



Title	Quantitative food webs of lepidopteran leafminers and their parasitoids in a Japanese deciduous forest
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1 Title:

2 **Quantitative food webs of lepidopteran leafminers and their parasitoids in a**
3 **Japanese deciduous forest**

4

5 Authors:

6 Toshihide Hirao and Masashi Murakami

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8 Affiliations and addresses:

9 Tomakomai Research Station, Hokkaido University Forests, Tomakomai, Japan

10

11 Address correspondence to:

12 Toshihide Hirao, Tomakomai Research Station, Hokkaido University Forests, Takaoka,

13 Tomakomai, Hokkaido 053-0035, Japan

14 E-mail: hirao@fsc.hokudai.ac.jp; Tel: +81-144-33-2171; Fax: +81-144-33-2173

1 **Abstract** Quantitative food webs were constructed to explore the community structure of
2 leaf-mining moths in the family Gracillariidae and their parasitoid wasps in a deciduous
3 forest in Hokkaido, Japan. A whole food web was constructed from data collected from
4 June to October, 2001. In the web, 16 leafminer species on seven tree species were
5 attacked by 58 species of hymenopteran parasitoid; 376 links between leafminers and
6 parasitoids were observed. Leafminers were specialist herbivores, but most parasitoids
7 were generalists. Five webs were constructed for the seasonal prevalence of leafminers
8 over the 1-year period to reveal the temporal dynamics in community structure. Among
9 the seasonal webs, the first web in June was distinctive because two tree species, Japanese
10 umbrella tree *Magnolia obovata* and Japanese magnolia *M. kobus*, supported the
11 community. Second to fourth webs from July to September were dominated by the
12 leafminer species on Japanese oak *Quercus crispula*, and fifth web was marked by that on
13 *Carpinus cordata*. The extent of potential apparent competition among leafminers was
14 evaluated using quantitative parasitoid overlap diagrams. These diagrams suggested that
15 abundant host species are likely to have large indirect effects on less-abundant species.
16 Moreover, the potential for apparent competition between leafminer species inhabiting
17 the different host tree species can occur, although leafminers sharing the same tree
18 species are prone to interact via shared parasitoids. In this system, particular leafminer
19 species as potential sources of apparent competition can affect other species as sinks, and
20 control whole-community dynamics. Directed apparent competition may potentially
21 occur around oak trees.

22

23 **Keywords** Apparent competition, Community structure, Deciduous forest,
24 Heterogeneity, Source-sink dynamics

1 **Introduction**

2

3 Food webs can be used not only to describe trophic interactions, but also to examine the
4 potential for indirect interactions, such as exploitative or apparent competition (Cohen et
5 al. 1990; Polis and Winemiller 1996). Exploitative competition may occur among
6 predators that share a limited resource, whereas prey species that share a common
7 predator may show apparent competition, which is defined as a reduction in the
8 population density of one prey species when that of another prey species increases, with
9 the interaction mediated by an increase in the predatory species (Holt 1977). Apparent
10 competition can be meaningful in structuring communities, such as host–parasitoid
11 systems, in which resource competition is not predominant (Abrams et al. 1996).
12 Host–parasitoid communities should be especially prone to apparent competition because
13 parasitoids have generation times similar to their hosts, show remarkable responses to
14 changes in host abundance, and constantly regulate host populations below carrying
15 capacity (Holt and Lawton 1993). However, there is little evidence from field studies to
16 support this hypothesis (but see van Nouhuys and Hanski 2000; Morris et al. 2001, 2004).

17 Most early studies of food webs (connectance webs, cf. Rott and Godfray 2000)
18 traced the presence or absence of trophic links between trophospecies (e.g., Cohen et al.
19 1990). On the other hand, some field research constructed food webs that included
20 quantitative information on trophic interactions and provided information on the potential
21 for apparent competition (Memmott et al. 1994; Müller et al. 1999; Rott and Godfray
22 2000; Valladares et al. 2001; Lewis et al. 2002). In host–parasitoid systems, an exact
23 quantitative food web can be constructed relatively easily because trophic interactions are
24 easier to trace.

1 In forest ecosystem, the density of leafminers varies considerably among tree
2 species, which can cause heterogeneity in a quantitative food web structure. Some tree
3 species can be inhabited by abundant leafminers; hence many parasitoids can aggregate
4 on the tree species. Some previous studies shows that the potential for apparent
5 competition between hosts was likely to have asymmetry or directionality in many pairs
6 because one direction of apparent competition was larger than another, and therefore, one
7 host species had a disproportionately greater effect on other hosts via shared parasitoids
8 (Müller et al. 1999; Rott and Godfray 2000; Valladares et al. 2001; Lewis et al. 2002). In
9 addition to the asymmetry of indirect interaction between hosts, Askew and Shaw (1974)
10 constructed semi-quantitative food webs for leafminer–parasitoid communities and then
11 hypothesised that a plant species is important in structuring the parasitoid community.
12 Rott and Godfray (2000) showed that host species sharing the same plant in a temperate
13 forest are likely to interact via shared parasitoids, although Lewis et al. (2002) reported
14 that plant effects were not observed in a tropical forest insect–parasitoid community.
15 These imply the needs for much more examples of quantitative food webs to reveal the
16 robust structures observed in natural communities especially from faunal rich Asian
17 temperate forest, which may help reveal the processes that structure the communities
18 (Valladares et al. 2001).

