

Effects of Parasitoid Community Structure upon the Population Dynamics of the Honeysuckle Leafminer, *Chromatomyia suikazuræ* (Diptera: Agromyzidae)

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Abstract. Population dynamics of a leafminer, *Chromatomyia suikazuræ* (Agromyzidae, Diptera) and its parasitoid community were studied for ten years at seven natural populations along an altitudinal gradient in Japan. This species which mines leaves of a forest shrub, *Lonicera gracilipes* (Caprifoliaceae), was attacked by 25 hymenopterous parasitoid species. Annually, the parasitoid community structure varied less within a population than among populations. The seven parasitoid communities were clustered into three groups corresponding to the altitudinal gradient: (a) lowland communities dominated by late-attacking, generalist pupal idiobiont eulophids and with highest species diversity, (b) hillside communities dominated by an early-attacking, specialist larval-pupal koinobiont braconid and (c) highland communities dominated by an early-attacking, generalist larval idiobiont eulophid. Annual changes of the host larval densities among the local populations were largely synchronous rather than cyclic. Among these populations, host density levels and mortality patterns greatly varied. By analyzing these inter-population differences of host mortality patterns, the following conclusions were drawn: (1) The host mortality patterns were determined by the host utilization patterns of the locally dominant species. (2) The host pupal mortality but not larval mortality was related to species diversity but not to species richness itself of each parasitoid community. (3) Density dependence was detected only in pupal mortality at a lowland population dominated by late-attacking pupal parasitoids. These results suggest that interspecific interactions of parasitoids add additive effects to host population dynamics dissimilarly among local populations with different parasitoid communities.

Key words: parasitoid community, altitudinal gradient, population dynamics, leafminer, density-dependence.

Introduction

Endophytic herbivores are subject to intense attack by many parasitoid species (Askew and Shaw 1986; Hawkins and Lawton 1987; Hespeneide 1991), host ranges of which are broader than parasitoids of exophytic host herbivore species (Hawkins et al. 1990). Species richness of the parasitoid community varies across host species (Hawkins 1990), and the levels of parasitoid species richness are related to structural refuges provided by the plants (Hochberg and Hawkins 1992, 1993, 1995). Within a host herbivore species, in addition, species richness of the parasitoid community differs among host plant species (Askew and Shaw 1974, 1986; Askew 1995; Mills 1995),

among habitats in ecological succession (Price 1973, 1995) and among altitudes (Randall 1982).

It is one of the major problems of population ecology how structure and complexity of parasitoid community influence upon the host population dynamics. This problem is closely related with the consequence of biological control (Mills 1995; Ehler 1995). There has been many theoretical models on dynamics and stability of host-parasitoid systems (cf. Hassell 1978; Hassell and Godfray 1992). Most insect systems, however, are considerably complex, and the degree to which conclusions from simple models can be applied to these more complex systems remains unresolved (Jones et al. 1995) since interactions among natural enemies sometimes result in nonadditive and higher-order effects on herbivore populations (Hurd and Emswiler 1990). A number of recent studies expand-

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ed on single parasitoid-single host systems to include three or more interacting species and examine the population dynamics and community stability of both hosts and parasitoids (Holt and Lawton, 1993; Jones et al. 1995).

Manipulative field experiments are the most elegant and least ambiguous way of quantifying species interactions, but they are also the most difficult to perform (Mills 1995). Another approach to detect the effects of parasitoid community structure upon host population dynamics is long-term field studies at several local populations which harbor differently structured parasitoid communities. Such long-term field studies are, however, very few.

This paper presents the results of a ten-year study of the population dynamics of seven natural local populations of a leafminer species along an altitudinal gradient. The studied leafminer, *Chromatomyia suikazuræ* Saksakawa, 1993, is subject to attack by 25 parasitoid species, responsible for more than 80% of host mortality (Kato 1985, 1994a). A preliminary survey suggested that the leafminer populations along an altitudinal gradient fostered differently-structured species-rich parasitoid communities.

First, in this paper, it is demonstrated that the parasitoid community structure varied more markedly among the populations than annually within a population. The variation corresponded to the altitudes of the seven sites. Secondly, dynamics of the seven local leafminer popula-

tions is described and analyzed. Some differences in host mortality patterns were found among local populations harboring differently structured parasitoid communities. To detect effects of the parasitoid community structure on the host mortality pattern, the following three hypotheses were tested: (1) Resource utilization patterns of locally dominant parasitoid species influence the host mortality patterns. (2) Species richness or species diversity of a parasitoid community affects the host mortality. (3) Parasitoid community structure affect density-dependency of the host mortality.

Materials and methods

The larva of *Chromatomyia suikazuræ* mines in the palisade parenchyma of newly opened leaves of several *Lonicera* species (Caprifoliaceae) (Kato 1985). The larval period lasts about 15 days. The third instar larva pupates in the leaf's spongy parenchyma by making a puparium just inside the lower leaf epidermis. Larvae and pupae, but not eggs, suffer high mortalities, most of which are caused by the parasitoids' attack (parasitism and host-feeding). Disease, predation by organisms other than parasitoid wasps, abscission of mined leaves, and intraspecific competition for food contributed only weakly

Table 1. Location of the seven study sites, arranged in an ascending order of altitude. Size of quadrat, number and density of *Lonicera gracilipes* shrubs, mean (\pm SD, across years) numbers of sampled host plants and leafmines and sampling dates at each site are also indicated

Site code	Locality	Latitude Longitude	Altitude (m)	Size of quadrat (m ²)	Number of host plants per quadrat	Density of host plants per hectare	Mean no. of sampled host plants (range)	Mean no. of sampled leaf-mines (range)	Sampling date
S1	Hino, Uji, Kyoto Prefecture	34°55'N 135°49'E	75	10 × 200	8	40.0	4.2 ± 1.2 (3–7)	1841 ± 1413 (223–3982)	Apr. 24–May 1
S2	Iwakura, Sakyo-ku, Kyoto, Kyoto Pref.	35°5'N 135°47'N	170	100 × 100	90	90.0	33.3 ± 15.8 (13–61)	12121 ± 16483 (1351–22827)	May 6–12
S3	Kibune, Sakyo-ku, Kyoto, Kyoto Pref.	35°8'N 135°46'N	475	20 × 750	5	3.3	2.7 ± 1.3 (2–3)	700 ± 497 (166–1872)	May 14–22
S4	Seryo, Sakyo-ku, Kyoto, Kyoto Pref.	35°9'N 135°45'N	640	60 × 100	7	11.7	2.7 ± 0.7 (2–4)	998 ± 789 (153–2251)	May 15–22
S5	Mt. Hiei, Sakyo-ku, Kyoto Pref.	35°4'N 135°50'N	800	100 × 100	7	7.0	2.9 ± 0.7 (2–4)	2322 ± 1632 (481–5624)	May 16–25
S6	Nakakaruzawa, Kita-saku-gun, Nagano Pref.	36°22'N 138°36'N	1005	10 × 200	12	60.0	2.5 ± 1.1 (1–4)	961 ± 889 (142–2721)	May 26–June 4
S7	Matsubara-ko, Minami-saku-gun, Nagano Pref.	36°3'N 138°27'E	1140	40 × 60	28	116.7	3.8 ± 1.3 (2–7)	1868 ± 1452 (65–5198)	May 26–June 4

to mortality.

