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Fungivorous *Pegomya* flies: spatial and temporal variation in a guild of competitors

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Fourteen species of *Pegomya* (Anthomyiidae) are the only significant primary fungivorous flies breeding in *Leccinum* (Boletaceae) sporophores in Finland. The length of the thorax in the flies is negatively correlated with the number of flies emerging from a sporophore, suggesting increasing larval competition with increasing numbers of larvae in sporophores. Further evidence of competition is provided by a geographical comparison: in Central Europe there are only 2 species of *Pegomya* that use *Leccinum*, but their abundance is as high as the pooled abundance of all *Pegomya* in Finland, i.e. 20 to 50 flies per sporophore. We demonstrate that *Pegomya* are intraspecifically aggregated amongst sporophores, which will contribute to the coexistence of many species in spite of competition. In Finland, the number of abundant species is about 7 throughout the country, though the species pool decreases from south (13) to north (7). Predation of full-grown larvae and pupae is also severe and may inflict up to 90% mortality. Prolonged diapause is common in *Pegomya* in Lapland but not in south Finland, probably because of increasing year-to-year variation in sporophore production with latitude.

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1. Introduction

Most fungivorous insects are conspicuously polyphagous, breeding in the sporophores of dozens of macrofungal species (Hanski 1988a and references therein). Polyphagy in fungivorous insects is generally explained by the scarcity of most of the host fungi, and by large year-to-year variation in their sporophore production, making host specialisation an unlikely evolutionary outcome (Hanski 1988a). Primary fungivorous flies in the genus *Pegomya* (Anthomyiidae) are a notable exception (Fig. 1), most species being restricted to a few species of *Leccinum*, especially *L. versipelle* and *L. scabrum* (Boletaceae). *Leccinum* are amongst the most abundant and largest mushrooms in coniferous forests in northern Europe (Ohenoja & Koistinen 1984), and as *Leccinum* are mycorrhizal fungi, their sporophores have a relatively predictable occurrence. These factors should improve the chances of oligophagous fungivores surviving on *Leccinum*. Boletaceae are structurally and chemically (Bruns 1984) unique amongst Agaricales (the family is often considered to form a separate order Boletales), which may also contribute to oligophagy in *Pegomya*.

The genus *Pegomya* consists primarily of leaf-mining and fungivorous species (Griffiths 1982–84). Hackman (1976, 1979) has reported on the life-history of several fungivorous *Pegomya* in Finland. His studies have demonstrated some differences between the species, e.g. in the site of oviposition, but most species are similar ecologically and colonize the same sporophores in large numbers. Hundreds of *Pegomya* larvae occur regularly together, and it seems probable that the larvae compete with each other. *Pegomya* comprise an interesting guild of many similar species using the same patchy and ephemeral resource (for a review of insects using such resources see Hanski 1987a).

In this paper we draw together ecological information on *Pegomya* based on our extensive rearing results from about 2500 *Leccinum* sporophores col-