19 Here, we describe a whole quantitative food web based on Lepidoptera
20 leafminer moths and their hymenopteran parasitoids. We present five seasonal food webs
21 following the seasonal prevalence of leafminers to examine the seasonal dynamics of
22 community structure. Based on these quantitative webs, we assessed the extent to which
23 the potential of apparent competition are likely to occur between leafminer species
24 inhabiting the different host tree species. Then, we constructed parasitoid overlap

1 diagrams to estimate the potential for seasonal apparent competition.

2

3

4 **Methods**

5

6 Study site

7

8 Surveys were performed in a secondary forest re-growth after a clear-cut about 40 years
9 ago located at Tomakomai Experimental Forest (TOEF; 42°43' N, 141°36' E; ca. 90 m
10 a.s.l.), Hokkaido, Japan. This cool-temperate deciduous forest received about 1.2 m of
11 annual precipitation and had an average annual temperature of 5.6°C. Oak (*Quercus*
12 *crispula* Bl.), maple (*Acer mono* Maxim.), and linden (*Tilia japonica* Miq.) dominated the
13 forest. The canopy ranged from 10 to 15 m in height, with saplings of the dominant tree
14 species growing on the forest floor. All of the surveys were conducted within five
15 sampling plots (30 × 30 m) with relatively uniform tree species composition. Deciduous
16 trees broke buds in early to mid-May and shed their leaves in late October. Seven tree
17 species, *A. mono* (Am), *A. palmatum* Thunb. (Ap), *Carpinus cordata* Bl. (Cac), *Magnolia*
18 *obovata* Thunb. (Mo), *M. kobus* DC. (Mk), *Q. crispula* (Qc) and *T. japonica* (Tj), were
19 attacked by lepidopteran leafminers, mainly from the genus *Phyllonorycter*
20 (Gracillariidae, Table 1). Other potential hosts for leafminers in this forest, *Sorbus*
21 *alnifolia* and *Ostrya japonica*, were rarely attacked by Lepidoptera leafmines, and thus,
22 were not examined.

23

24 Food web construction

1

2 The quantitative food web was constructed in three steps. First, the total biomass of
3 leaves for each individual of seven tree species at the site was estimated. The leaf biomass
4 was calculated only once at August 2001. To estimate the biomass of leaves (g dry
5 weight), the diameter at breast height (DBH) was measured in millimetres. The total
6 biomass of leaves was estimated for each tree individual using the allometry of DBH and
7 leaf biomass derived from a neighbouring site in TOEF (Takahashi et al. 1999). In
8 addition, the average leaf biomass per three branches for each tree species in our plots
9 was calculated from 30 randomly chosen branches.

10 The leafminer community was sampled by collecting mines from 903 individual
11 trees within the five sampling plots. For these trees, three branches on three randomly
12 chosen directional positions in the upper canopy were sampled with a pruning hook. All
13 mines collected in the field were taken to the laboratory for rearing. Mines were kept in
14 transparent plastic containers with moistened tissue paper to maintain the proper
15 humidity at ambient air temperature. Emerged adult moths and hymenopteran parasitoids
16 were collected and preserved in dry condition for moths and in 70% ethanol respectively
17 in glass vials. Both leafminer and parasitoid specimens were identified to species and
18 counted. The total numbers of leafminer and parasitoid species on each tree individual
19 were estimated as follows

20

21
$$\frac{\text{sampled number of leafminers or parasitoids}}{\text{leaf biomass per branch}} \times \text{total biomass of leaves in the tree}$$

22

23 This sampling and rearing procedure was performed each month from June to October
24 2001, at 30-day intervals.

1 It was impossible to identify leafminer species from which parasitoids had
2 enclosed, because the pupae were fully consumed by the parasitoid larvae and the species
3 were practically indistinguishable in the shape of the mines only (Kumata personal
4 communication). Therefore, it was assumed that parasitoid species sharing the same plant
5 species had trophic interactions with leafminer species in equal proportion to the
6 abundance of each leafminer species on the shared plant (cf. Rott and Godfray 2000). A
7 summary quantitative food web comprising the total numbers of leafminer and parasitoid
8 individuals, and five monthly food webs corresponding to the five sampling periods, were
9 constructed.

10 In most parasitoid species, one parasitoid individual emerged per mine, but
11 *Holcothorax* sp. was a polyembryonic species, and multiple parasitism was observed in
12 *Achrysocharoides* species. The number of emerged individuals per host leafminer was
13 about six for *Holcothorax* sp. and about three for *Achrysocharoides*. In the present study,
14 the webs were constructed with the density of parasitoids measured in units of either
15 numbers of individuals (see Rott and Godfray 2000).

16

17 Potential for apparent competition

18

19 A necessary condition for apparent competition between two hosts to occur is that the two
20 species are sharing natural enemies. Different host leafminer species are linked using a
21 quantitative measure, d_{ij} , representing the probability that a parasitoid attacking species i
22 potentially developed on species j . It is assumed that adult parasitoids disperse within the
23 site prior to ovipositing, and that parasitoid species are not biased by host species race.
24 The quantitative index, d_{ij} , for each pair of leafminer species in generation t is calculated

1 as

2

$$3 \quad d_{ij} [t] = \sum_k \left[\frac{\alpha_{ik} [t] \alpha_{jk} [t-1]}{\sum_l \alpha_{il} [t] \sum_m \alpha_{mk} [t-1]} \right]$$

4

5 where $\alpha_{ik}[t]$ is the strength of the link between host i and parasitoid k in the food web in
6 generation t . The sums of k and l include all parasitoids and that of m includes all hosts.

