmental stage, on the species
composition of mycophagous insect communities, it was impor-
tant to exclude as many other factors as possible and therefore a
partial CCA (a CCA with covariates: ter Braak & Šmilauer,
2002) was performed. The size of mushrooms varies among
fungal genera (Yamashita & Hiji, 2003) and therefore could
affect the composition of the mycophagous insect community
(Worthen et al., 1996, 1998; Yamashita & Hiji, 2003). Thus,
the fresh weight of mushrooms was included in the analysis as a
covariate. Month and year of mushroom collection were treated
covariates.

The total inertia, which is the total variance in the species
data, was divided into three components: environmental data,
covariates, and unexplained factors, and used to describe the
extent to which the variance in the mycophagous insect commu-
nity can be affected by these components (ter Braak & Šmilauer,
2002). If A denotes the total inertia and D denotes the
sum of all eigenvalues, the covariates explain [(A−B)/A]*100%
of the inertia. If C denotes the sum of all canonical eigenvalues,
our environmental variables explain (C/A)*100%, and the
remainder is the unexplained fraction.

Each mushroom’s genus was used as the environmental vari-
able, and the month and year of collection and weight of mushroom
rooms were treated as covariates. The genus of mushroom,
month, and year were treated as dummy variables. The data for
mushroom fresh weight was log10-transformed before analysis.

An analysis based on the number of emergents has many
advantages but the number of individuals reared does not
always represent an independent sample, because female insects
tend to lay eggs in clutches. Therefore, both the datasets based
on the number of emergents and on the presence or absence of
insects were analyzed and the results were compared. The
number of individual insects was log-transformed (log10 (No. of
individuals + 1)) before analysis. Families or species of insects
that emerged from fewer than 5 mushrooms were not included in
the analysis of the presence/absence data, which focused on
the dominant insects. For both the analyses, mushroom genera
with fewer than 10 samples were pooled and treated as a refer-
cence group. Parasitoids and predatory insects were excluded.

The explanatory variables were tested by the automatic forward
selection procedure in Canoco 4.5 (9999 randomizations).
Biplots were focused on inter-species distances.
RESULTS

Composition of mycophagous insect communities

During the survey period, 2457 mushrooms belonging to 27 genera were collected (Table 1). The fresh weight of the mushrooms ranged from 0.0002 g to 104 g. For each of the genera *Amanita*, *Collybia*, *Lactarius*, *Marasmius*, *Mycena* and *Rhodophyllus*, more than 10 individuals at each developmental stage were collected. A total of 4616 insects belonging to 16 families emerged from 439 mushrooms (Table 2). *Nitidulidae*, *Cecidomyiidae*, *Drosophilidae*, *Mycetophilidae*, *Phoridae* and *Psychodidae* were dominant in terms of numbers of individuals (more than 100 individuals). They were frequently observed throughout the survey period, with members of each family emerging from more than 50 mushrooms. Only *Hymenoptera* were identified as parasitoids and no predatory insects were reared. A total of 844 drosophilid insects belonging to 9 species emerged from 85 mushrooms (Table 3). *Drosophila bizonata* Kikkawa & Peng, *D. orientacea* Grimoldi, *James & Jaenike*, *D. unispina* Okada, *Hirtodrosophila albovialis* Momma & Takada and *H. sexvittata* Okada each emerged from more than 10 mushrooms.

HOST USE BY MYCOPHAGOUS INSECTS IN RELATION TO MUSHROOM TRAITS

Whole insect community

Using the abundance (the number of individuals that emerged) data, a partial CCA for the whole survey period was performed. Total inertia at stage 1, 2, 3 and 4 was 5.66, 7.84, 6.45 and 5.85, respectively. Fungal genera and covariables explained 28%–55% of the inertia. Fungal genera explained 14% at stage 1, 15% at stage 2, 13% at stage 3 and 10% at stage 4. On the other hand, a partial CCA based on the presence/absence data showed that total inertia at stage 1, 2, 3 and 4 was 2.00, 4.70, 3.45 and 4.59, respectively. Fungal genera and covariables explained 32%–78% of the inertia. Fungal genera explained 12% at stage 1, 17% at stage 2, 19% at stage 3 and 10% at stage 4. Automatic forward selection revealed that, at stage 1, *Marasmiellus* and *Collybia* significantly affected the