Population studies of *Chro. suikazuræ* were carried out at seven sites in Honshu, Japan (Table 1). The five sites in Kyoto Prefecture (S1 to S5) were about 270 km from the two sites in Nagano Pref. (S6 and S7). The altitudes of the sites ranged from 75 to 1140 m above sea level. S1 and S2 were sites covered with secondary natural forests, dominated by deciduous *Quercus* spp., and also containing evergreen *Q. glauca*. *Lonicera gracilipes* shrubs and *L. japonica* vines occurred at the forest floor and the forest margin, respectively. The three sites, S3, S4 and S5, were covered by temperate montane deciduous forests and had much snow in winter. The densities of the host plants were lowest there (Table 1). S6 and S7 in Nagano Prefecture were covered with cool temperate larch forests together with some *Q. mongolica* or *Ulmus davidiana*. On the forest floor at all these sites, *L. gracilipes* was distributed. At some sites, other *Lonicera* species such as *L. morrowii*, *L. maackii*, *L. praefflorens* and *L. vidalii* were also distributed. A quadrat (see Table 1 for size) was set at each site and all *Lonicera* plants in each quadrat were mapped and numbered.

Chromatomyia suikazuræ passes two or three generations on *Lonicera* species. The shrubby deciduous *Lonicera* species flush leaves only in spring, but the climbing evergreen *L. japonica* does so continuously from early spring to fall. Thus, flushing patterns of the *Lonicera* species determine the temporal patterns of resource availability for the leafminer. At S1 and S2, *Chro. suikazuræ* passes two generations on *L. gracilipes* and/or *L. japonica* in spring and one generation on *L. japonica* in autumn (Kato 1985, 1994a). At the other sites, *Chro. suikazuræ* passes the first and the third generations on evergreen *L. japonica* and the second on *L. gracilipes*. At S6 and S7, *L. japonica* was rare and the first and the third generations on *L. japonica* might be spent at warmer sites of lower altitudes nearby. Five *Lonicera* species were utilized by the leafminer for the second generation, but normal development of larvae seemed to be impeded on *L. maackii*, *L. praefflorens* and *L. vidalii*. At every site, the first generation was free from parasitoid attack but the second and third generations were subject to intense parasitoid attack.

Complete stratified sampling of leaf-mines in the second generation (stratified across plants) was made on *L. gracilipes* at the seven sites from 1981 to 1990 (samples at S1 in 1981 and at S7 in 1982 failed). All mined leaves on haphazardly selected plants were sampled from late April to early June (Table 1). The sampling date at each site was adjusted to the season two weeks after the completion of the host's pupation, because a preliminary study at S2 showed that the parasitoid community experience succession through interspecific within-host competition, and that community diversity peaked two weeks after the

pupation of healthy leafminers was completed (Kato 1994a, b). The data in the third week of succession at S2 (Kato 1994b) were used for comparison with other populations. At the time of sampling, the total number of leaves on each sampled shrub was also counted. Total numbers of sampled host plants and leaf-mines are shown in Table 1.

All sampled mined leaves on *L. gracilipes* only were sorted visually by leafminer's stage (first to third instar larvae and pupa) and state (bitten out by predators, removed or intact), and the number of each type was counted. Most leaves contained only a single leaf-mine. If a leaf contained more than one mine, it was cut and sorted separately. The sorted mined leaves were incubated separately in glass bottles (7 cm in diameter, 13 cm in height) covered with parafilm (American Can Company) perforated by a pin. The number of perforations was regulated to keep appropriate moisture. This incubation method, which provided the best conditions for development of both hosts and parasitoids, had been established in a preliminary study in 1980. Parasitoid emergence started one week after sampling and continued until September. After October, when all host flies and parasitoids had emerged, their numbers were counted separately by species and sex.

The relative frequency of parasitoid numbers for each species were used as variables for principal component analysis and cluster analysis (Ward's method) of parasitoid community structure. The leafminer density per leaf was estimated by dividing the number of sampled leafminers by the total number of leaves of sampled plants. To analyze the population dynamics of this species, densities were converted to their logarithm. The density-dependence of larval and pupal mortalities was tested by applying the logistic regression of Hails and Crawley (1992). The proportion of leafminers that died (p) was transformed into the odds-ratio, $\log[p/(1-p)]$, by assuming a binomial distribution of sampling error, and regressed against \log host density.

In order to examine the effect of climate on population dynamics, I obtained meteorological data from two locations in Kyoto and Nagano Prefectures. The former location is the Kamigamo Experimental Forest of Kyoto University (35°4.2'N, 135°46.1'E, alt. 135 m) 3.3 km southwest of S2 (Kyoto University Forest 1981–1990), and the latter is the Karuizawa Meteorological Station (36°20.3'N, 138°33.0'E, alt. 999 m) 4.1 km southwest of S6 (Nagano Prefectural Meteorological Station 1981–1990).

Results

Parasitoid community structure

Twenty-five species of hymenopterous parasitoids were

reared from the seven *Chro. suikazurae* populations; three braconids, three pteromalids and 19 eulophids (Table 2). The three braconids were solitary larval-pupal koinobionts, which lay eggs in the host larva. The hatched parasitoid larva feeds on the growing host larva without killing it until just after pupation, and the adult emerges from the host pupa. The three pteromalids were solitary pupal idiobionts. All eulophids but one were solitary idiobionts; the exception was a gregarious idiobiont,

Tetrastichus sp. 5, which laid 4.0 eggs per host on an average. Of the 19 eulophids, five species were pupal parasitoids, nine were larval parasitoids and five of them attacked host larvae and occasionally pupae. While most parasitoid species were polyphagous on various taxa of leafminers, *Opius katoei* was specific to *Chro. suikazurae* and related agromyzid species, and *Chrysocharis pubens* was restricted to agromyzid pupae.

Although the overall parasitoid faunae were largely

Table 2. A list of parasitoid wasp species which emerged from *Chromatomyia loniceriae*, and some ecological attributes of parasitism. Relative abundance of parasitoid species in the annual mean percentage in seven local populations and Shannon diversity index (H') of the parasitoid community are also shown.