7 The first quantity within the square brackets represents the relative importance of
8 parasitoid species k for host species i in generation t . The second quantity is the
9 proportion of parasitoid species k that emerged from host species j in the previous
10 generation $t - 1$. When host species i is equal to species j , hence d_{ii} , the index value
11 indicates a fraction of parasitoids from host i developing on the same host species. The
12 extent to which leafminer species were intergenerationally linked was conventionally
13 represented using parasitoid overlap diagrams (Müller et al. 1999). These diagrams
14 consist of a set of vertices, each representing a leafminer species. Two leafminer species
15 are connected by an edge when they share at least one parasitoid species.

16 However, this representation using parasitoid overlap diagrams can be
17 complicated to get information which links are relatively important, when many overlaps
18 are observed. In order to avoid the point, we offer matrix representations of the potential
19 interactions, together with the parasitoid overlap diagram. In the matrix, each row shows
20 species in a focal sampling season, and each column shows species from the previous
21 sampling season. The potential for apparent competition is represented as a monochrome
22 colour gradient corresponding to the quantitative index of the parasitoid overlap. All
23 graphics and computing were performed in the R environment for statistical computing

1 (R Development Core Team 2005).

2

3

4 **Results**

5

6 Structure of tree–leafminer–parasitoid community

7

8 The summary quantitative food web was constructed as a whole community structure
9 using leafminer and parasitoid abundance estimated from all samples (Fig. 1). The web
10 was based on 18733 sampled leafminers and 7 tree species. A total of 16 leafminer
11 species and 58 parasitoid species were represented, and there were 376
12 leafminer–parasitoid links. *Quercus crispula* was the most dominant tree species at the
13 study site (75.5% in leaf biomass), followed by *T. japonica* (9.8%), *A. mono* (7.5%), *C.*
14 *cordata* (3.1%), and *A. palmatum* (1.6%). Both *M. obovata* and *M. kobus* were rare (1.2%
15 and 1.0%, respectively). Four leafminer species were emerged from *Q. crispula*, three
16 from both *A. mono* and *C. cordata*, two from both *A. palmatum* and *M. kobus*, and one
17 from both *T. japonica* and *M. obovata* (Table 1). Of the parasitoid species, 50 belonged to
18 the family Eulophidae, 7 to Braconidae, and 1 to Encyrtidae (Table 1). The leafminer
19 species were completely specialized on the host tree species. The parasitoid species were
20 generalists for leafminers, and one parasitoid species preyed on an average of $6.483 \pm$
21 0.541 host species. The ratio of host to parasitoid species was 0.276. The realised
22 connectance was 0.139.

23

24 Seasonality of leafminer–parasitoid community

1

2 The number of leafminer and parasitoid species changed seasonally throughout the five
3 months from June to October (Fig. 2). The host/parasitoid species ratio also changed
4 seasonally, and was higher in June (0.500) and September (0.480) than in July (0.326),
5 August (0.375), and October (0.257). The realised connectance of the seasonal web was
6 highest in June (0.163) compared to the other months (0.112, 0.143, 0.137, and 0.147 for
7 July–October, respectively). These findings indicate that distinctive assemblages were
8 organised in early summer (June) and autumn (September and October) because the early
9 summer web was dominated by leafminer species on *M. obovata* and *M. kobus*, whereas
10 in the autumn webs the abundance of leafminer species on *C. cordata* was
11 disproportionately enhanced in the autumn webs.

12

13 Potential for apparent competition

14

15 The potential for apparent competition was represented as a monochrome colour gradient
16 (Fig. 3) corresponding to the quantitative index of the parasitoid overlap, d_{ij} , between 0
17 (no potential) and 1 (maximum potential). In the quantitative parasitoid overlap diagram
18 (Fig. 4) of early summer (June–July), the majority of parasitoids attacking leafminer
19 species on *M. obovata* tended to have developed on the same host species, which likely
20 played a role as a major source of parasitoids attacking other host species (Figs. 3a, 4a).
21 According to the overlap diagrams of subsequent seasons (July–August,
22 August–September and September–October), leafminer species on *Q. crispula* were
23 likely the predominant source of parasitoids attacking other host species (Figs. 3b–d,
24 4b–d). On the other hand, leafminer species *Phyllonorycter issikii* (Kumata) on *T.*

1 *japonica* was relatively specialised by the parasitoid species on that tree species (Figs.
2 3b–d, 4b–d).

3

4

5 **Discussion**

6

7 We constructed and described a summary quantitative food web of a community structure
8 including 16 leafminer species and 58 parasitoid species. Parasitoid diversity was higher
9 than that observed in previous work on leafminer–parasitoid communities in temperate
10 forests (Rott and Godfray 2000). The connectance of the seasonal webs ranged from
11 0.112 to 0.163 (average of 0.140 ± 0.008). These values are lower than those in review of
12 terrestrial food webs (mean of 0.31 [Schoenly et al. 1991]), but approximately consistent
13 with those reported by Rott and Godfray (2000) for Lepidoptera leafminers and
14 parasitoids in a temperate deciduous forest (0.13–0.16), which correspond to those in
15 aquatic food webs (mean of 0.14 [Martinez 1992]). At the tree–leafminer trophic level, 16
16 of 253 possible associations were observed (realised connectance of 0.063), reflecting the
17 monophagous feeding of leafminer moths.

