

# Coexistence mechanisms of mycophagous drosophilids on multispecies fungal hosts: aggregation and resource partitioning

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## Summary

1. In nature, various mechanisms that provide some refuges for inferior species to escape from competition act together to promote the species coexistence in a local community. We propose a method to evaluate simultaneously the relative importance of different mechanisms for the species coexistence, focusing on a mycophagous drosophilid community depending on a multispecies fungal host system, where two mechanisms – aggregation over patches of single fungal species and resource partitioning at the fungal species level – can act together. The data are based on the numbers of adult insects emerging from naturally occurring fungi collected from a temperate forest in northern Japan.

2. We confirm the finding of Sevenster & van Alphen (1996) that large patches are low-density refuges despite the large absolute numbers of competitors on them, and therefore adopt new measures for intra- and interspecific aggregations and the species-persistence criterion, which were developed by Sevenster (1996) to take account of variable patch sizes in calculating the aggregation measures.

3. The calculated measures are compared among three analyses for fungal resources: AR-analysis (the original data-set from multispecies fungal patches) in which both aggregation and resource partitioning can act together; R-analysis (combining the data for all patches of each fungal species) in which only resource partitioning at the fungal species level can act; and A-analysis (calculating the measures independently for each fungal species) in which only aggregation process can act as a coexistence mechanism.

4. Intraspecific aggregation over multispecies fungal patches is strengthened by both aggregation and resource partitioning processes.

5. We reconfirm the finding of Sevenster & van Alphen (1996) that interspecific associations are consistent over years, and support their claim that such consistent associations should be taken as real aspects of the community structure.

6. Measures for the persistence criterion ( $T$ ), the ‘relative effect of competitor aggregation’, are less than unity, satisfying the necessary and sufficient condition for the species persistence, in most drosophilid species concerned; these tend to be smaller in AR-analysis than in R- or A-analysis, suggesting facilitation of the species coexistence by both aggregation and resource partitioning in the mycophagous drosophilid community studied.

7. Differences in  $T$ -value between AR- and R-analyses and between AR- and A-analyses may indicate relative contributions of aggregation and resource partitioning, respectively, to the species coexistence. We propose a method to compare various communities in a multi-dimensional space with regard to the relative importance of different coexistence mechanisms.

*Key-words:* association, community, competition, northern Japan, patch size.

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## Introduction

Small, discrete, and ephemeral resources, such as dung, carrion, fruits or fungi, often support large numbers of species (Elton 1966; Heed 1968; Kimura *et al.* 1977; Shorrocks 1982). Atkinson & Shorrocks (1981) and Shorrocks & Rosewell (1986) proposed a model whereby competitors coexist on such resources without resource partitioning: if the competitively superior species is aggregated over resource patches, independently of the inferior species, it by chance leaves refuges in low-density patches where the inferior species is safe from competition (Shorrocks 1990). Ives & May (1985) and Ives (1988a, 1988b, 1991) developed an analytical version of the aggregation model. Hanski (1981) and de Jong (1982) each independently developed equivalent models describing how spatial aggregation facilitates coexistence of ecologically similar forms in patchy environments. Increasing evidence supports this 'aggregation model' (Atkinson & Shorrocks 1984; Kneidel 1985; Hanski 1987; Rosewell, Shorrocks & Edwards 1990; Shorrocks, Rosewell & Edwards 1990; Ives 1991; Jaenike & James 1991; Shorrocks 1991; Sevenster & van Alphen 1996). Most studies that brought such evidence focused on a single type or species of food resource to exclude another factor, resource partitioning, from the analyses or experiments. As Shorrocks (1990, 1996) mentioned, however, in nature any mechanisms that provide refuges for inferior competitors act together to make the coexistence easier; there are many possible mechanisms that may help to explain the local coexistence (diversity) of species. Shorrocks (1996) called it 'a problem with too many solutions'. It remains to be investigated in natural communities to what extents different mechanisms promote the coexistence separately and in combination (Sevenster & van Alphen 1996).

Mycophagous drosophilids seem to be prime candidates to study multiple mechanisms, especially aggregation and resource partitioning, that act together to promote the species coexistence in a community. Rosewell *et al.* (1990) documented on the basis of data of adult emergence from naturally occurring fungi that the distribution of each drosophilid species over patches of single fungal species was significantly aggregated in 58 out of 62 cases examined. Jaenike & James (1991) also obtained similar results in field experiments using fruiting bodies of *Agaricus bisporus* Lange as breeding sites. On the other hand, it is known that members of a mycophagous drosophilid community as a whole breed on a wide range of fungal species, with various degrees of resource partitioning among them (Lacy 1984; Kimura & Toda 1989; Courtney, Kibota & Singleton 1990; Toda & Kimura 1997). These two processes, aggregation and resource partitioning, which enhance the coexistence of community members, have never been investigated at the same time covering the whole range of host fungi.