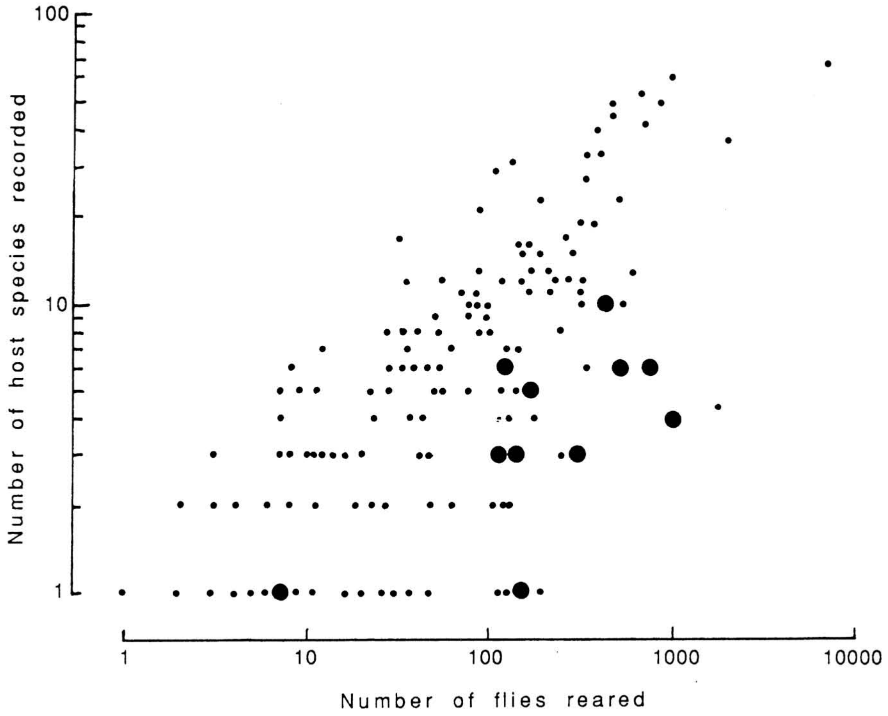

Fig. 1. Number of macrofungal host species recorded for *Pegomya* (large dots) and other fungivorous species (data from Hackman & Meinander 1979). The increasing host range with increasing number of flies (total number reared) is largely or entirely a sampling effect, but note that for a given number of flies reared *Pegomya* have a clearly narrower host range than fungivorous flies on average.

lected from different parts of Finland. Our results confirm that *Pegomya* larvae compete in the sporophores, but we also show that predation is important. We demonstrate temporal responses in *Pegomya* to seasonal and annual variation in sporophore numbers, and we suggest that aggregated distributions of larvae in sporophores significantly contribute to the coexistence of 14 species in the regional species pool.

2. Material and methods

Leccinum sporophores were collected for fly rearing at four localities in Finland over several years. In southern Finland, at Tvärminne (59°50′N, 23°15′E) and Espoo (60°15′N, 24°30′E), sporophores were collected by W. Hackman and M. Meinander in 1974, and in Lammi (61°05′N, 25°05′E) by I. Hanski in 1981 and 1982, and by E. Ribeiro in 1983 and 1984. In northwestern Finnish Lapland, at Kilpisjärvi (69°03′N, 20°50′E), G. Ståhls collected sporophores in 1985 and 1986. The numbers of sporophores collected at each site are given in Table 1. Generally, most of the sporophores found were collected or used for field rearing (see below).

Sporophores collected for laboratory rearing were kept in paper bags in the field to avoid cross-contamination. In the laboratory, the sporophores were placed in plastic containers on a layer of peat, in which the larvae could pupate, and the containers were covered with nylon gauze. The few mycetophilids that use Boletaceae in Finland (Hackman & Meinander 1979) emerged in about two weeks, during which time the rearing containers were kept in the shade outdoors. The main inhabitants of Boletaceae are *Pegomya* (Hackman & Meinander 1979), which hibernate. Hibernating pupae were kept at about +4°C for about four months.

About half of the sporophores at Lammi were not brought to the laboratory but the insects were allowed to develop in the field. The sporophore was surrounded by a metal cylinder, which was forced 15 cm deep into the soil around the sporophore (the total height of the cylinder was 30 cm, diameter 15 cm). Full-grown larvae descended to the soil inside the cylinder to pupate. Predators such as staphylinid beetles could enter the cylinders by flying in from above. After the sporophore had

Table 1. Numbers of *Pegomya* reared from *Leccinum* sporophores during several years at four localities in Finland. The column headings give the locality and year. Locality codes are: E Espoo, T Tvärminne, L Lammi and K Kilpisjärvi.