18 Leaf biomass and the density of leafminer species differed greatly according to
19 tree species (Fig. 1). These variations create heterogeneity for parasitoids, causing
20 heterogeneous leafminer–parasitoid interactions. In June and October, leafminer species
21 on *M. obovata* and *C. cordata* became disproportionately large, respectively (Fig. 2a, e),
22 whereas in July–September, leafminer species on *Q. crispula* dominated (Fig. 2b–d). This
23 suggests that both the configuration of tree species in space and the phenology of
24 leafminer species may affect the heterogeneity of leafminer–parasitoid interactions, and

1 even the emergence of apparent competition in the community.

2 Regarding the apparent competition between hosts via a shared parasitoid,
3 inferences about dynamic interactions from static quantitative webs provide necessary,
4 but insufficient, evidence to confirm the occurrence of apparent competition. However,
5 we found a great potential for the occurrence of apparent competition, which likely to be
6 caused by a predominant leafminer species on rare species. Although Askew and Shaw
7 (1974) argued that plant species had a major effect on parasitoid fauna, the present study
8 shows that the presence of a common host tree species *Q. crispula* supporting a large
9 population of a parasitoid may strongly affect the rare leafminer species on different host
10 tree species, i.e., asymmetric apparent competition (Müller et al. 1999; Lewis et al. 2002),
11 in which leafminer species, particularly *Phyllonorycter bicinctella* (Matsumura), on *Q.*
12 *crispula* were likely the predominant source of parasitoids attacking other host species.
13 However, we simultaneously found that a subset of our food webs are distinctively
14 compartmentalised, especially on *T. japonica*, which suggested that the parasitoid species
15 on *T. japonica* is rather specialise on the leafminer species, in this case *Phyllonorycter*
16 *issikii*, on that tree species. The bottom-up effect of tree species may apply to the overall
17 community dynamics.

18 The asymmetric apparent competition observed in the parasitoid overlap
19 diagrams suggests the effect of background spatial habitat structure on the dynamics in
20 leafminer and parasitoid community, which would underpin the observed structure of the
21 quantitative food webs. Asymmetric apparent competition may provide insights into the
22 relationship between the horizontal spatial structure of habitats and quantitative food
23 webs. Holt (1996) theoretically highlighted the spatial aspect of apparent competition,
24 and Morris et al. (2005) tried to introduce spatial scale into measurements of the potential

1 for apparent competition. Apparent competition can theoretically occur in space (Holt
2 1996), and spatial perspectives have been considered in recent years (e.g., Bonsall and
3 Hassell 2000; Holt and Barfield 2003). Recently, McCann et al. (2005) also argued that
4 the spatial structure of food webs affects their stability. If two hosts share a common
5 parasitoid, but occur on spatially isolated plants that rarely grow in close proximity, the
6 opportunities for apparent competition between these herbivores may be substantially
7 diminished (Morris et al. 2005). In our system, individual trees can be regarded as
8 habitats for leafminer–parasitoid assemblages. If asymmetric apparent competition
9 between leafminer species occurs via a shared parasitoid, it is expected that adult
10 parasitoids would disperse from tree species on which the predominant leafminer species
11 feeds to other tree species. Assuming that tree species show no biased distributions in the
12 forest, parasitism would aggregate around individual trees of species preferred by the
13 predominant host. The spatial aggregation of ecological events like this has been called
14 “spillover predation” (e.g., Lidicker 2000; Kristan and Boarman 2003; Power and
15 Mitchell 2004), which is *sense lato* allochthonous input intensively studied in the
16 context of food webs (e.g., Polis et al. 1997). The spatial aggregation of parasitism or
17 spillover-like parasitism from predominant patches to other patches has been suggested in
18 host–parasitoid systems (Brodmann et al. 1997; Maron and Harrison 1997).

19 Quantitative food webs and parasitoid overlap diagrams offer promise for future
20 studies. Because quantitative food webs have been constructed using standardised
21 methods based on Müller et al. (1999) in a variety of communities and climates (e.g., Rott
22 and Godfray 2000; Valladares et al. 2001; Lewis et al. 2002), comparing these food webs
23 would offer an opportunity to study geographic variation in the potential for apparent
24 competition and macroecological patterns in food web structure. Furthermore, we

1 hypothesise that parasitism would aggregate around the plant species on which each host
2 species specialises, and in particular, around individuals of a plant species preferred by
3 the predominant host species in the community, where there is a potential for asymmetric
4 apparent competition to occur. The spatial pattern of parasitism in host–parasitoid
5 communities with spatially structured habitats (e.g., tree species) with a potential for
6 asymmetric apparent competition deserves to be investigated in detail. Approaches to
7 link spatial perspectives to the analysis of quantitative food webs may afford new insights
8 into food web ecology.

9
10

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16
17

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1 Figure legends

2

3 **Fig. 1** Summary quantitative web using pooled data from the whole study period. The
4 three series of black bars represent leaf biomass (bottom), leafminer abundance (middle),
5 and parasitoid abundance (top), drawn at different scales. The code numbers for species
6 interactions are listed in Table 1. The length of edge in links between leafminers and
7 parasitoids illustrate the relative strength of each leafminer–parasitoid interaction.

8

9 **Fig. 2** Seasonal quantitative webs for (a) June, (b) July, (c) August, (d) September, and (e)
10 October, corresponding to turnover of leafminer species. The webs were constructed as in
11 Fig. 1, and the arrangement of species is retained.

12

13 **Fig. 3** Matrix representation of the potential interactions between leafminer species. (a)
14 June–July; (b) July–August; (c) August–September; (d) September–October. Each row
15 shows species in a focal sampling season, and each column shows species from the
16 previous sampling season. The potential for apparent competition is represented as a
17 monochrome colour gradient corresponding to the quantitative index of the parasitoid
18 overlap, d_{ij} , between 0 (no potential) and 1 (maximum potential). Full black squares
19 represent maximum potential interaction between two corresponding species, whereas
20 complete white squares show no potential interaction between leafminer species. Species
21 code numbers are listed in Table 1.