Although Shorrocks & Sevenster (1995) and Shorrocks (1996) attempted to evaluate the relative importance of aggregation and resource partitioning by comparable measures of intra- and interspecific aggregations, respectively, there has been no appropriate method in the aggregation model to analyse data taken from a wide range of resources variable in patch size. Recently, Sevenster (1996) improved this point, substituting the density for the number in measures of intra- and interspecific aggregations to take account of variable patches.

In this study, the new measures and criterion developed by Sevenster (1996) are adopted to compare aggregations, associations, and conditions for coexistence of mycophagous drosophilids among the following three systems of fungal resources: (i) single-type (corresponding here to fungal species) system with discrete patches; (ii) multi-type system without discrete patches in each type; and (iii) multi-type system with discrete patches in each type. Each system is based on different assumptions: in the first system only the aggregation can act as a mechanism for coexistence; in the second only the resource partitioning at the fungal species level can do so; and in the third both mechanisms can act together.

The data were based on the numbers of drosophilid and non-drosophilid adults emerging from naturally occurring fungi. Two data-sets were taken in successive years 1995 and 1996, to compare interspecific associations over resource patches between the two years.

## Methods

### SAMPLING OF FUNGI AND EMERGENT INSECTS

Collection of fungi was carried out during a limited period within a rather small, isolated area, the Botanic Garden of Hokkaido University, to avoid overestimates of aggregation due to temporal and spatial variations in population density and/or host utilization (cf. Sevenster & van Alphen 1996). The Botanic Garden covers 13.5 ha and contains some natural groves but is located in the centre of Sapporo City, surrounded by the urban area and therefore isolated, if not completely, from other mycophagous drosophilid habitats. Fungal samples were collected twice a week during June, when most mycophagous drosophilid species are synchronously in their first breeding season because the generation has overwintered as adults (Kimura *et al.* 1978; Watabe *et al.* 1985; Toda *et al.* 1986; Kimura & Toda 1989).

All fruiting bodies were collected from each fungal patch. A separate patch was defined as the fruiting body or bodies within a small area that might be reached by larvae during their development. Considering the temporal variation of host use in the process of decay among different drosophilid species

(Kimura 1976, 1980; Kimura & Toda 1989), we sampled fungi at an appropriate stage when larvae of all the consumer species were likely to be present. Each sample was weighed and placed on damp sand (in 1995) or vermiculite (in 1996) and leaf litter in a 1-litre plastic container with a cotton-plugged ventilation hole in the lid. The sand and leaf litter were sterilized by drying at 105°C for 24 h before use. The containers were kept in an outdoor insectary and emerging adult insects were collected every 1 or 2 days for almost 5 months until early November. All drosophilids were identified to species, but other insects to family.

## ANALYSIS

### Measures for aggregation model

The following three measures for intraspecific aggregation, interspecific aggregation (association), and coexistence criterion, which were improved by Sevenster (1996) to incorporate the density, not the number, of potential competitors on each patch into the 'aggregation model', were calculated only for drosophilids.

Intraspecific aggregation was quantified by  $J$ , the increase in the average density of competitors encountered relative to a random distribution:

$$J = (\sum e_i / N^2) \cdot \{ \sum n_i (n_i - 1) / e_i \} - 1 \quad \text{eqn 1}$$

where  $n_i$  is the number of adult individuals having emerged from patch  $i$ ,  $e_i$  is the size of patch  $i$ , quantified by the wet weight (in g) of fungal sample, and  $N$  is the total number of individuals.  $J = 0$  indicates a random distribution,  $J > 0$  an aggregated distribution, and  $J < 0$  the tendency of a uniform distribution.

Association between species was quantified by  $C$  as a measure of interspecific aggregation, i.e. the increase in the average density of heterospecific competitors encountered relative to a random distribution:

$$C_{xy} = (\sum e_{ij} N_x N_y) (\sum n_{xij} n_{yij} / e_i) - 1 \quad \text{eqn 2}$$

where subscripts  $x$  and  $y$  indicate species.  $C_{xy} < 0$  indicates that the two species encounter each other, on average, less frequently than at random, and  $C_{xy} > 0$  indicates more frequent encounters than at random.

Sevenster (1996) proposed  $T_{xy}$ , the 'relative effect of competitor aggregation', as a new criterion for the persistence of species  $x$ :

$$T_{xy} = (1 + C_{xy}) / (1 + J_x) \quad \text{eqn 3}$$

$T_{xy} < 1$  is a necessary and sufficient condition for the persistence of species  $x$  in the presence of species  $y$ . However, species do not compete in pairs. We therefore calculated the relative effect of aggregation of all potential competitors,  $T_{x-x}$ , on the persistence of each species, combining the data of all other drosophilids ( $T_{\text{dro}}$ ) or of all other dipterans ( $T_{\text{all}}$ ).