	Laboratory rearing						Field rearing			
	E74	T74	L83	L84	K85	K86	L81	L82	L83	L84
Pegomya species										
P. flavoscutellata (Zett.)	82	27	113	24	459	44	14	6	5	8
P. notabilis (Zett.)	–	262	42	4	144	55	2	1	1	2
P. zonata (Zett.)	94	280	218	24	636	20	35	10	7	46
P. scapularis (Zett.)	–	150	329	10	2649	921	157	84	–	9
P. circumpolaris Ackland & Griffiths	–	–	21	27	40	85	–	8	2	16
P. incisiva Stein	15	–	–	–	80	16	–	–	–	–
P. fulgens (Meigen)	–	103	40	129	–	–	8	24	1	221
P. transgressa (Zett.)	–	–	–	–	654	845	–	–	–	–
P. vittigera (Zett.)	1	3	90	–	+	–	13	1	1	–
P. furva Ringdahl	45	196	–	–	+	–	15	–	–	–
P. winthemi (Meigen)	37	23	–	–	–	–	–	–	–	–
P. tabida (Meigen)	3	161	4	–	–	–	2	7	–	–
P. tenera (Zett.)	–	–	4	–	–	–	1	6	–	–
P. pulchripes (Loew)	–	–	9	–	–	–	–	–	–	–
Unidentified ♀♀			1228	266			238	173	36	333
Total	227	1205	2078	484	4662	1986	485	317	53	635
Number of sporophores	11	8	68	99	203	39	85	79	131	100
Pegomya per sporophore	22.6	156.0	30.5	4.8	22.9	50.9	5.7	4.0	0.4	6.4
Number of species	7	9	10	6	7	7				
Species / 200 ind. mean	6.70	8.40	9.20	6.00	6.80	6.69				
SD	0.47	0.51	0.73	0.01	0.41	0.51				
Mydaea spp.	–	2	157	4	4	–	59	42	9	8
Hymenoptera spp.	+	+	16	+	+	+	180	98	28	2

Notes: Only males have been identified to species in the rearing experiments from Lammi (the total number of females is given separately). Hymenoptera were not counted from Kilpisjärvi, Tvärminne or Espoo, though they were present. Older but not rotting sporophores were chosen for the E74 and T74 samples (Hackman & Meinander 1979). In the other samples nearly all the sporophores found were collected.

entirely decayed in three to four weeks, the soil inside the cylinder was removed intact and placed in a plastic pot of the same diameter. The pots were kept at about +4°C for about four months, after which time they were brought to the laboratory to permit the flies to emerge.

After the rearing containers had been moved to room temperature, flies started to emerge in about two weeks, and the emergence continued for at most six weeks. The containers were checked every second day for flies, which were collected with an exhaustor and killed in ethylene acetate. Flies were either pinned, which is preferable for identification, or preserved in 70% alcohol (most of the material from Lammi).

The 1986 rearings from Kilpisjärvi were moved back to +4°C after a couple of weeks since emergence had completely ceased. Following the second cold treatment (about 4 months) the rearing containers were once more brought to room temperature to allow flies to emerge. After emergence had ceased, the cold treatment was repeated for the third time.

3. Results

3.1. Guild composition

Table 1 gives the numbers of *Pegomya* reared from *Leccinum* at four localities in several years. Species number decreases from 13 in southern Finland to 9 in Lapland, but of the latter only 7 are regularly observed. One species, *P. transgressa*, is restricted to Lapland, where it replaces *P. fulgens*, a closely related species (V. Michelsen pers. comm.). The dominant 4–5 species tend to be the same everywhere, apart from the species pair *P. transgressa-fulgens*, while at any one locality there are additionally several other, usually rarer, species (Table 1).

Our results indicate large year-to-year variation in the species composition, e.g. *P. scapularis* was the dominant species at Lammi in 1981 and *P. fulgens* was rare, while the situation was reversed in 1984.

The number of species varied from 6 to 10 in the different sets of samples, but part of this variation is simply due to varying sample size. A random subsample of 200 individuals included 6.0 to 9.2 species (Table 1). Our data thus do not indicate any clear decrease in the rarefied species number with increasing latitude, although the regional species pool decreases from 13 in South Finland to 7 regular species in Lapland.