22

23 **Fig. 4** Quantitative parasitoid overlap diagrams. (a) June–July; (b) July–August; (c)
24 August–September; (d) September–October. The numbered vertices show leafminer

1 species; circle sizes indicate the contribution of the focal leafminer species as a source of
2 its own parasitoids. Polygons between leafminer species denote shared parasitoid
3 numbers, where the width of the link at each species represents the potential effect
4 derived from another leafminer species as a source of parasitoids. Species code numbers
5 are listed in Table 1.

1 **Table 1** Summary of observed species and trophic interactions. The leafminer species (Lepidoptera: Gracillariidae) are listed across the top
 2 of the table with their code numbers and the tree species on which they feed. The parasitoid species are listed in the left column of the table,
 3 along with the species code number. Asterisks denote observed trophic interactions between leafminer and parasitoid species. The original
 4 species names of abbreviated codes of tree species are *Acer mono* Maxim. (Am), *A. palmatum* Thunb. (Ap), *Carpinus cordata* Bl. (Cac),
 5 *Magnolia obovata* Thunb. (Mo), *M. kobus* DC. (Mk), *Quercus crispula* Bl. (Qc) and *Tilia japonica* Miq. (Tj).

	Am	Ap	Cac	Mk	Mo	Qc	Tj
A. <i>Phyllonorycter jezioniella</i> (Matsumura)							
B. <i>Caloptilia sp.1</i>							
C. <i>Stigmella sp.</i>							
D. <i>Phyllonorycter orientalis</i> (Kumata)							
E. <i>Cameraria nipponica</i> Kumata							
F. <i>Phyllonorycter sp.2</i>							
G. <i>Phyllonorycter turugisana</i> (Kumata)							
H. <i>Phyllonorycter sp.1</i>							
I. <i>Caloptilia sp.2</i>							
J. <i>Gibbovalva kobusi</i> Kumata and Kuroko							
K. <i>Gibbovalva magnoliae</i> Kumata and Kuroko							
L. <i>Phyllonorycter bicinctella</i> (Matsumura)							
M. <i>Caloptilia sp.3</i>							
N. <i>Phyllonorycter matsudai</i> Kumata							
O. <i>Phyllonorycter acutissimae</i> (Kumata)							
P. <i>Phyllonorycter issikii</i> (Kumata)							
							Species code

Eulophidae

Eulophinae

<i>Elachertus fenestratus</i> Nees		+	+			+	+	29
<i>Elachertus inunctus</i> Nees		+	+	+		+		30
<i>Elachertus sp.2</i>						+	+	31
<i>Cirrospilus lyncus</i> Walker	+	+	+		+	+		24
<i>Cirrospilus diallus</i> Walker	+	+	+			+		25
<i>Cirrospilus sp.1</i>						+		26
<i>Cirrospilus sp.2</i>			+		+	+	+	27
<i>Sympiesis laevifrons</i> Kamijo			+		+	+		49
<i>Sympiesis sericeicornis</i> (Nees)		+	+		+	+		50
<i>Sympiesis acalle</i> (Walker)						+		48
<i>Sympiesis sp.1</i>						+		51
<i>Sympiesis sp.2</i>			+					52
<i>Sympiesis sp.3</i>		+			+	+		56
<i>Sympiesis sp.4</i>						+		53
<i>Sympiesis sp.5</i>						+		54
<i>Sympiesis sp.6</i>						+		55
<i>Pnigalio sp.1</i>	+				+			44
<i>Pnigalio sp.2</i>					+			45
<i>Pnigalio sp.3</i>				+	+			46
<i>Pnigalio katonis</i> (Ishii)	+	+		+	+	+		43