## Data analysis

First, the above three measures were calculated for each of the original data-sets in 1995 and 1996, which consisted of the data of emergent insects from multiple patches of multiple fungal species. In such a situation the intra- and interspecific aggregation measures,  $J$  and  $C$ , are very likely to be affected by two factors, aggregation over patches of single fungal species and resource partitioning among multiple fungal species. Usually, the combined effects of both mechanisms are expected to reduce the  $T$ -value, i.e. to promote the coexistence of the species. This analysis is henceforth called 'AR-analysis', since aggregation and resource partitioning can contribute together.

Next, to evaluate the relative importance of the two mechanisms for coexistence, the analyses were made based on the following two assumptions. In the first analysis we summed up the data for all patches of each fungal species to exclude the effect of aggregation, assuming that each fungal species produces only a single, very large fruiting body or 'superpatch'. This analysis is called 'R-analysis', since only resource partitioning can contribute to the aggregation measures. The second analysis was made independently for each fungal species. Since the effect of resource partitioning at the fungal species level is excluded and only aggregation over patches of single fungal species can contribute to the aggregation measures, this is called 'A-analysis'.

In all the three analyses only drosophilid species with  $N \geq 10$  were subjected to the analyses. In AR- and R-analyses, fungal samples (patches) that produced no drosophilids were excluded from the analyses, and in A-analysis only fungal species with seven or more samples were subjected to the analysis. In consequence, the values of  $J$ ,  $C$ , and  $T$  were compared between AR- and R-analyses and between AR- and A-analyses only for the species or species pairs of which the corresponding values were calculated in all the three analyses. For example, a total of 43 individuals of *Drosophila makinoi* Okada emerged in 1996, but from *Oudemansiella brunneomarginata* L. Vasilieva and *Flammulina velutipes* (Fr.) Sing. of which samples were six and two, respectively. Therefore, *D. makinoi* was excluded from A-analysis and eventually from the comparisons.

## Results

In total, 103 fungal patches of 23 species from 9 families and 95 patches of 16 species from 8 families were sampled in 1995 and 1996, respectively. Of these, 97 and 90 fungal samples yielded insects, and the total numbers of reared insects were 18 641 and 31 016, respectively. Diptera comprised 99.3% and 98.6% of these totals, including 17 and 19 families, respectively (Table 1). The Drosophilidae was the top-ranked among them, 9844 individuals (52.8% of the total)

**Table 1.** Insects reared from fungal samples in 1995 and 1996

	1995	1996
<b>DROSOPHILIDAE</b>		
<i>Leucophenga maculata</i> (Dufour)	50	333
<i>Le. quinquemaculipennis</i> Okada	49	28
<i>Mycodrosophila poecilogastra</i> (Loew)	–	3
<i>Hirtodrosophila quadrivittata</i> (Okada)	–	22
<i>H. ussurica</i> (Duda)	113	–
<i>H. trivittata</i> (Strobl)	189	3
<i>H. trilineata</i> (Chung)	156	52
<i>H. sexvittata</i> (Okada)	3669	2164
<i>H. alboralis</i> (Momma & Takada)	676	332
<i>H. histrioides</i> (Okada & Kurokawa)	2543	2155
<i>Drosophila makinoi</i> Okada	16	43
<i>D. orientacea</i> Grimaldi, James & Jaenike	560	3063
<i>D. histrio</i> Meigen	37	–
<i>D. brachynephros</i> Okada	1152	1178
<i>D. curvispina</i> Watabe & Toda	514	113
<i>D. unispina</i> Okada	109	14
<i>D. nigromaculata</i> Kikkawa & Peng	–	137
<i>D. auraria</i> Peng	11	12
<i>Scaptomyza pallida</i> (Zetterstedt)	–	17
<i>Lordiphosa collinella</i> (Okada)	–	1
Total	9844	9670
<b>Other DIPTERA</b>		
Anisopodidae	1244	851
Cecidomyiidae	1	40
Chironomidae	4	–
Chloropidae	7	34
Culicidae	–	1
Dolichopodidae	–	1
Empididae	–	5
Fanniidae	4	4
Heleomyzidae	122	205
Limnobiidae	440	1410
Lonchaeidae	4	447
Muscidae	57	76
Mycetophilidae	1238	1615
Phoridae	3505	7643
Platypezidae	8	21
Psychodidae	1710	197
Scatopsidae	162	7812
Sciaridae	149	362
Sphaeroceridae	20	200
Total	8675	20924
COLEOPTERA	1	57
COLLEMBOLA	–	2
DERMAPTERA	1	–
HYMENOPTERA	120	357
LEPIDOPTERA	–	6
Total	18641	31016

of 15 species and 9670 (31.2%) of 18 species having emerged from 96 fungal samples (23 species, 9 families) and 85 samples (15 species, 8 families) in 1995 and 1996, respectively (Table 1).