The sporophores that were brought directly to the laboratory yielded from 5 to 156 flies per sporophore in the six sets of containers in Table 1. However, the highest figure is not representative, because Hackman & Meinander (1979) selectively sampled a small number of heavily infested sporophores. Omitting the highest and the lowest figures leaves average yields varying only a little, from 23 to 51 flies per sporophore. This range is even smaller if only the flies which emerged after one winter (cold treatment) are included for the 1986 Kilpisjärvi sample, which is the only material in which prolonged diapause was studied systematically (Section 3.3); the range is then from 23 to 40 flies per sporophore.

The mushrooms that were allowed to decay in the field yielded much smaller numbers of flies, i.e. from 4 to 6 per sporophore (Table 1, excluding the lowest value of 0.4). It is likely that the difference between the two kinds of rearing experiments is largely due to predation of larvae and pupae in the field by e.g. predatory staphylinid beetles, which are common in decaying mushrooms and their surroundings (Benick 1952). Whatever the exact causes of mortality, only about 10% of individuals survived in the field until the beginning of winter (calculated on the basis of emerging adults; Table 1). If the predators are most abundant in and around sporophores where the pooled numbers of prey are highest, predation may further enhance the coexistence of many *Pegomya* in spite of larval competition (Hanski 1981).

Two notable natural enemies of *Pegomya* in the sporophores are *Mydaea* flies (Muscidae) and parasitic Hymenoptera (Hackman & Meinander 1979). Their occurrence has however been sporadic (Table 1), and apparently they do not impose a heavy mortality on *Pegomya.*

3.2. Phenology

Fungivorous insects need to cope with temporal variability in resource availability at several time scales, including seasonality of sporophore production, which depends greatly on weather conditions during the summer. Ohenoja & Metsänheimo (1982) report that in Lapland good fruiting occurs only in years when the mean daily temperature for the latter half of August and all of September remains above +10°C, while precipitation seems to have a primary effect on the timing of the beginning of frutification. On average, the yields are highest between 15 August and 10 September in Lapland (Ohenoja & Metsänheimo 1982). The average duration of sporophore

Table 2. Numbers of *Pegomya* caught in a malaise trap operated in Sipoo in 1983. Pooling the material before and from August reveals significant phenological differences between the species ($\chi^2=25.16$, df=7, $P<0.0007$; *P. pulchripes*, *P. furva* and *P. winthemi* excluded). The Roman numbers refer to the 4 quarters of each month.

Species	Jun III	Jun IV	Jul I	Jul II	Jul III	Jul IV	Aug I	Aug II	Aug III	Aug IV	Sep I	Sep II	Sep III
P. geniculata	1	1	12	5	12	1	2	3	4	15	12	18	33
P. notabilis	1	2	3	3	3	–	1	3	–	14	16	8	6
P. flavoscutellata	10	1	17	2	11	2	8	1	21	105	42	7	10
P. winthemi	1	–	–	–	–	–	–	–	–	–	–	–	–
P. zonata	–	2	2	–	2	1	–	2	2	17	9	5	9
P. fulgens	–	–	5	–	–	–	–	–	–	–	4	–	6
P. incisiva	–	–	1	–	–	–	–	–	9	8	7	1	5
P. vittigera	–	–	–	–	2	3	–	2	–	7	10	6	13
P. scapularis	–	–	–	–	1	–	1	–	2	14	15	9	11
P. pulchripes	–	–	–	–	–	1	–	–	2	–	–	–	–
P. furva	–	–	–	–	–	–	–	–	–	–	–	–	3

production in northern Finland and Lapland was 2.5 months in 1976, four months in 1977 and three months in 1978 (Ohenoja & Koistinen 1984). In southern Finland *Leccinum* sporophores can occur as early as June and the season extends until the end of October.