SUBORDER Family Subfamily	Code	Species	Mode of parasitism ^a	Host stages of oviposition/ emergence ^b	Mean % of emerged wasps						
					Site						
					S1	S2	S3	S4	S5	S6	S7
ICHNEUMONOIDEA											
Braconidae											
Opiinae	1	<i>Opius katoei</i> Fischer	K	L/P	18.82	11.82	52.45	53.00	11.96	7.37	2.31
Alysiinae	2	<i>Dapsilarthra</i> sp.	K	L/P	9.38	0.38	0.73	1.64	2.80	0.15	0.01
	3	<i>Dacnusa nipponica</i> Takada	K	L/P	0.10	0.18	6.73	1.32	0.27	1.80	0.92
CHALCIDOIDEA											
Pteromalidae											
Miscogasterinae	4	<i>Sphaeripalpus</i> sp.	I	P/P	0.00	0.38	0.73	4.96	0.38	0.29	2.20
	5	<i>Merismus</i> sp.	I	P/P	0.73	0.04	0.49	3.48	2.26	3.31	3.05
	6	<i>Halticoptera</i> sp.	I	P/P	0.00	0.46	0.00	0.00	0.00	0.00	0.06
Eulophidae											
Elachertinae	7	<i>Cirrospilus diallus</i> Walker	I	L/L(P/P)	0.31	1.16	0.30	0.40	10.06	0.45	1.51
Eulophinae	8	<i>Diglyphus minoens</i> (Walker)	I	L/L	4.23	12.41	4.66	15.76	37.65	62.17	72.17
	9	<i>Pnigalio katonis</i> (Ishii)	I	L/L(P/P)	4.89	0.67	1.02	4.74	0.34	0.46	0.08
	10	<i>Pnigalio</i> sp.	I	L/L	1.73	0.42	2.01	0.30	0.16	1.34	0.29
Tetrastichinae	11	<i>Tetrastichus</i> sp. 1	I	L/L	0.42	1.14	0.01	0.14	0.03	0.06	0.04
	12	<i>T.</i> sp. 2	I	L/L	1.15	2.08	0.00	0.18	0.07	0.05	0.02
	13	<i>T.</i> sp. 3	I	L/L	0.87	0.86	0.00	0.04	0.02	0.49	0.00
	14	<i>T.</i> sp. 4	I	L/L	0.00	0.05	0.42	0.09	1.41	0.61	1.08
	15	<i>T.</i> sp. 5	I	P/P	0.44	8.30	0.02	0.11	0.00	0.10	0.18
	16	<i>T.</i> sp. 6	I	L/L	0.51	0.00	0.00	0.00	0.72	0.01	0.26
Entedontinae	17	<i>Chrysocharis pubens</i> (Delucchi)	I	P/P	21.11	26.16	19.97	4.71	10.77	1.69	1.16
	18	<i>C. phryne</i> (Walker)	I	P/P	6.51	3.17	0.16	2.23	5.47	8.89	5.54
	19	<i>C. pentheus</i> (Walker)	I	L/L	23.72	26.44	5.32	4.61	13.22	2.30	2.09
	20	<i>C. albipes</i> (Ashmead)	I	L/L(P/P)	0.01	0.03	0.54	0.61	1.89	1.28	0.78
	21	<i>C. ujiyei</i> Kamijo	I	L/L(P/P)	0.07	0.08	0.00	0.03	0.15	3.84	1.06
	22	<i>Cotterellia japonica</i> Kamijo	I	P/P	0.04	0.40	0.00	0.00	0.00	0.13	0.12
	23	<i>Closterocerus trifasciatus</i> Westwood	I	L/L(P/P)	0.52	1.60	0.31	0.20	0.28	0.54	4.47
	24	<i>Teleopteris erxias</i> (Walker)	I	L/L	2.35	0.78	4.14	1.47	0.37	0.26	0.04
	25	<i>Pediobius acantha</i> (Walker)	I	P/P	1.33	1.12	0.00	0.00	0.00	1.49	0.32
Shannon diversity index (H') of annual mean parasitoid community					3.17	3.04	2.37	2.53	2.93	2.28	1.86
Annual mean of Shannon diversity index (H') of yearly parasitoid communities					2.62	2.70	1.84	1.86	2.42	1.95	1.57

^a I, idiobiont; K, koinobiont.

^b L, larva; P, pupa.

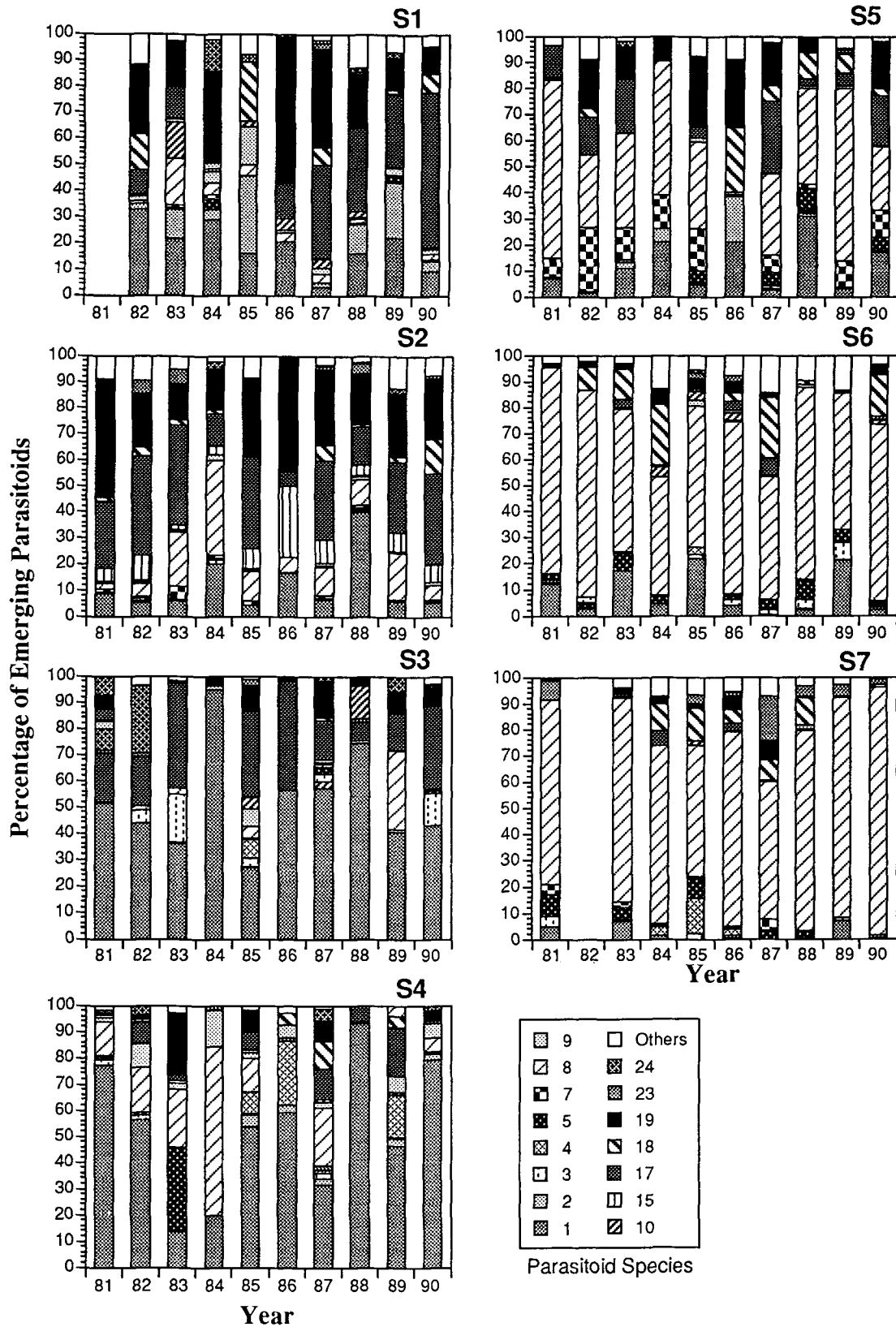


Fig. 1. Ten-year changes in composition of parasitoid species emerging from *Chromatomyia suikazurae* leaf-mines sampled at seven local populations. Parasitoid species codes are shown in Table 2.