#### DENSITY OF DROSOPHILIDS PER FUNGAL PATCH

Sevenster & van Alphen (1996) revealed, based on the data of insects having emerged from fallen fruits of

*Spondias mombin* L. in a tropical forest of the Barro Colorado Island (BCI), that the number and the density of competitors in a patch had opposite correlations with patch size: while large patches seemed to be aggregated when numbers were considered, they in fact tended to be low-density refuges. To confirm whether the same tendency is also present in the fungal system of a temperate forest, we plotted the number and the density of drosophilid emergents per fungal patch against patch size on log-log scales, based on

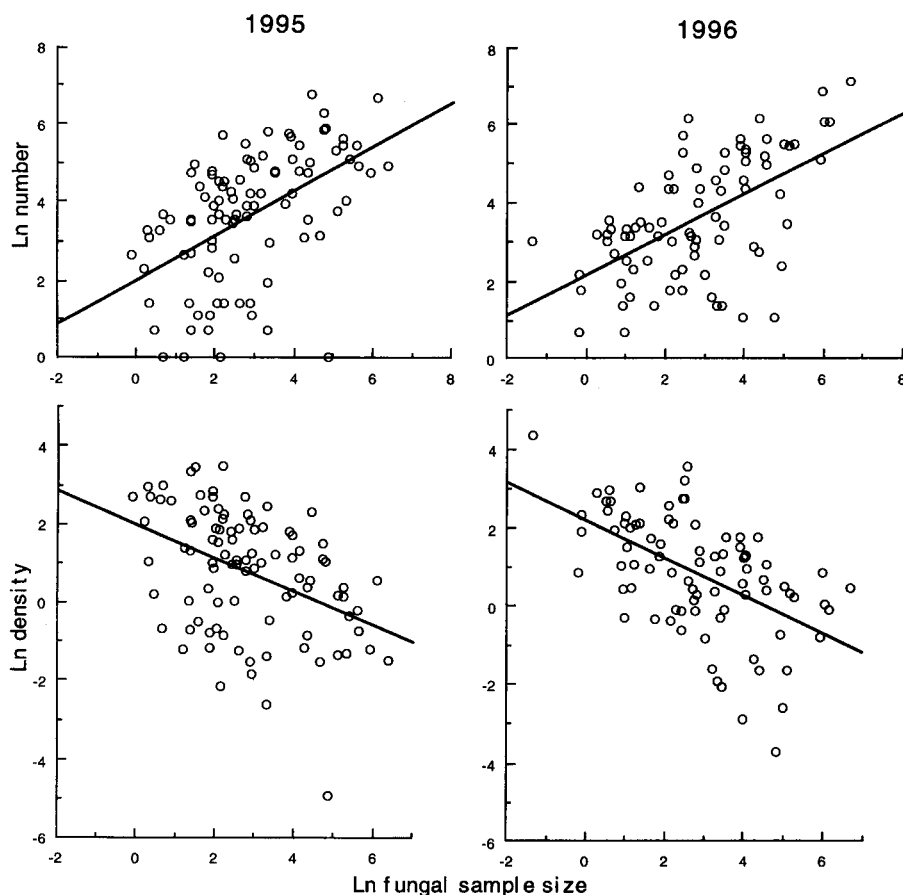
the data from the whole data-sets of 1995 and 1996 but separately for each year (Fig. 1). Log-log regression analyses revealed that within both years, the number of drosophilid emergents had a significantly positive relationship with fungal patch size, whereas the density declined significantly with increasing patch size (Fig. 1, Table 2). Furthermore, we examined these relationships separately for each fungal species with seven or more patches sampled in each year; 12 data-subsets were subjected to the regression analysis (Table 2). Log-log regressions of the number of drosophilids on fungal patch size were positive in all the cases except for *Pleurotus ostreatus* (Fr.) Quél. in 1996, though significant only in two cases, *Coprinus mica-ceus* (Fr.) Fr. in 1996 and *Pluteus cervinus* (Secr.) Quél. in 1995. On the other hand, the density showed a negative regression coefficient on patch size in all the cases, though significant only in three cases, *P. cervinus* in 1996, *Coprinus atramentarius* (Fr.) Fr. in 1995, and *P. ostreatus* in 1996. In addition, the amounts of variance in the number and the density of individuals per patch explained by patch size were much more in the present fungal multi-type system (26.9 or 31.9% for the number and 18.1 or 29.5% for the density, Table 2) than in *S. mombin* fruit single-type system (5.7 or 6.0% and 6.4 or 6.6%, respectively; Sevenster & van Alphen 1996).