Results from a malaise trap operated in Sipoo (60°20′N, 25°20′E) in southern Finland show that *Pegomya* occur from June to October (Table 2). In June, July and August both sexes were trapped, but from September onwards only females occurred in the trap. By the end of July, 9 out of 10 species had been caught, but the greatest numbers of individuals occurred in the middle of August (Table 2). An early emergence may be an adaptation to take advantage of summers when the sporophores appear exceptionally early, but it is also possible that females need to feed for a prolonged period of time to reach maturity (Tiensuu 1935, Hackman & Meinander 1979). Some species occur earlier than others (Table 2). Of the dominant species (Table 1) only *P. scapularis* had a late occurrence in August–September, while the other common species first appeared in June–July (Table 2).

3.3. Diapause

All fungivorous *Pegomya* have a pupal diapause. As *Pegomya* are exceptionally oligophagous for fungivorous flies (Fig. 1), and as the numbers of sporophores vary substantially from one year to another, one could expect that these species would have a high frequency of prolonged diapause (individuals staying in diapause for two or more winters; for a review see Hanski 1988b). In southern Finland, prolonged diapause has however been recorded rarely for only one species, *P. furva* (Hackman 1976). In contrast, in Lapland prolonged diapause occurs in all the seven common species (Ståhls 1987; Table 3), though the frequency of prolonged diapause seems to vary widely between the species, from 4 to 68% in the material in Table 3. Some individuals of *P. transgressa* diapaused three "winters" (cold treatments; Table 3). Perhaps significantly, this is the only species in the assemblage having an exclusively northern and montane distribution (Table 1; V. Michelsen pers. comm.).

It is probable that the reason for the difference in the frequency of prolonged diapause between southern and northern Finland is greater year-to-year variation in sporophore production in the north than in the south. Ohenoja & Metsänheimo (1982) give data on total sporophore production (fresh weight, kg/ha) of macrofungi during 6 years in Lapland, and they found the maximum and minimum figures in birch forests to be 363 and 0.3 kg/ha, respectively. Equally extreme low values have not been reported for southern Finland (Ohenoja & Koistinen 1984). Sjöblom et al.'s (1979) study on sporophore production during a three-year period (1976–1978) in Ekenäs (59°50′N, 23°20′E) in southern Finland gave a maximum of 225 kg/ha and a minimum of 60 kg/ha.

Table 3. Numbers of *Pegomya* emerging after one (I), two (II) and three (III) cold treatments. Material collected from Kilpisjärvi in 1986. — Diap. = percent in prolonged diapause. Abund. = relative abundance (%) in 1985–86.

Species		I	II	III	Diap.	Abund.
P. zonata	♀	11	1	–	20	10
	♂	5	3	–		
P. incisiva	♀	6	2	–	13	1
	♂	8	–	–		
P. flavoscutellata	♀	6	16	–	68	17
	♂	8	14	–		
P. notabilis	♀	29	1	–	7	2
	♂	22	3	–		
P. circumpolaris	♀	29	1	–	4	2
	♂	53	2	–		
P. scapularis	♀	415	53	–	16	47
	♂	360	93	–		
P. transgressa	♀	303	126	4	30	21
	♂	298	118	8		

If prolonged diapause has significant population dynamic consequences, we could expect some relationship between the frequency of prolonged diapause and the relative abundance of the species (see models by Chesson 1983, Bulmer 1984). To estimate the latter, we calculated a pooled measure of relative abundance for the years 1985 and 1986, for which data are available (Table 1). None of the rearings were given two cold treatments in 1985, and we have therefore added to the 1985 figures the expected number of flies in prolonged diapause, estimated from the 1986 results. Thus calculated, we obtained the relative abundances given in Table 3. This measure of relative abundance is significantly correlated with the frequency of prolonged diapause in 1986 ($P<0.05$, Olmstead-Tukey's corner test; Sokal & Rohlf 1981). We therefore conclude that prolonged diapause has significant population dynamic consequences for *Pegomya* in Lapland.