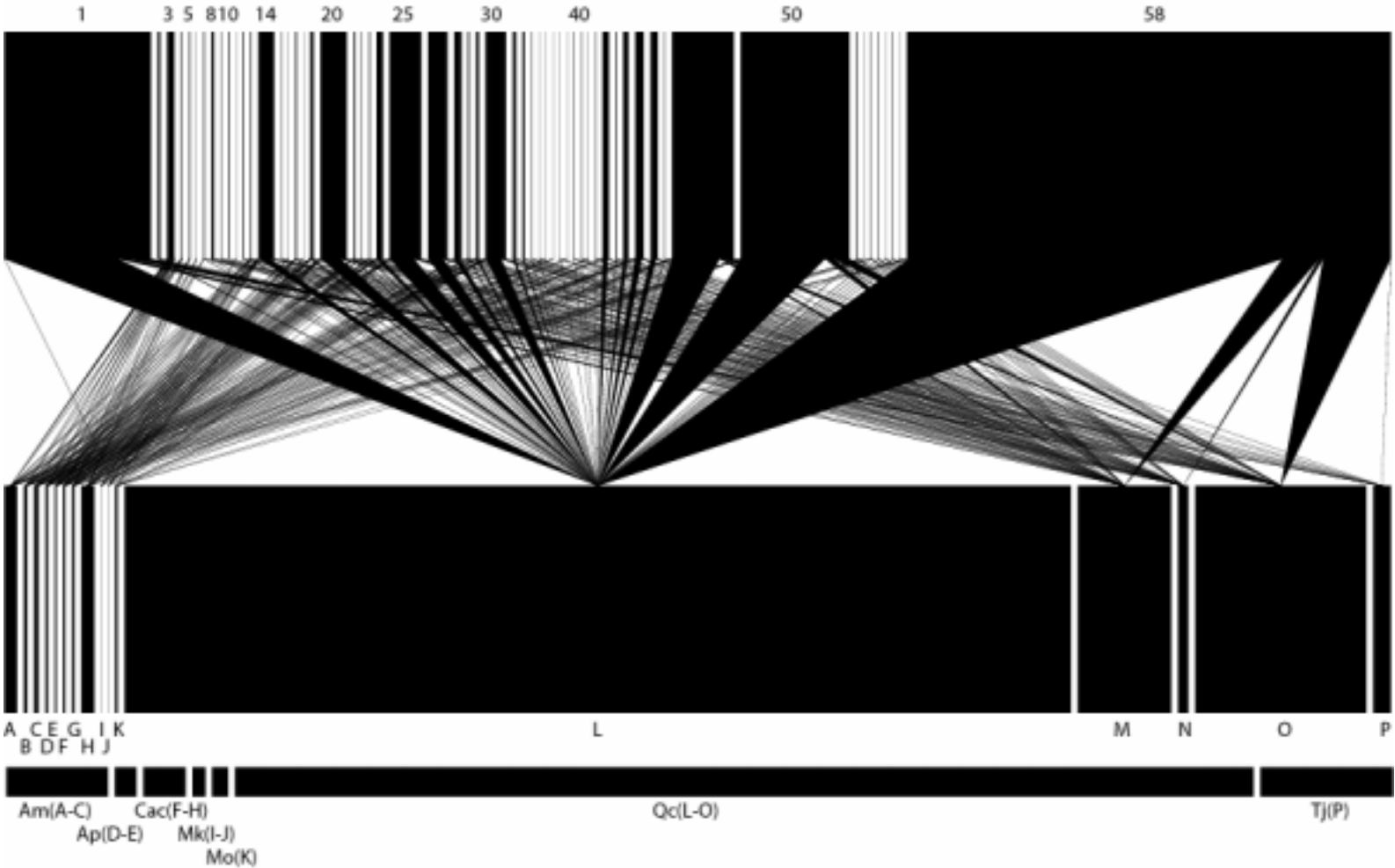
	<i>Pnigalio sp.5</i>									+				57
	<i>Pnigalio sp.6</i>									+				47
	<i>Eulophinae sp.1</i>									+		+		42
Entedontinae														
	<i>Achrysocharoides sp.1</i>									+		+		1
	<i>Achrysocharoides sp.2</i>											+		2
	<i>Achrysocharoides sp.3</i>			+	+	+								3
	<i>Achrysocharoides sp.4</i>			+	+									4
	<i>Achrysocharoides sp.5</i>												+	5
	<i>Achrysocharoides sp.6</i>												+	6
	<i>Achrysocharoides sp.7</i>											+	+	7
	<i>Achrysocharoides sp.8</i>												+	8
	<i>Achrysocharoides sp.9</i>												+	9
	<i>Achrysocharoides sp.10</i>													10
	<i>Achrysocharoides sp.11</i>									+				11
	<i>Achrysocharoides sp.12</i>												+	12
	<i>Chrysocharis laomedon</i> (Walker)			+	+	+		+				+		20
	<i>Chrysocharis ujiyei</i> Kamijo					+	+					+	+	23
	<i>Chrysocharis sp.1</i>			+	+	+						+		21
	<i>Chrysocharis sp.2</i>			+								+	+	22
	<i>Pleurotropposis japonica</i> (Kamijo)									+		+		28
	<i>Closterocerus trifasciatus</i> Westwood												+	35

	<i>Entedontinae sp.1</i>							+	32
	<i>Entedontinae sp.2</i>							+	34
	<i>Entedontinae sp.4</i>						+		36
	<i>Entedontinae sp.5</i>						+		37
	<i>Entedontinae sp.6</i>							+	38
	<i>Entedontinae sp.7</i>						+		39
	<i>Entedontinae sp.8</i>							+	40
	<i>Entedontinae sp.9</i>							+	41
	<i>Entedontinae sp.10</i>						+		33
Braconidae									
	<i>Dolichogenidea dilecta</i> (Haliday)							+	13
	<i>Pholetesor sp.</i>							+	14
	<i>Orgilus kumatai</i> Watanabe							+	15
	<i>Choeras sp.</i>								16
	<i>Dolichogenidea sp.</i>							+	17
	<i>Rhysipolis sp.</i>							+	18
	<i>Glyptapanteles mygdonia</i> (Nixon)							+	19
Encyrtidae									
	<i>Holcothorax sp.</i>							+	58

1

Parasitoids (scale: hosts × 2.30)