Thus, we reconfirmed Sevenster & van Alphen's (1996) finding that large patches are low-density refuges despite the large absolute numbers of competitors on them. This may be applicable to various systems consisting of patchy resources, probably as a general rule. We therefore support their claim of the general need to take patch size into account when quantifying aggregation.

#### MEASURES FOR AGGREGATION MODEL

##### Intraspecific aggregation

Table 3 shows the degrees of intraspecific aggregation, quantified by  $J$ , in the three (AR, R, and A) analyses separately for each year.  $J$ -values were calculated for 10 and 9 drosophilid species in AR- and R-analyses and 30 and 31 drosophilid-fungal species combinations in A-analysis in 1995 and 1996, respectively. All the calculated  $J$ -values were positive, indicating more or less aggregated distributions. Within both years, as expected,  $J$ -values were larger in AR-analysis than in R- or A-analysis. The differences were significant in comparisons of AR vs. R (Mann-Whitney (MW)  $U$ -test,  $P = 0.0343$ ) and AR vs. A ( $P = 0.0014$ ) in 1995 and AR vs. A ( $P = 0.0367$ ) in 1996 but non-significant in AR vs. R ( $P = 0.1711$ ) in 1996. This



**Fig. 1.** Log-log regressions of the number and the density of drosophilid emergents per fungal patch on patch size (in g) for the two years 1995 and 1996.

**Table 2.** Regressions of log (drosophilid number) and log (drosophilid density) on log (fungal sample size). Fungal sample size in g

Data	<i>n</i>	Number			Density		
		Slope	<i>r</i> <sup>2</sup> (%)	<i>P</i>	Slope	<i>r</i> <sup>2</sup> (%)	<i>P</i>
ALL '95	96	0.564	26.9	< 0.001**	-0.436	18.1	< 0.001**
ALL '96	85	0.514	31.9	< 0.001**	-0.486	29.5	< 0.001**
COM '95	15	0.457	11.9	0.209	-0.543	15.9	0.141
COM '96	17	0.758	28.7	0.027*	-0.242	3.9	0.446
PLC '95	9	0.774	45.9	0.045*	-0.226	6.7	0.500
PLC '96	15	0.162	2.3	0.589	-0.838	38.7	0.013*
POS '95	7	0.767	47.2	0.088	-0.233	7.6	0.550
POS '96	7	0.726	47.6	0.086	-0.274	11.4	0.458
PEV '95	9	0.097	0.4	0.875	-0.903	24.7	0.174
OUB '95	9	0.829	17.8	0.258	-0.171	0.9	0.807
COA '95	7	0.106	5.2	0.623	-0.894	79.7	0.007**
PLO '96	11	-0.503	8.2	0.393	-1.503	44.3	0.025*
POT '96	7	0.688	38.5	0.137	-0.312	11.4	0.459
MYH '96	7	0.649	30.7	0.197	-0.351	11.5	0.457

\**P* < 0.05, \*\**P* < 0.01.

Code of fungal species name: COM, *Coprinus micaceus* (Fr.) Fr.; PLC, *Pluteus cervinus* (Secr.) Quél.; POS, *Polyporellus squamosus* (Fr.) Karst.; PEV, *Peziza vesiculosa* Fr.; OUB, *Oudemansiella brunneomarginata* L. Vassilieva; COA, *Coprinus atramentarius* (Fr.) Fr.; PLO, *Pleurotus ostreatus* (Fr.) Quél.; POT, *Polyporus tuberaster* Fr.; MYH, *Mycena haematopus* (Fr.) Quél.

**Table 3.** Intra- and interspecific aggregations of drosophilid emergents in the three analyses for fungal resources

Year:	1995			1996		
	AR	R	A	AR	R	A
Intraspecific aggregation ( <i>J</i> )						
<i>n</i>	10	10	30	9	9	31
Median	10.25	5.40	2.75	9.97	4.38	2.39
Maximum	238.50	51.34	115.70	203.00	16.06	43.47
Minimum	2.81	0.45	0.29	1.25	0.32	0.17
Interspecific aggregation ( <i>C</i> )						
<i>n</i>	31	31	65	30	30	68
Positive association	21*	17	55**	14	16	35
Negative association	10*	14	10**	16	14	33
Median	0.86	0.07	1.17	-0.15	0.15	0.11
Maximum	20.13	7.12	17.34	16.50	11.51	15.81
Minimum	-0.95	-0.97	-1.00	-1.00	-0.92	-1.00

 $\chi^2$  test: \**P* < 0.05, \*\**P* < 0.01.

means that both aggregation and resource partitioning act together to strengthen more or less intraspecific aggregations over multitype fungal patches.