3.4. Competition

If competition occurs amongst larvae developing in sporophores, we could expect competition first to lead to a decrease in the size of the emerging adults, and only very severe competition to increase mortality (cf. Grimaldi & Jaenike 1984).

To estimate the degree of competition, we measured the tibia and thorax lengths of 299 individuals of *P. scapularis* reared from 17 sporophores of *Leccinum scabrum*, of which one half of each sporophore was taken for rearing. This material was collected from Lapland, where *P. scapularis* is the numerically dominant species (Table 1). Thirty randomly chosen individuals were measured per sporophore, or all individuals were measured if there were less than 30 flies from the sporophore. The analyses were run both for individual flies and for the mean values for sporophores. The two sets of measurements gave similar results, and we report here the thorax measurements only.

Table 4 gives the results of ANCOVA (individual flies) and multiple regression (mean values for sporophores) with the cap diameter of the sporophore and the logarithm of the numbers of *Pegomya* reared from the sporophore as two covariates. Females are significantly larger than males, but the sex ratio was roughly equal and it did not explain variation in the average size of flies between sporophores. As expected, the thorax length decreased with increasing numbers of *Pegomya* per sporophore (Table 4). Unexpectedly, the size of the flies also decreased with increasing sporophore size. This is surprising because larger sporophores should provide more food for the larvae than small ones, and hence yield larger flies because of decreased competition. However, larger sporophores are also more advanced in their decay and possibly less suitable than somewhat smaller and younger ones for *Pegomya*, which feed on fresh fungal tissue. We also repeated the analyses for the numbers of *P. scapularis* only, with similar results, but as this species may compete with other species, it seems better to use the total numbers of *Pegomya* in the analysis.

Table 4. Results of ANCOVA (individual flies) and multiple regression (means for sporophores) for the thorax length of *P. scapularis*. — ** $P<0.01$; *** $P<0.001$.

	Flies (n=299)			Sporophores (n=17)		
	MS	F	P	coeff.	t-value	P
Main effect: sex	1496	92.5	***	sex ratio: no effect		
Covariates:						
no. of *Pegomya*	99	6.14	**	–1.57	–3.73	***
cap diameter	304	18.84	***	–0.87	–3.96	***

This evidence is not conclusive for competition affecting individual size and hence e.g. female fecundity. One complicating factor is that strong scramble competition could produce small numbers of small flies per sporophore (low survival). However, our test is conservative in this respect, and we conclude that competition is the most likely reason why flies tend to be small when their numbers are large per sporophore.

3.5. Larval aggregation

Recent theoretical (Shorrocks et al. 1979, Hanski 1981, Atkinson & Shorrocks 1981, Ives & May 1985, Ives 1988a, 1990) and experimental studies (Kneidel 1985, Hanski 1987b, Ives unpubl.) have demonstrated how two species breeding in ephemeral and patchy microhabitats, such as fungal sporophores, may coexist regionally in spite of strong competition within resource patches. Regional coexistence is possible if the numbers of larvae are more or less independently aggregated in the resource patches, increasing intraspecific but not interspecific competition and thereby facilitating coexistence (Hanski 1987c, Ives 1988b).

We have analysed between-sporophore variation in emerging *Pegomya* in the material collected from Lapland. Following Ives' (1988b) recommendation, we use the index $J(1) = [(v_1/x_1)-1]/x_1$ to characterize intraspecific aggregation for species 1, where x_1 and v_1 are the mean and the variance in the sample. $J(1)$ measures the relative increase in the average number of conspecific competitors a larva of species 1 must face above the number of conspecific competitors of females ovipositing randomly (Ives 1988b). Similarly, interspecific aggregation was measured by $C(1,2) = \mathrm{cov}\,(x_1, x_2)\,/\,x_1x_2$. Table 5 summarizes the results for the seven common species in Lapland. Calculations were repeated for the total material of 151 sporophores and the 56 sporophores with a cap diameter greater than 10 cm (the latter was done to minimize differences between the sporophores). In both cases the result is the same: there is substantial intraspecific aggregation and much weaker and in most cases nonsignificant interspecific aggregation. For coexistence, the important thing is aggregation of