| TABLE 1. Number of mushrooms collected and their average fresh weight plus standard deviation for each fungal genus at each developmental stage. |
|---------------------------------|----------------|----------------|----------------|----------------|
|                                | Stage 1        | Stage 2        | Stage 3        | Stage 4        |
| Agaricaceae                    | Lepiota        | 4 (0.0 ± 0.0)  | 6 (0.0 ± 0.0)  | 15 (0.0 ± 0.0) | 1 (0.0)        |
| Amanitaceae                    | *Amanita*      | 13 (7.3 ± 8.4) | 16 (15.5 ± 21.6)| 17 (5.5 ± 6.8) | 12 (10.9 ± 12.6)|
| Boletaceae                     | *Leccinum*     | –              | 1 (15.1)       | 1 (13.9)       | 2 (35.5 ± 27.5) |
|                                | *Saillus*      | 3 (5.9 ± 6.7)  | 7 (19.3 ± 16.8)| 3 (10.1 ± 10.7)| 2 (1.4 ± 1.1)   |
|                                | *Tylopilus*    | 1 (30.8)       | 1 (103.7)      | –              | –              |
| Coprinaceae                    | *Psathyrella*  | 1 (2.1)        | 1 (1.6)        | –              | –              |
| Cortinariaceae                 | *Cortinarius*  | 4 (1.0 ± 0.2)  | 19 (2.0 ± 1.9) | 3 (2.7 ± 2.1)  | 4 (0.9 ± 0.6)  |
|                                | *Dermocybe*    | –              | 3 (1.9 ± 0.3)  | 2 (3.3 ± 0.5)  | –              |
|                                | *Inocybe*      | 8 (2.6 ± 2.5)  | 28 (1.0 ± 1.7) | 24 (1.9 ± 3.3) | 13 (2.0 ± 3.0) |
| Gomphidiaceae                  | *Gomphidius*   | –              | 3 (3.4 ± 1.5)  | –              | 1 (8.4)        |
| Hygrophoraceae                 | *Camaeophyllum*| –              | 2 (0.6 ± 0.6)  | –              | –              |
|                                | *Hygrocybe*    | 11 (0.1 ± 0.0) | 6 (0.2 ± 0.1)  | 3 (0.6 ± 0.5)  | 1 (0.2)        |
| Paxillaceae                    | *Paxillus*     | –              | 3 (3.4 ± 2.2)  | 2 (3.9 ± 0.4)  | –              |
| Phuteaceae                     | *Pluteus*      | –              | 1 (1.5)        | –              | –              |
| Rhodophyllaceae                | *Rhodophyllus* | 27 (1.1 ± 1.0) | 113 (2.8 ± 2.6)| 48 (3.4 ± 3.3) | 30 (3.0 ± 3.0) |
| Russulaceae                    | *Lactarius*    | 43 (1.1 ± 0.8) | 99 (3.1 ± 2.2) | 56 (4.7 ± 3.4) | 25 (3.0 ± 2.4) |
|                                | *Russula*      | 3 (7.6 ± 4.7)  | 9 (9.6 ± 5.4)  | 5 (4.7 ± 4.4)  | 10 (3.4 ± 2.1) |
| Strophariaceae                 | *Kuehneromyces*| –              | 3 (0.4 ± 0.1)  | 3 (0.3 ± 0.2)  | –              |
|                                | *Naematoloma*  | –              | –              | 1 (3.0)        | –              |
| Tricholomataceae               | *Clitocybe*    | –              | 3 (0.8 ± 0.4)  | 2 (0.5 ± 0.1)  | 1 (0.4)        |
|                                | *Collybia*     | 45 (0.1 ± 0.1) | 37 (0.4 ± 0.3) | 35 (0.5 ± 0.6) | 50 (0.3 ± 0.4) |
|                                | *Laccaria*     | 5 (1.1 ± 0.4)  | 4 (2.2 ± 2.3)  | 2 (0.9 ± 0.7)  | 1 (3.3)        |
|                                | *Marasmiellus* | 13 (0.0 ± 0.0) | 17 (0.0 ± 0.0) | 13 (0.0 ± 0.0) | 7 (0.0 ± 0.0)  |
|                                | *Marasmius*    | 74 (0.1 ± 0.1) | 206 (0.2 ± 0.1) | 158 (0.2 ± 0.2) | 85 (0.2 ± 0.2) |
|                                | *Mycena*       | 132 (0.0 ± 0.0)| 420 (0.1 ± 0.2) | 213 (0.1 ± 0.2) | 130 (0.1 ± 0.1) |
|                                | *Oudemansiella*| –              | –              | –              | 1 (1.8)        |
|                                | *Tricholomopsis*| –             | 2 (0.3 ± 0.0)  | –              | –              |
| Unidentified                   | –              | –              | –              | –              | –              |

Stage 1 – immature, soon after appearance; stage 2 – fresh, with pileus expanded; stage 3 – intermediate, with pileus fully expanded; stage 4 – entirely decayed or dried out.
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**TABLE 2.** Insects that emerged from agaric mushrooms at developmental stages 1, 2, 3 and 4.