#### Association

The degree of association was quantified by  $C_{xy}$ , a pairwise interspecific aggregation measure, for 31 and 30 drosophilid pairs in AR- and R-analyses and 65 and 68 pairs in A-analysis in 1995 and 1996, respectively (Table 3). *C*-values differed significantly neither between AR- and R-analyses nor between AR- and A-analyses (MW, *P* > 0.05). The numbers of positive

and negative associations are also shown in Table 3. The proportion was significantly deviated from 1:1 toward positive association in AR- and A-analyses in 1995 ( $\chi^2$ -test, *P* = 0.0482 and *P* < 0.0001, respectively).

Sevenster & van Alphen (1996) found that associations between competitor species on *S. mombin* fruit patches were consistent over years. We also examined correlations between corresponding *C*-values of 1995 and 1996 in the three analyses. Kendall rank correlation coefficients were significantly positive for 55 pairs in AR- and R-analyses ( $\tau$  = 0.34 and 0.40, respectively, *P* < 0.001 in both; Table 4). For A-analy-

**Table 4.** Kendall rank correlations between corresponding C-values of 1995 and 1996 for drosophilid species

System	Data	<i>n</i>	$\tau$	<i>P</i>
AR	ALL	55	0.34	< 0.001**
R	ALL	55	0.40	< 0.001**
A	COM	6	0.87	0.015*
	PLC	6	0.20	0.573
	POS	6	0.33	0.348

\**P* < 0.05, \*\**P* < 0.01.

sis only three fungal species, *C. micaceus*, *P. cervinus*, and *Polyporellus squamosus* (Fr.) Karst., provided the data, C-values of six pairs in each fungal species, applicable to this analysis. Kendall rank correlation was significantly positive ( $\tau = 0.87$ , *P* = 0.015) for *C. micaceus* but non-significant for *P. cervinus* and *P. squamosus*. These results reconfirm Sevenster & van Alphen's (1996) finding and claim that interspecific associations are consistent between years, and should be taken as real aspects of the community structure, although Shorrocks *et al.* (1990) suggested that associations are essentially random. Furthermore, the consistent associations in our fungal multitype system are attributed mostly to similarities and differences in host preference for fungal species between drosophilid species. The consistent associations observed on a single fungal species, *C. micaceus*, suggests the possibility of resource partitioning on a finer scale than at the fungal species level, probably due to differences in microhabitats of drosophilids and/or conditions of the fungal fruiting bodies.

#### Coexistence criterion

Relative effects of aggregation of all potential drosophilid or dipterous competitors,  $T_{dro}$  and  $T_{all}$ , on persistence were calculated and compared among the three (AR, R, and A) analyses for 10 and 9 drosophilid species in 1995 and 1996, respectively (Table 5). Although both  $T_{dro}$  and  $T_{all}$  values tended to be smaller in AR-analysis than in R- or A-analysis, the differences were not significant in the MW test for the combined *T*-values (*P* > 0.05, Table 6). However, in pairwise comparisons by Wilcoxon signed rank test after log-transformation of *T*-values, where mean *T*-value (weighted by the number of emergents from each fungal species) were used for A-analysis, significant differences were detected for  $T_{all}$  between AR and R in 1995 (*P* = 0.0051),  $T_{all}$  between AR and A in 1995 (*P* = 0.0367),  $T_{dro}$  between AR and R in 1996 (*P* = 0.0109), and  $T_{all}$  between AR and R in 1996 (*P* = 0.0077).

Differences in *T*-value between AR- and R-analyses and between AR- and A-analyses may indicate relative contributions of aggregation and resource partitioning, respectively, to the species coexistence. In

**Table 5.** Relative effect of aggregation of all potential competitors,  $T_{x-x}$ , on persistence of each drosophilid species.  $T_{dro}$  was calculated for all potential drosophilid competitors, and  $T_{all}$  for all potential dipterous competitors