Table 5. Variance-covariance structure for a guild of 7 *Pegomya* breeding in *Leccinum scabrum* and *L. versipelle* sporophores in Lapland. The indices *J* and *C* are defined in the text. The first *J* (a) is for the total material of 151 sporophores, while the second *J* (b) is for the 56 sporophores with a cap diameter greater than 10 cm. The upper-right corner of the matrix is for the total material, and the lower-left corner is for the 56 largest sporophores.

Species	$J(i)^a$	$J(i)^b$	$C(i,j)$						
			1	2	3	4	5	6	7
1. *P. flavoscutellata*	7.08	4.28	—	1.39	0.12	0.69	0.12	0.46	–0.39
2. *P. scapularis*	4.57	1.82	0.63	—	0.48	2.08	1.79	2.36	0.00
3. *P. notabilis*	14.65	4.37	–0.04	0.59	—	1.65	0.93	0.88	–0.66
4. *P. zonata*	5.40	2.37	0.04	0.65	0.47	—	0.89	2.17	–0.21
5. *P. circumpolaris*	18.81	9.07	–0.30	0.45	1.24	0.03	—	–0.37	–0.07
6. *P. transgressa*	10.34	4.48	0.12	0.73	–0.38	0.51	–0.69	—	–0.42
7. *P. incisiva*	10.62	6.24	–0.56	–0.24	–0.68	–0.41	–0.52	–0.51	—

clutches if females do not oviposit eggs singly (Ives 1988b). Some *Pegomya* species oviposit eggs singly while others lay small clutches (Hackman & Meinander 1979); hence the results in Table 5, based on the numbers of emerging flies, may give a somewhat but not seriously inflated picture of the level of aggregation facilitating coexistence.

An elegant result recently derived by Ives (unpubl.) allows one to estimate the minimum effect of aggregation on 2-species coexistence measured in terms of larval competition. Let α_0 and β_0 be the threshold values of larval competition above which coexistence is impossible in the case of random distribution of species, and α_a and β_a denote the corresponding thresholds when species are aggregated. The threshold values α_a and β_a are given by the inequality

$$\alpha_a \beta_a > \alpha_0 \beta_0 [J(1)+1][J(2)+1] / [C(1, 2)+1]^2.$$

The average values of *J* and *C* in the restricted set of 56 sporophores in Table 5 are 4.66 and 0.05, respectively. Using these values, the minimum estimate for the effect of aggregation on coexistence is 0.97, in other words the observed level of aggregation would be enough to allow coexistence even if the larval competition coefficients were about 30 times greater than the threshold values allowing coexistence in randomly distributed species. The meaning of this result is that the species will coexist almost regardless of the strength of larval competition. Although this result is still limited to only two species, and no quantitative prediction for guild size may be given, the implication is surely that aggregation must very significantly facilitate coexistence in fungivorous *Pegomya*.

4. Discussion

4.1. Geographical patterns

Bruns (1984) reports that the diversity of insects he found in his investigations of the insects of Boletaceae in the Midwest in the USA is comparable to that reported from European fleshy fungi. Many species of both insects and hosts in the US Midwest are identical with those reported from Europe, while in other cases congeneric insect species occupy niches similar to those of their European counterparts. In North America very little breeding work has yet been done, and anyone willing to undertake comprehensive rearings of insects from mushrooms will easily make new discoveries (Griffiths 1982–84). Of the eight species of *Pegomya* that Bruns (1984) reared all but one (*Pegomya mallochi*, with Nearctic distribution; Table 6) are also found breeding in Boletaceae in Finland, where they appear to fill similar or identical niches to those in North America. The *Pegomya* species are primarily Holarctic in distribution (Griffiths 1982–84).