Stage 1: immature, soon after appearance; Stage 2: fresh, with pileus expanded; Stage 3: intermediate, with pileus fully expanded; Stage 4: entirely decayed or dried out.
Table 3: Drosophilids that emerged from agaric mushrooms at developmental stages 2, 3 and 4.

<table>
<thead>
<tr>
<th>Genera</th>
<th>Dang</th>
<th>Dbiz</th>
<th>Dori</th>
<th>Duni</th>
<th>Dsp1</th>
<th>Dsp2</th>
<th>Halb</th>
<th>Hmac</th>
<th>Hsex</th>
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</table>

Dang – Drosophila anguralis; Dbiz – D. bizonata; Dori – D. orientacea; Duni – D. unispina; Dsp1 – Drosophila sp. 1; Dsp2 – Drosophila sp. 2; Halb – Hirtodrosophila alboralis; Hmac – H. macromaculata; Hsex – H. sexvittata; Unid – Unidentified individuals

Stage 1 – immature, soon after appearance; Stage 2 – fresh, with pileus expanded; Stage 3 – intermediate, with pileus fully expanded; Stage 4 – entirely decayed or dried out. No drosophilids emerged from mushrooms at Stage 1.

The composition of the insect community using either the abundance data or the presence/absence data. At stage 2, Amanita, Collybia, Cortinarius and Lactarius significantly affected the composition of the insect community based on the abundance data, and Amanita, Collybia, Lactarius and Marasmiellus based on the presence/absence data. At stage 3, Collybia, Lactarius and Marasmius, and at stage 4, only Collybia significantly affected the composition of the insect community using either datasets. At stage 3 based on presence/absence data, Marasmiellus also significantly affected community composition.

There were no significant differences in the number of genera of fungi that significantly affected the insect community composition at the different developmental stages (G test for contingency table: \( G = 3.42, p = 0.331 \) for the abundance data, \( G = 4.407, p = 0.221 \) for the presence/absence data).

Partial CCA based on the abundance data revealed that only the fungal genus Marasmiellus, which is attacked by Nitidulidae, significantly affected the composition of the insect community at stage 1 (Figures are not shown). At stage 2, Cecidomyiidae and Psychodidae were associated with Amanita, Heleomyzidae with Lactarius and Cecidomyiidae with Marasmiellus. At stage 3, Nitidulidae were associated with Collybia, Mycetophilidae with Lactarius and Cecidomyiidae with Marasmiellus and Marasmius. At stage 4, only Collybia affected the composition of the insect community. Thus, relationships between Collybia and Nitidulidae at stage 2, between Lactarius and Heleomyzidae at stage 2, between Collybia and Nitidulidae at stage 3 and between Collybia and Nitidulidae, Chlorophoridae, and Heleomyzidae at stage 4 were observed both in the datasets based on abundance and on presence or absence.

Drosophilid community

Based on the abundance data, fungal genera and covariables explained more than 50% of the inertia both at stage 3 and at stage 4. Fungal genera explained 34% of the variance at stage 3 and 19% at stage 4. On the other hand, fungal genera and covariables explained about 65% of the inertia for the dataset based on presence or absence of insects. Fungal genera explained 27% of the variance at stage 3 and 25% at stage 4.

At stage 3, forward selection in partial CCA based on the abundance data revealed that 5 fungal genera, Ama-
nita, Collybia, Inocybe, Mycena and Rhodophyllus significantly affected the species composition of the drosophilid community at stage 3 (Fig. 2). Drosophila orientacea was associated with the genus Amanita, H. alboralis with Collybia, D. bizonata with Inocybe and D. unispina with Mycena and Rhodophyllus. At stage 4, however, only Collybia significantly affected the species composition of the drosophilid community (Fig. 2). Hir-todrosophila alboralis was associated with the genus Collybia.

Based on the presence/absence data, only Amanita significantly affected the species composition at stage 3, and Collybia, Lactarius, Marasmius and Mycena at stage 4. At stage 4, H. alboralis was associated with the genera Collybia and Mycena, and D. orientacea with Lactarius (Figures not shown). Thus, the relationship between H. alboralis and Collybia at stage 4 was observed both in the datasets based on abundance and on presence/absence of drosophilids.

There were no significant differences in the number of the fungal genera that significantly affected the species composition of the drosophilid community at the different fungal developmental stages ($G$ – test for contingency...
DISCUSSION

Our hypothesis that a difference in the fungi may exert a direct influence on the composition of mycophagous insect communities was supported, but the other hypothesis that the relative importance of fungal genera compared to other fungal traits may change as the mushrooms decay was not supported by our analyses. In the whole insect community, however, the percentage of variance explained by the environmental variable were rather small (10–19%). Thus, although there is no clear evidence, it seems that differences in fungal genera do not greatly influence the composition of the whole insect community. Although they attack decaying mushrooms, members of the drosophilid community appear to be relatively sensitive to difference in the chemical traits of fungal genera, which has an effect on the species composition of the community.