Analysis	1995						1996					
	$T_{dro}$			$T_{all}$			$T_{dro}$			$T_{all}$		
	AR	R	A (mean)	( <i>n</i> )	AR	R	A (mean)	( <i>n</i> )	AR	R	A (mean)	( <i>n</i> )
<i>Le. maculata</i>	0.38	0.28	1.36	(1)	0.47	0.53	1.08	(1)	0.22	0.28	0.90	(2)
<i>Le. quinque maculipennis</i>	0.28	0.44	0.58	(1)	0.26	0.59	0.46	(1)	0.14	0.32	0.46	(1)
<i>H. trilineata</i>	2.35	1.56	1.33	(1)	1.40	1.47	1.38	(1)	0.34	0.37	0.53	(1)
<i>H. sexvittata</i>	0.64	0.70	0.78	(5)	0.87	1.30	1.10	(5)	1.28	1.86	0.58	(6)
<i>H. alboralis</i>	0.47	0.50	0.47	(5)	0.54	0.77	0.43	(5)	0.73	1.07	0.46	(4)
<i>H. histrioides</i>	0.14	0.14	0.33	(3)	0.18	0.36	0.30	(3)	0.12	0.15	0.63	(3)
<i>D. orientacea</i>	0.34	0.28	0.66	(3)	0.25	0.41	0.42	(3)	0.23	0.29	0.57	(6)
<i>D. histrio</i>	0.44	0.34	0.71	(2)	0.38	0.45	0.62	(2)	—	—	—	—
<i>D. brachynephros</i>	0.54	0.52	0.73	(5)	0.52	0.61	0.55	(5)	0.83	1.15	0.87	(6)
<i>D. curvispina</i>	1.17	1.10	1.09	(4)	1.01	1.10	1.00	(4)	2.02	1.86	1.04	(2)
Median	0.46	0.47	0.72	(30)	0.50	0.60	0.59	(30)	0.34	0.37	0.58	(31)
Mean	0.68	0.59	0.80	(30)	0.59	0.76	0.73	(30)	0.66	0.82	0.74	(31)

**Table 6.** *P* values in Mann–Whitney *U* (MW) and Wilcoxon signed rank (WR) tests for the differences in  $T_{dro}$  and  $T_{all}$  between AR- and R-analyses and between AR- and A-analyses

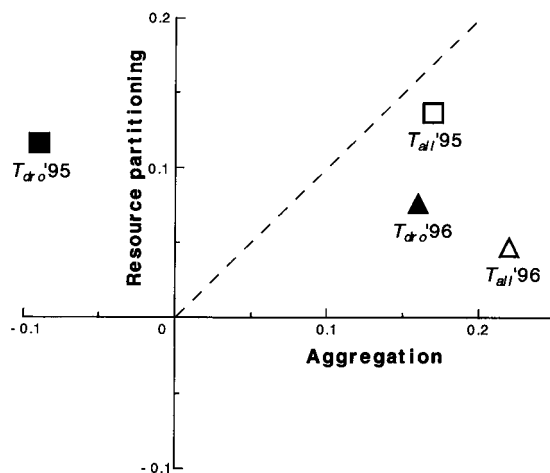
	MW		WR	
	$T_{dro}$	$T_{all}$	$T_{dro}$	$T_{all}$
1995				
AR vs. R	0.8497	0.2265	0.4413	0.0051**
AR vs. A	0.0889	0.2899	0.0506	0.0367*
1996				
AR vs. R	0.4527	0.1118	0.0109*	0.0077**
AR vs. A	0.3536	0.2692	0.2135	0.1731

\* $P < 0.05$ , \*\* $P < 0.01$ .

Fig. 2, four points for  $T_{dro}$  and  $T_{all}$  of the two years are plotted in a two-dimensional space with regard to the degrees of importance of aggregation and resource partitioning as coexistence mechanisms: the two dimensions of this space are  $\bar{T}(R) - \bar{T}(AR)$  and  $\bar{T}(A) - \bar{T}(AR)$ , respectively, since the coexistence becomes easier with decreasing  $T$ -value. The plot for  $T_{dro}$  in 1995 indicates a negative effect of aggregation on the species coexistence, probably due to somewhat larger (positive) interspecific aggregations over patches of each fungal species, i.e.  $C$ -values in A-analysis (Table 3). In addition, the figure suggests a yearly variation in the relative importance of the two coexistence mechanisms: resource partitioning tended to be more important in 1995 than in 1996, but aggregation was *vice versa*.

## Discussion

Most of the calculated  $T_{dro}$  and  $T_{all}$  values were less than unity even in the R- and A-analyses (Table 5):

**Fig. 2.** Relative contributions of aggregation and resource partitioning as mechanisms for the species coexistence in a mycophagous drosophilid community in the two years 1995 and 1996, evaluated by  $\bar{T}(R) - \bar{T}(AR)$  and  $\bar{T}(A) - \bar{T}(AR)$ , respectively.

the necessary and sufficient condition for persistence of those species was satisfied only by resource partitioning at the fungal species level or aggregation over patches of single fungal species. There were, however, a few species whose  $T_{dro}$  and  $T_{all}$  values exceeded unity in R- and/or A-analyses. This does not necessarily mean their extinction. Some of them can persist on natural fungal multispecies patches (AR-analysis), due to the combined effects of resource partitioning and aggregation, as seen in *Leucophenga maculata* (Dufour) and *Hirtodrosophila sexvittata* (Okada) in 1995 and *Hirtodrosophila alboralis* (Momma & Takada) and *Drosophila brachynephros* Okada in 1996 (Table 5). Thus, the species coexistence (diversity) in the studied mycophagous drosophilid community was regarded as being promoted, on average, by both resource partitioning and aggregation, although the relative importance of the two mechanisms varied more or less between years.