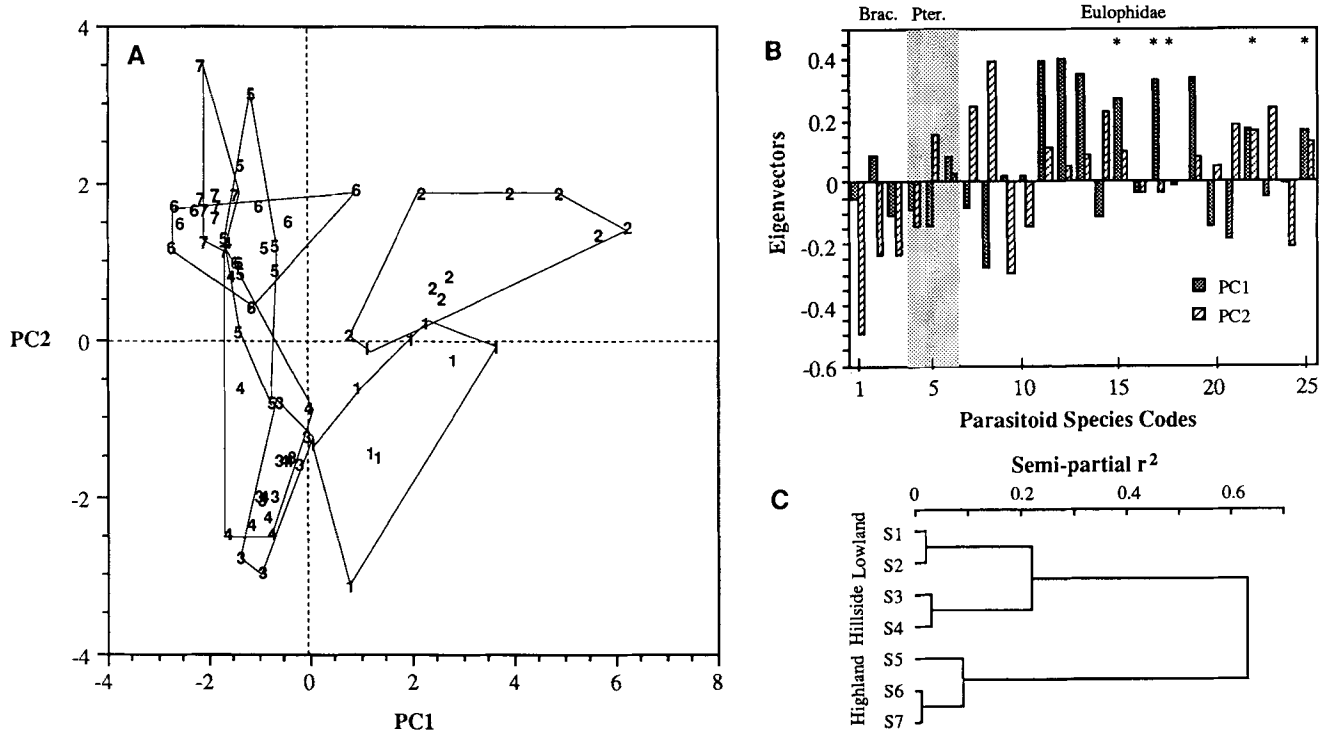


Fig. 2. Analyses of parasitoid community structure of *Chromatomyia suikazuriae*. A, A result of a principal component analysis on parasitoid communities at seven populations. Plots of the first and the second principal components are shown by site code number. B, Eigenvectors of 25 parasitoid species upon the first and the second primary components (PC1 and PC2) in a primary component analysis on parasitoid communities. Asterisks denote pupal parasitoids. C, Clustering (with Ward's method) of seven parasitoid communities by relative abundance of emerged parasitoids.

similar among the seven local populations, the dominant species varied among the sites (Table 2). The dominant species were *Chry. pubens* and *Chry. pentheus* at S1 and S2, *O. katoii* at S3 and S4, and *Diglyphus minoensis* at S5, S6 and S7. Since sampling intensity varied among sites, the relative abundance of rare parasitoids may be biased. Figure 1 shows ten-year changes in the relative abundance of parasitoids which emerged at the seven populations. The Shannon diversity indices of yearly parasitoid communities at S1, S2 and S5 were significantly higher than at S3, S4, S6 and S7 (t test of each pair, $df=16-18$, $P < 0.05$) (Table 2).

To detect trends in the variation of parasitoid communities, a principal component analysis on the parasitoid communities was carried out. The variables used for the analysis were the relative abundance of emerged parasitoids, as shown in Fig. 1. Two principal components (PC1 and PC2) accounted for 24.8% of the standardized variance and three components explained 32.9%. Figure 2B shows the loadings of each parasitoid species on the two primary components. PC1 had high positive loadings on *Chry. pubens*, *Chry. pentheus* and most *Tetrastichus* spp. and high negative loadings on *D. minoensis*. PC2 shows high positive loadings on *D.*

minoensis and *Cirrospilus diallus* and high negative loadings on *O. katoii* and *Pnigalio katonis*.

Figure 2A shows that scatter plots of parasitoid communities of the same population gathered on axes of PC1 and PC2. S1 and S2, with positive loadings on PC1, are characterized by the dominance of *Chry. pubens*, *Chry. pentheus* and *Tetrastichus* spp. and a scarcity of *D. minoensis*. S3 and S4, with negative loadings on both PC1 and PC2, are characterized by the dominance of *O. katoii*. S6 and S7, with negative loadings on PC1 and positive loadings on PC2, are characterized by the dominance of *D. minoensis*. S5 was intermediate between the latter two groups. Inter-population means of annual within-population variances of PC1 and PC2 were 0.951 ± 1.214 (± 1 SD) and 0.752 ± 0.438 , respectively, which were significantly less than the annual means of inter-population variances (4.404 ± 2.496 and 2.988 ± 0.848 , respectively) (PC1, $t=3.78$, $P < 0.005$, $df=13$; PC2, $t=7.10$, $P < 0.001$, $df=13$).

By a cluster analysis of relative abundance of emerged parasitoid species in the annual mean percentage (with Ward's method), three clusters were detected at 0.22 in semi-partial r^2 (Fig. 2C). These clusters corresponded to the altitudes of the sites. Hereafter, the three clusters are referred to as lowland (S1 and S2), hillside (S3 and S4) and

highland populations (S5, S6 and S7).

From the standpoint of parasitoid resource utilization patterns, the parasitoid species can be grouped into three categories: larval (idiobiont eulophids), larval-pupal (koinobiont braconids) and pupal parasitoids (idiobiont eulophids and pteromalids). The comparisons from this standpoint suggest that (1) the percentage of larval-pupal parasitoids was significantly higher at S3 and S4 than at other sites (t -test, $df=16-18$, $P<0.05$), (2) the percentage of larval parasitoids was higher at S6 and S7 than at other sites excluding S5 (t -test, $df=16-18$, $P<0.05$), (3) the percentage of pupal parasitoids was higher at S1 and S2 than at other sites excluding S5 (t -test, $df=16-18$, $P<0.05$), and (4) parasitoid communities at S3, S4, S6 and S7 were dominated by early attackers, i.e., braconids and *D. minoews*.

The mean annual emergence rate (i.e., the number of emerging parasitoids divided by the number of killed host leaf-miners) was highest at S3 ($51.0\pm 4.8\%$, mean ± 1 SD), followed by S4 ($48.3\pm 5.6\%$), S2 ($46.9\pm 2.4\%$), S5 ($43.1\pm 4.6\%$), S7 ($42.5\pm 4.4\%$), S6 ($39.3\pm 3.8\%$) and S1 ($38.0\pm 4.3\%$); each pair of sites did not significantly differ

(t -test, $df=16-18$, $P>0.05$). No significant correlation was detected between the mean annual emergence rate and the host larval density at each site (F -test, $df=9$, $P>0.05$).

Host population dynamics

These analyses suggested that annually the parasitoid community structure varied less within a population than among populations. Thus, the author now addresses the problem as to whether the inter-population differences of parasitoid community structure result in differences in host population dynamics.

Ten-year changes in log number of host larvae, pupae and emerging adult flies per 1,000 leaves of *L. gracilipes* at seven sites are shown with annually averaged parasitoid food webs in Fig. 3. The emerging adult densities at S3, S4 and S5 were very low or zero, suggesting that local extinction sometimes occurred at these sites. Log larval density reached 2.75 in 1988 at S6 and 2.64 in 1988 at S5, suggesting 56.2% and 43.7% of the total leaves were mined, respectively. The annual-mean log density was highest at S6 (2.25, suggesting 17.8% of leaves were mined) and

Table 3. Results of two-way analysis of variance comparing densities and mortalities across ten years and three site clusters of study sites.