In the drosophilid community, there was no overall effect of fungal genera, but some fungal genera significantly affected the species composition (Fig. 2). Drosophilid larvae feed on yeast or bacteria on substrates on which their parent lay eggs, and some drosophilids show a preference for specific yeasts or bacteria (Kearney & Shorrocks, 1981; Oakeshott et al., 1989). The growth of some microbes is inhibited by sesquiterpenes produced by certain species of Agaricales (Lactarius velleucus: Sterner et al., 1985). Thus, it is likely that microbial floras differ among fungal genera, and drosophilid species may choose their hosts accordingly.

Bruns (1984) divided mycophagous insects into two groups: primary fungivores and secondary fungivores. Primary fungivores, such as Mycetophilidae and Phoridae, feed on fungal tissues and secondary fungivores, such as Drosophilidae and Psychodidae feed on the microbes living on mushrooms. In the partial CCA diagram, Mycetophilidae and Phoridae tended to be closely associated, as were the Drosophilidae and Psychodidae (Fig. 1). This suggests that there is some relationship between preference for particular developmental stages of fungi and that for particular fungal genera, although many insect families and drosophilid species in these plots occurs close to the origins, suggesting that they were likely to be polyphagous. Amanita mushrooms remain fresh for a shorter period than those of Lactarius (Yamashita & Hijii, 2004), which suggests that Amanita mushrooms decay more quickly than those of Lactarius. Thus, differences in the perishability of mushrooms belonging to different fungal genera may affect the composition of the insect community exploiting mushrooms at a particular stage.

Mycophagous insects are adapted to the toxins present in fungal fruiting bodies (Hanski, 1989), at least those of their hosts. In the whole insect community, Nitidulidae, with only one species (Neopalpodes inermis Reitter), occurs close to Collybia in the partial CCA ordination diagram (Fig. 1). Some species of Collybia produce cyanide, which is toxic to non-mycophagous insects, such as Drosophila melanogaster Meigen (Drosophilidae) and Spodoptera littoralis Boisdouval (Noctuidae; Mier et al., 1996). Jaenike et al. (1983) tested the insecticidal properties of α-amanitin and showed that it is not harmful to mycophagous drosophilids, but is a highly effective defense against non-mycophagous drosophilids.

The correspondence between the longevity of fungal hosts and the larval period of insects may also explain the pattern of host selection by mycophagous insects. Diptera have a short larval period and dominate in the short lived agaric fungi (Kimura, 1976; Hackman & Meinander, 1979; Lacy, 1984; Yamashita & Hijii, 2003), and Coleoptera a long larval period and dominate long lived polyphores (Aphyllophorales; Pielou & Verma, 1968; Hågvar, 1999, Jonsell et al., 2001). In mycophagous drosophilids, the longevity of their fungal host’s fruiting body is similar to that of their larval period (Toda & Kimura, 1997). In
our previous study, we showed that nitidulid beetles, which have a long larval period, attack mushrooms of Collybia soon after they appeared (Yamashita & Hijii, in press), when they may be toxic; thus, nitidulid beetles appear to select mushrooms that will last for a long time. These findings suggest that in mycophagous insects, selection pressure may be greater to use fruiting bodies with a suitable longevity rather than those that contain little or no defensive chemicals.

Our study showed that fungal genera, which may represent chemical compounds, only slightly affected the species composition of a mycophagous insect community, even during the early stages of development of the fungi. This finding suggests that for mycophagous insect communities, the chemical compounds produced by fungi are less likely to be important than other selection pressures. Thus, the quality hypothesis (Hanski, 1989) is the most likely explanation of the polyphagy in our system.

Our study did not evaluate the effect of low predictability of mushroom occurrence. Courtney et al. (1990) proposed that mushrooms produced by mycorrhizal fungi are more predictable resources for insects than those produced by saprophytic fungi, because mycorrhizal fungi have specific associations with particular tree species. In the study plots, however, the distribution of fruiting bodies of saprophytic fungi tended to be aggregated and changed very slowly (Yamashita & Hijii, 2006). In addition, the insect communities did not show a clear association with either of these two fungal groups (Fig. 1). Thus, this study indicates that there is little difference in the predictability of the spatial distribution of mycorrhizal (Amatina, Cortinarius, Inocybe, Lactarius and Russula) and saprophytic fungi (Collybia, Marasmiellus, Marasmius, Mycena and Rhodophyllus). The low predictability of the occurrence of agaric mushrooms is likely to select for polyphagy in mycophagous insects, but its relative importance compared to other factors must be evaluated by further studies of the factors determining the structure of mycophagous insect communities on mushrooms.

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REFERENCES


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