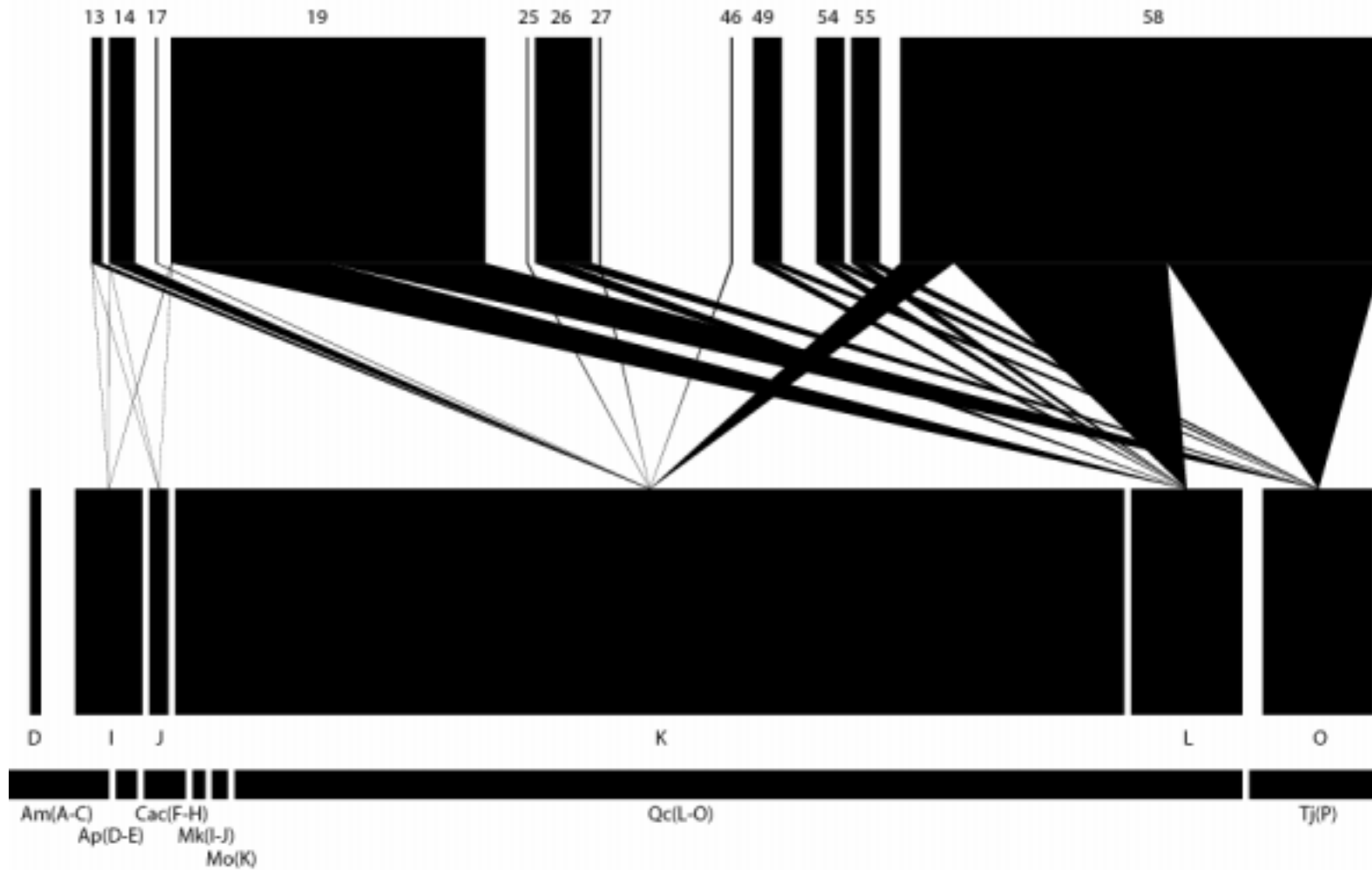
Hirao and Murakami Fig. 1

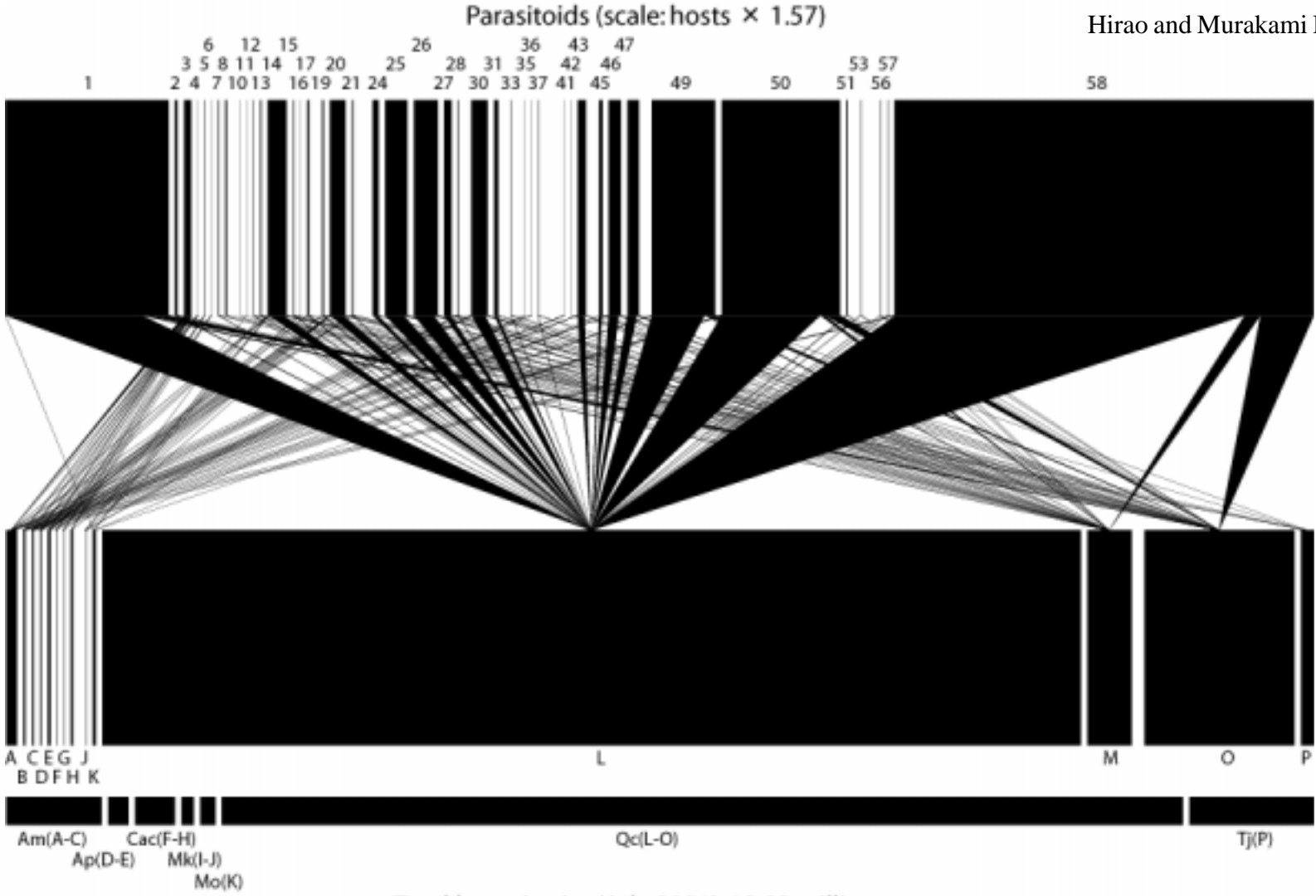


Total hosts in site (all generations): 46.42 million