Dependent variables	Source of variation	df	SS	F	P
Log larval density	Year	9	8.225	7.840	<0.0001
	Altitude	2	6.691	28.690	<0.0001
	Year \times Altitude	18	2.908	1.390	ns
	Error	38	4.431		
Log pupal density	Year	9	6.434	3.701	<0.005
	Altitude	2	3.039	7.867	<0.005
	Year \times Altitude	18	3.142	0.904	ns
	Error	38	7.340		
Log adult density	Year	9	2.132	0.810	ns
	Altitude	1	13.908	47.577	<0.0001
	Year \times Altitude	9	7.261	2.760	<0.05
	Error	17	4.970		
Log larval mortality	Year	9	0.835	1.471	ns
	Altitude	2	2.155	17.083	<0.0001
	Year \times Altitude	18	0.931	0.820	ns
	Error	38	2.397		
Log pupal mortality	Year	9	3.621	1.380	ns
	Altitude	1	5.578	19.136	<0.0005
	Year \times Altitude	9	4.442	1.693	ns
	Error	17	4.952		
Log mortality	Year	9	5.701	2.117	ns
	Altitude	1	1.935	6.473	<0.05
	Year \times Altitude	9	7.697	2.861	<0.05
	Error	17	5.082		

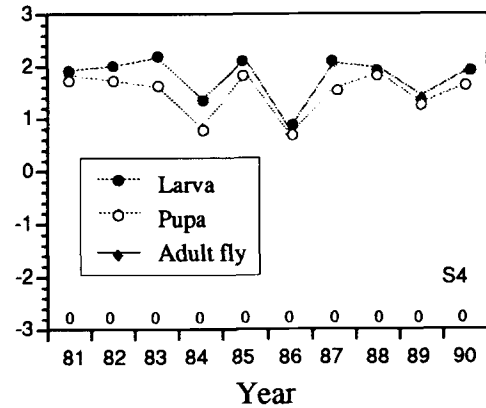
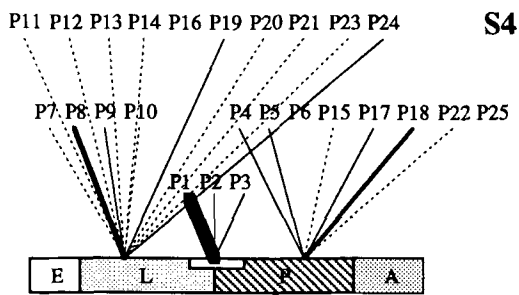
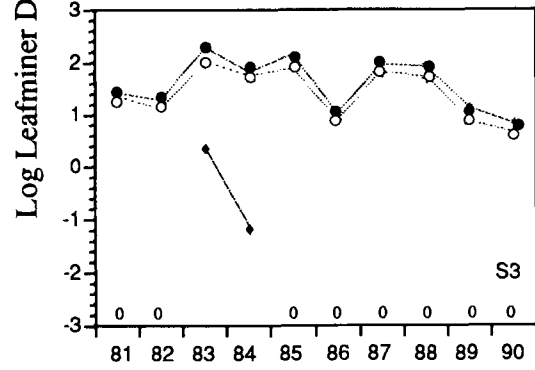
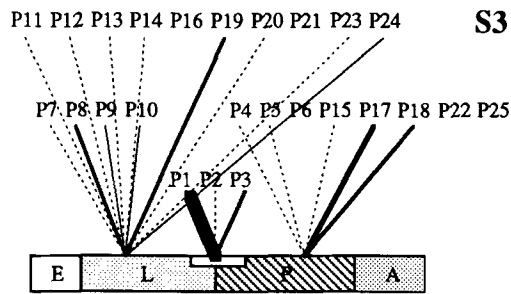
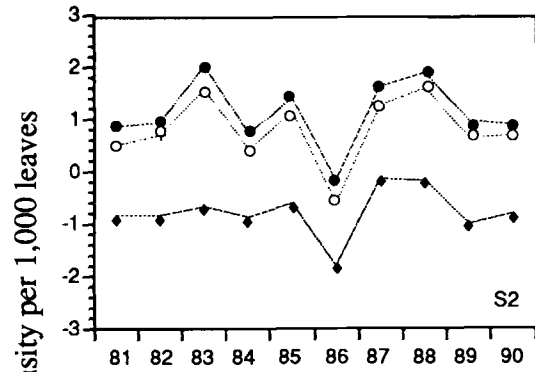
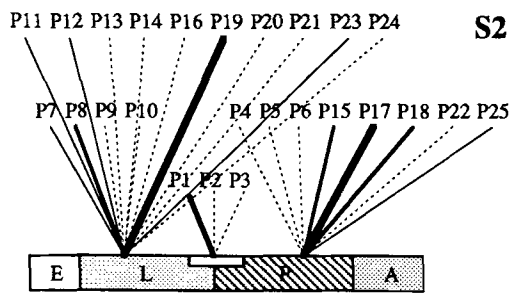
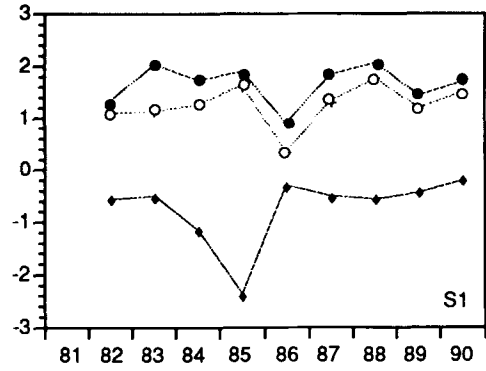
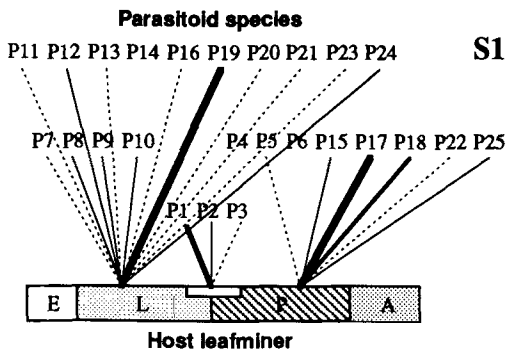


Fig. 3.