In spite of the combined effects of these two mechanisms,  $T$ -values of a very few species, e.g.  $T_{dro}$  and  $T_{all}$  of *Hirtodrosophila trilineata* (Chung) in 1995 and  $T_{dro}$  of *H. sexvittata* in 1996, exceeded unity in the AR-analysis. However, their  $T$ -values were less than unity in the other year, respectively. This means that the criterion conditions for persistence of these species fluctuate between years. The long-term, averaged effect of such an annual variation in  $T$  may allow their persistence, although their populations would fluctuate yearly to a larger extent than those of other species.

On the other hand, *Drosophila curvispina* Watabe & Toda constantly showed  $T$ -values more than unity in both years. Is the species going extinct from the Botanic Garden? This does not seem to be the case. This species has been constantly recorded from the Garden for at least 10 years (M.J. Toda, unpublished). In addition, this species is almost specialized to breed on fungi, and it therefore rarely, if ever, utilizes materials other than fungi as breeding sites. If the population of this species sinks in the season studied at the Botanic Garden, its persistence should be sustained by recovery in other seasons or by immigration from other habitats. This implies that seasonal resource partitioning and/or habitat segregation may play a role in the persistence of this species.

Although the present study was consciously quite limited in space and time, the species coexistence and diversity in a community should be understood on a larger spatio-temporal scale where various mechanisms would act together to ensure the persistence of inferior competitors by providing many kinds of refuges. It was impossible, however, to evaluate the relative importance of such concurrent mechanisms until Sevenster (1996) improved the aggregation measures and coexistence criterion to incorporate the density, not the number, of competitors into the aggregation model. In this study, by manipulating the original data-set, we present a technique to exclude



the effects of aggregation and resource partitioning by combining the data, not only the number of insects but also patch size, for each fungal species and then dividing the data-set into subsets of individual fungal species. This technique would be applicable to wider spatio-temporal situations to evaluate the relative importance of more coexistence mechanisms at the same time. Such an extended analysis will be analogous to the 'niche dimensionality analysis' (Levins 1968; Shorrocks 1975; Atkinson & Shorrocks 1977), whereby the relative importance of multiple niche components is evaluated by partitioning the total community diversity into subsets of diversity explained along each niche dimension.

Such an analysis, which makes it possible to evaluate simultaneously the relative importance of various kinds of species-coexistence mechanisms, will open a door for comparison of communities over a wider range. To understand the mechanisms of global patterns of biodiversity on the earth, we have to compare the relative importance of coexistence mechanisms among different communities. The method proposed in this study will be effective for such a comparison: each community is placed in a space comprising multiple dimensions of coexistence mechanisms, as shown in Fig. 2. It is expected that different mechanisms contribute in different proportions to the species coexistence and diversity among different communities. For example, principal mechanisms may be different between species-poor and species-rich communities. Studying a species-rich, frugivorous *Drosophila* community in a tropical forest of BCI, Sevenster (1992) and Sevenster & van Alphen (1996) revealed that the process of aggregation over *S. mombin* fruit patches enhanced the species coexistence and diversity, but that the degree of aggregation was weaker in that community than in temperate communities studied previously. Furthermore, they pointed out at the same time that other mechanisms, such as resource partitioning between seasons or at the fruit species level, acted together to stabilize the species coexistence and to increase the diversity in the whole frugivorous *Drosophila* community of BCI.

Refuges provided by the aggregation process are probabilistic in principle for inferior competitors. Genetic changes in a population that cause niche differentiation in any dimension should stabilize the species coexistence and become fixed in the population, if environmental conditions allow. Analysing a simple genetic model of ecological character displacement, Gotelli & Bossert (1991) showed that where there is more than one resource type, coexistence due to resource partitioning may be an evolved state resulting from interspecific competition. Otherwise, invading species occupying very different niches from those of the residents can establish their populations more easily. Thus, it is expected that, during the process of community development and saturation, the probability refuge provided by the aggrega-

tion process will decrease in relative importance as a mechanism for species coexistence. This prediction can be tested by comparing communities with different histories of interspecific interactions, e.g. tropical vs. temperate, or continental vs. insular communities.

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