Table 6 compares the numbers of fly species reared from *Leccinum* species, in the *L. scabrum* (*L. scabrum, L. holopus, L. carpini, L. variicolor*) and *L. versipelle* groups (*L. versipelle, L. aurantiacum, L. vulpinum, L. roseotinctum, L griseum*; according to Ulvinen 1976). In Central European investigations (Burla & Bächli 1968, Eisfelder 1954, 1955, 1956, Dely-Draskovits 1972a, 1972b, 1974, Dely-Draskovits & Mihàlyi 1972, Papp 1972) only two *Pegomya* species, *P. winthemi* and *P. notabilis*, have been reared from Boletaceae. The great abundance of *Leccinum* species especially in boreal regions may explain the decrease in the number of *Pegomya* spe-

Table 6. Geographical comparison between the numbers of species reared from *Leccinum* species in the *L. versipelle* and *L. scabrum* groups.

	Finland	Central Europe	North America	Soviet Carelia	England
Pegomya spp.	14	2	8	11	9
other Anthomyiidae	2	1	–	2	2
Tipulidae	2	–	1	3	–
Anisopodidae	–	–	2	1	–
Drosophilidae	4	1	2	3	7
Heleomyzidae	–	2	–	2	2
Muscidae	8	6	6	6	5
Mycetophilidae	3	4	2	17	14
Phoridae	–	3	2	5	2
Scatopsidae	–	1	1	1	1
Sphaeroceridae	3	1	–	5	2
Syrphidae	2	1	2	1	–
Total	36	22	25	51	44

cies reared with decreasing latitude: 14 in Finland, 11 in Soviet Carelia (Yakovlev & Osipova 1985), 8 in Michigan in North America (Bruns 1984), 9 in the UK (Chandler 1979, Buxton 1960), and 2 in Central Europe. The number of mycetophilid species reared is very variable, perhaps due to varying degrees of sampling.

Dely-Draskovits & Mihàlyi (1972) reported high densities for the two Central European *Pegomya*, 16 (*P. notabilis*) and 59 (*P. winthemi*) individuals per sporophore. These densities are an order of magnitude higher than those we found for these species in Finland (Table 1), and the pooled density of these two species in Central Europe is comparable with the pooled density of the 14 *Pegomya* in Finland (Table 1). These results suggest density-compensation, and present another line of evidence for resource competition in *Pegomya*.

4.2. Aggregation and guild size

The theoretical studies on competition in ephemeral resources cited in Section 3.5 deal with only two species, and although it seems probable that the results extend to many species, one would like to know whether this mechanism is likely to allow 3, 10 or perhaps 100 competitors to coexist on the same resource. Shorrocks & Rosewell (1986) have made a start in answering this question. They used a simulation model and empirical data on fungivorous *Drosophila* to predict the guild size of competitors, based only on independently aggregated larval distributions in species using the same resource. They predicted a modal guild size of 5, which agreed well with the observed value of 7. Unfortunately, their data base includes guilds which do not satisfy the model assumptions; for example some of the fungivorous guilds include species which do not use the same host fungi or which are saprophagous (Hanski 1988a). The most convincing demonstrations of competition in fungivorous *Drosophila* are from North America (Grimaldi & Jaenike 1984).

Our results on guild size in *Pegomya* suggested that the number of common species is limited to 6 to 8 species locally (Table 1). By increasing the sample size one could undoubtedly collect all the possible species from one locality in South Finland, but many of them would be very rare, and their occurrence at many sites in many years could be due to dispersal from elsewhere.

The prediction of Shorrocks & Rosewell (1986) was based on empirical results on *Drosophila*. Unfortunately, we do not have such results for *Pegomya*, and it cannot now be concluded whether the agreement between Shorrocks & Rosewell's (1986) prediction and our observations on guild size is more than a coincidence. Further development of this theory for many species and its quantitative testing are major challenges for insect ecologists.

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