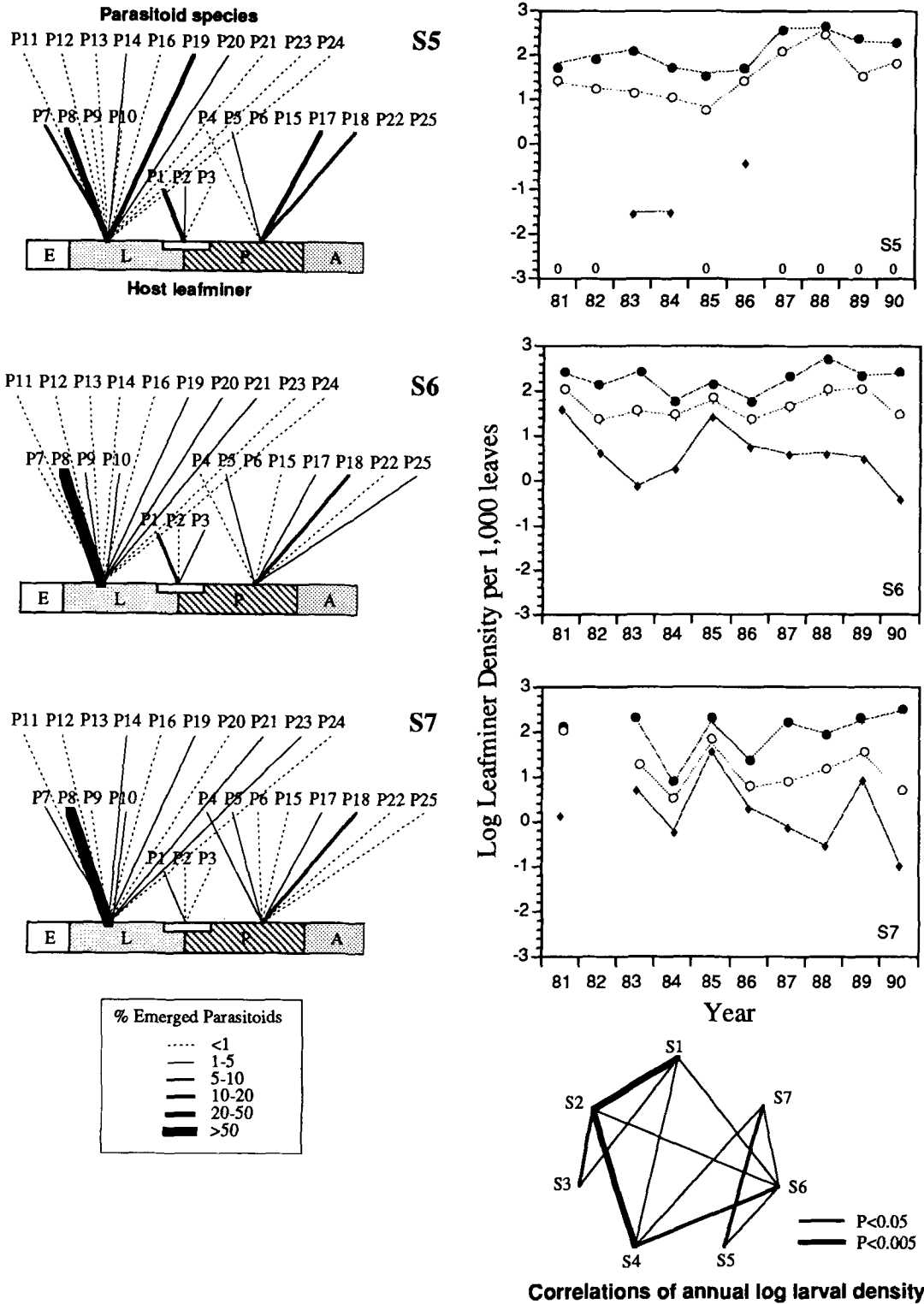


Fig. 3. Annually averaged parasitoid food webs (left) and ten-year changes in log densities of larvae, pupae and adults of *Chromatomyia suikazuræ* per 1,000 *Lonicera gracilipes* leaves (right) at seven local populations. Parasitoid species utilized larvae (L), pupae (P) or both, but did not utilize eggs (E) and adults (A). Absence of adult fly emergence is shown by zero. At S3, S4 and S5, emergence of adult flies was not observed in most years. The diagram in the bottom right represents correlations of annual log larval density among seven local populations. Significant correlations are shown by solid lines.

lowest at S2 (1.11, suggesting 1.29%). Host larval and pupal densities varied significantly across years and across the three altitudes (Table 3). In general, larval density was highest at highland sites, and lowest at lowland sites. This altitudinal trend was obscured by pupal density. Host adult density varied significantly across the three altitudes but not across years (Table 3). Emerging adult density was significantly higher at highlands than at lowlands. The variances of population fluctuations did not significantly differ among the populations (F test, $df=7-8$, $P>0.05$) except for larval density between S2 and S6 ($F=4.95$, $df=8$, $P<0.05$).

The population fluctuations did not show clear cycles (Fig. 3) unlike those found in some lepidopteran herbivores in coniferous forests (e.g., Royama 1984; Turchin 1990; Swetnam and Lynch 1993). Significant correlations in larval densities among populations were detected, as shown in Fig. 3. Population fluctuations were more synchronous between closer populations. The larval density of the second generation at S2 had a high correlation with that of the first generation, which had the highest correlation with the monthly mean of daily maximum temperature in February (Kato 1994a). The larval density at S6 had a higher correlation with the monthly mean of maximum daily temperature in March ($r=0.381$, but not significant, $t=1.165$, $P>0.05$) than in February ($r=$

0.040), April ($r=0.307$) and May ($r=0.091$). The monthly mean of maximum daily temperature in February at S2 had a significant correlation with that in March in S6 ($t=3.393$, $P<0.01$, $r=0.768$) but not with that in February ($t=1.255$, $P>0.05$, $r=0.406$). Both February in S2 and March in S6 correspond to the seasons of the first generation of this leafminer.

Figure 4 shows changes in total and partial log mortalities (k_1-k_3 , k_p) of *Chro. suikazuræ* at four local populations (S1, S2, S6 and S7). Mortalities of 1st- and 2nd-instars were generally much lower than those of 3rd-instars. The total log mortality K varied greatly; the annual-maximum amplitude was largest in S7 (2.6), followed by S1 (2.5), S6 (2.0) and S2 (1.4). These k -values of larval, pupal and total mortalities varied significantly across the three altitudes (Table 3). In general, larval mortality was highest at highland sites, followed by lowland and hillside sites. In contrast, pupal and total mortalities were higher at lowland than at highland sites. The larval mortality at S3, where the parasitoid community was dominated by a koinobiont braconids, was significantly lower than at all other populations.

Effects of parasitoid community structure

To detect the effects of parasitoid community structure

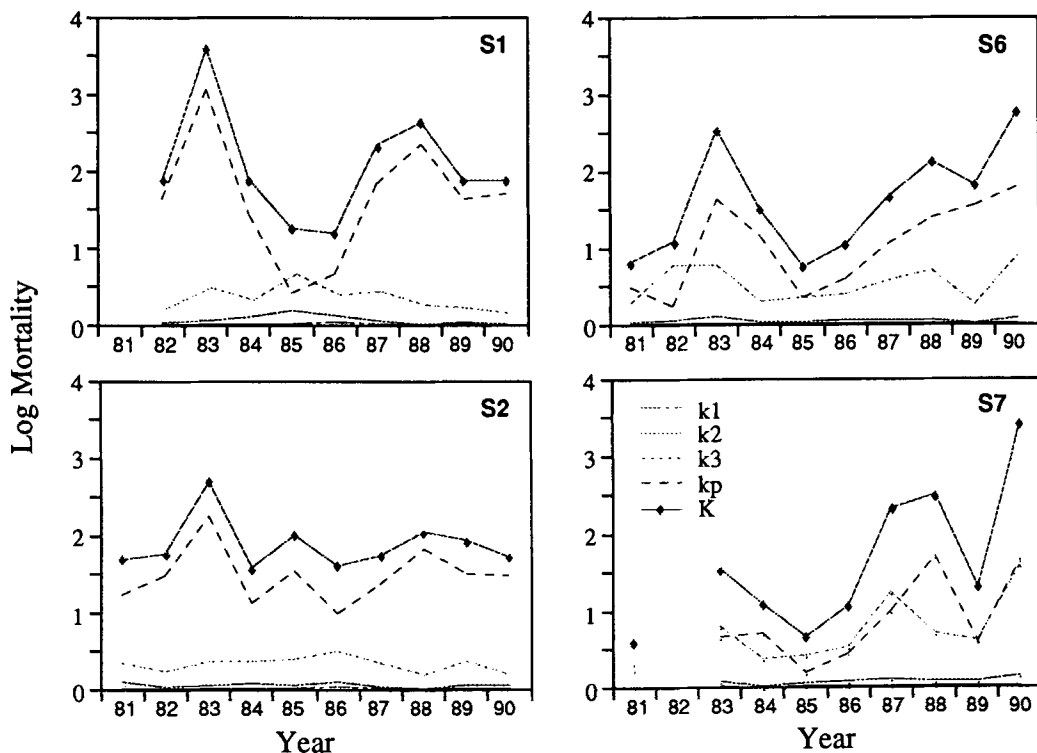


Fig. 4. Changes in log mortalities of 1st–3rd instar larvae and pupae of *Chromatomyia suikazuræ* at four sites (S1, S2, S6 and S7). K , total mortality; k_p , pupal mortality; k_{1-3} , 1st–3rd instar larval mortalities.

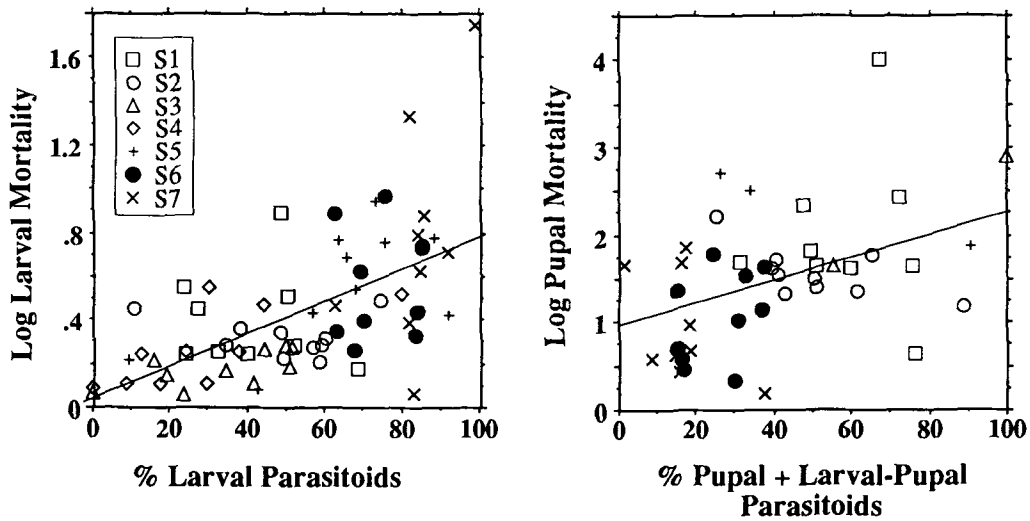


Fig. 5. A relationship of log larval mortality against percentage of emerged larval parasitoids (left) and a relationship of log pupal mortality against percentage of pupal and larval-pupal parasitoids (right). The regression lines are $y=0.044+0.007x$ ($r=0.606$) and $y=0.982+0.013x$ ($r=0.410$), respectively.

upon host population dynamics, the following three hypotheses were tested. The first hypothesis is that resource utilization patterns of locally dominant parasitoid species influence host mortality patterns. Log larval mortality had a significant correlation with the percentage of larval parasitoids in total emerging parasitoids (F -test, $df=66$, $F=38.4$, $P<0.0001$, Fig. 5). Log pupal mortality had a significant correlation with the percentage of pupal and larval-pupal parasitoids (F -test, $df=41$, $F=8.3$, $P<0.01$, Fig. 5). Thus, this hypothesis was confirmed.

The second hypothesis is that species richness or species diversity of a parasitoid community affects the host mortality. No significant correlations were found between larval/pupal mortality and species richness of each para-

sitoid community (F -test, $df=66$, $P>0.05$). A significant correlation was found between log pupal mortality and Shannon diversity index, H' (F -test, $df=36$, $F=7.2$, $P<0.05$, Fig. 6), but not between log larval mortality and H' (S3, S4 and S5 were excluded in this analysis; F -test, $df=66$, $F=1.2$, $P>0.05$, Fig. 6). These results suggest that the species diversity of the parasitoid community is related to host pupal mortality.

The third hypothesis is that parasitoid community structure affects density-dependency of host mortality. Density-dependence of larval and pupal mortalities was tested with logistic regression (Hails and Crawley 1992). Analyses of annual sequential data suggested that larval mortalities were not significantly density-dependent within the populations; correlations between the log-odd ratio

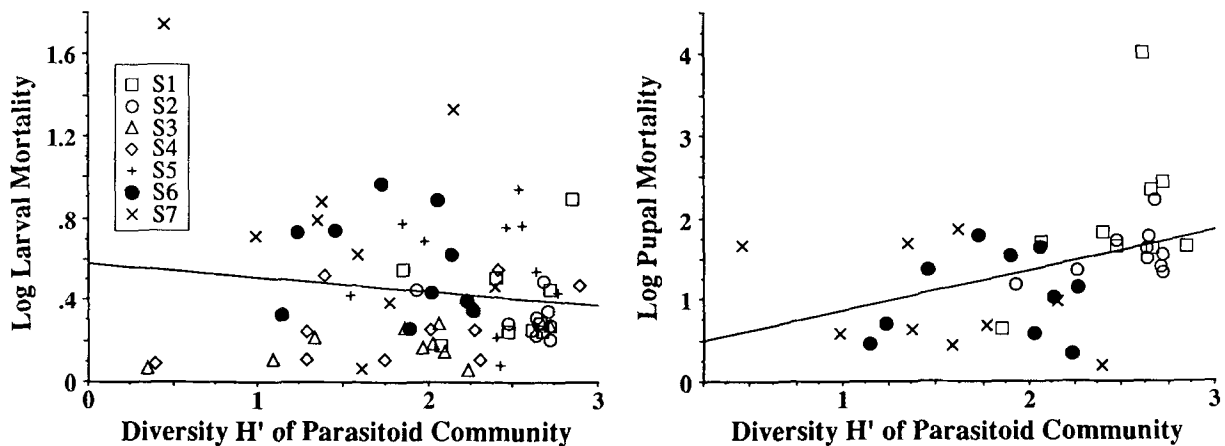


Fig. 6. Relationships of log larval and pupal mortality against Shannon diversity index (H') of parasitoid community. The regression lines are $y=0.573-0.068x$ ($r=0.132$) and $y=0.938+0.275x$ ($r=0.409$), respectively.

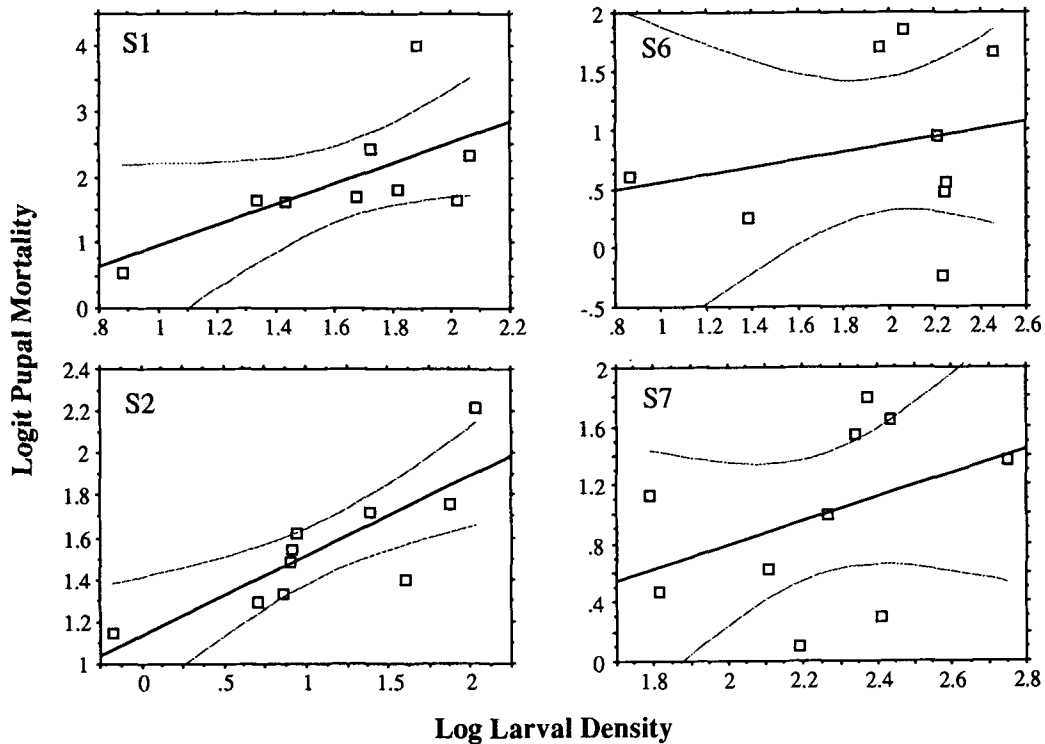


Fig. 7. Relationships between the log-odd ratio (=logit) of pupal mortality and log larval density at four sites. Maximum likelihood regression equations are: S1, $y=1.577x-0.628$, $r^2=0.404$, $t=2.179$, $P>0.05$; S2, $y=0.38x+1.129$, $r^2=0.655$, $t=3.901$, $P<0.05$; S6, $y=0.813x-0.833$, $r^2=0.156$, $t=1.217$, $P>0.05$; S7, $y=0.314x+0.248$, $r^2=0.049$, $t=0.601$, $P>0.05$.

(=logit) of larval mortality and log larval density were not significant at seven sites ($P>0.05$). For pupal mortality, significant temporal density-dependence was detected only at S2 where the Shannon diversity index of parasitoid community and the percentage of late-attacking pupal parasitoids were highest ($r^2=0.655$, $t=3.901$, $P<0.05$; Fig. 7). These results suggest that density-dependency in pupal mortality is related to parasitoid community structure, especially with the species diversity of the parasitoid community or with percentages of late-attacking pupal parasitoids.

Discussion

The seven populations of *Chro. suikazurae* along the altitudinal gradient were associated with differently-structured parasitoid communities (Fig. 1), and the inter-population differences involved species richness and relative frequencies of emerging parasitoids (Table 2). Thus, the dominant parasitoid species of each population differed in family (Braconidae vs. Eulophidae), resource utilization pattern (idiobiont vs. koinobiont), host stage attacked (larva vs. pupa), host range (specialist vs. generalist) and attacking phase in the succession of the

parasitoid community (early-attacker vs. late-attacker). The seven parasitoid communities were clustered into three groups (Fig. 2): (1) lowland communities (S1 and S2) dominated by late-attacking, generalist pupal idiobiont eulophids, (2) hillside communities (S3 and S4) dominated by an early-attacking, specialist larval-pupal koinobiont braconid, and (3) highland communities (S5, S6 and S7) dominated by an early-attacking, generalist larval idiobiont eulophid.

A study (Kato 1994b) on parasitoid community dynamics at S2 showed that the parasitoid community experienced succession through asymmetric interspecific competition even over a few weeks within a generation, and that early-attackers such as *D. minoensis* and *O. katoi* were displaced by late attackers such as *Chry. pentheus* and *Chry. pubens*, respectively. The trend that the early-attackers are displaced by the late-attackers was common to the populations but the rate of displacement seems to be different among the populations. With respect to this displacement process, the parasitoid communities in hillsides and highlands can be regarded as "neotenous" communities dominated by early-attackers. Why were these early-attackers not displaced by late attackers in hillsides and highlands? On hillsides where the host plant density was very low, only a specialist parasitoid, *O. katoi*,

rather than a late-attacking generalist eulophid, would be able to track the highly-scattered host population. In highland populations, since an early-attacking idiobiont larval parasitoid, *D. minoews*, was dominant, the host pupal density was too low to support enough late-attacking, pupal parasitoids.

Apart from the intra-generational process of parasitoid community organization, there should be other factors creating the observed inter-population differences in the parasitoid community structure. One possible factor is climatic conditions. Since parasitoid communities at adjacent altitudes were clustered together, climatic conditions appear to play an important role in organizing the parasitoid communities. Another factor may be local leafminer community structure. Although data are still lacking, the leafminer community at each host population can be an important factor in organizing the parasitoid community, because most parasitoid species are generalists and inevitably must shift host leafminer species throughout the several months when they are active.

Before demonstrating the inter-site differences in population dynamics, I will first summarize the population attributes common to the populations. Host populations suffered most mortalities in the larval and/or pupal stages and the main mortality factor was parasitism. Mortality in the larval stages increased as the larval instar proceeded (Fig. 4). The larval mortalities were temporally density-independent. Populations fluctuated unicyclically and the variances did not significantly differ among populations. Since the larval density was much lower than the number of available leaves (annual-mean percentages of mined leaves ranging from 1.28% in S2 to 17.7% in S6), the populations in the second generation were not resource-limited.

In contrast to these inter-population resemblances, differences of host population dynamics were detected among the populations which harbored differently-structured parasitoid communities. I will now discuss three effects of parasitoid community structure upon host population attributes. First, resource utilization patterns of the dominant parasitoid species (i.e. a pupal idiobiont at lowland, a larval-pupal koinobiont at hillside, and a larval idiobiont at highland) directly influenced the host mortality pattern (Table 2, Fig. 5). Pupal mortality was significantly higher at lowland than at highland sites. Conversely, larval mortality was significantly lower in lowlands and hillsides than in highlands. Thus, the demographic pattern in a parasitoid-active generation was directly determined by the parasitoid community structure rather than by resource availability or intraspecific competition for resource as has been observed in lepidopteran leafminers (Bultman and Faeth 1986; Auerbach 1991; Preszler and Price 1993).

Secondly, host pupal mortality had positive correlations

with species diversity but not with species richness of the parasitoid community itself (Fig. 6). This result suggests that the interspecific interactions had an additive effect on host pupal mortality. This additive effect is considered to be related to the long successional chains of late-attacking pupal parasitoids. The theoretical models of biological control predicted that the addition of a second parasitoid may lead either to a lower host density (May and Hassell 1981) or to a higher host density (Takehashi et al. 1984, Briggs 1993), and this inconsistency resulted from different assumptions on niche and competition properties of parasitoids. Although the detailed mechanisms are still unknown, higher species diversity of parasitoid communities, i.e., higher frequencies of interspecific interactions seem to result in reduction of host densities in natural ecosystems.

Thirdly, density-dependency of host mortality was affected by the parasitoid community structure, especially by the foraging characteristics of the dominant parasitoid species. The late-attacker, *Chry. pubens*, by not only hyperparasitizing early-attackers but also attacking unparasitized host leafminers, was a density-dependent mortality agent at S2 (Kato 1994b). While this species was present at all sites, it acted as a density-dependent agent only at S2. This suggests that the population-regulatory activity of the species was displayed only when it was dominant in the parasitoid community and when its attack was preceded by intense attack of the early-attacker, *O. katoi*. The density-dependence in mortality at S2 was not accompanied by significantly density-dependent parasitism, probably because the host mortality due to the parasitoid's host-feeding and inter-specific within-host competition increases in a density-dependent fashion (Kato 1994a).

Irrespective of these differing effects of the parasitoid community structure on host population dynamics, the host population fluctuations were synchronized (Fig. 3). In the first parasitoid-free generation in early spring, larval density was limited by the number of newly opened leaves and the larval mortality was influenced by the size distribution of the leaves (Kato 1985, 1994a). Since climatic change was largely synchronous among all the populations, the synchronous population fluctuation was thought to originate from synchronous changes in resource availability, which were driven by changes in temperature from February to March.

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