Parasitoids (scale:hosts × 0.33)

Hirao and Murakami Fig. 2a

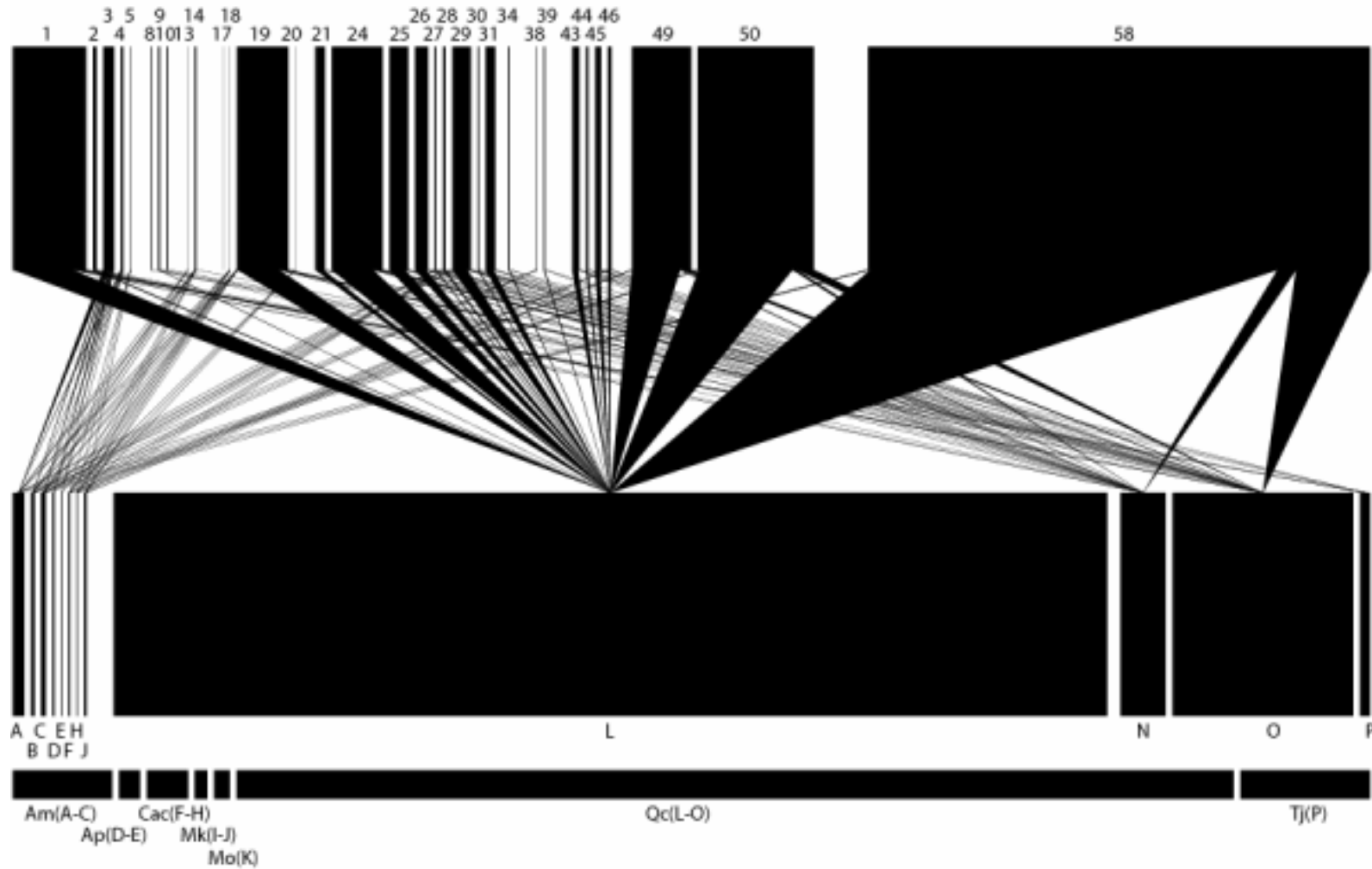




Total hosts in site (July 2001): 18.53 million

Parasitoids (scale: hosts × 2.88)

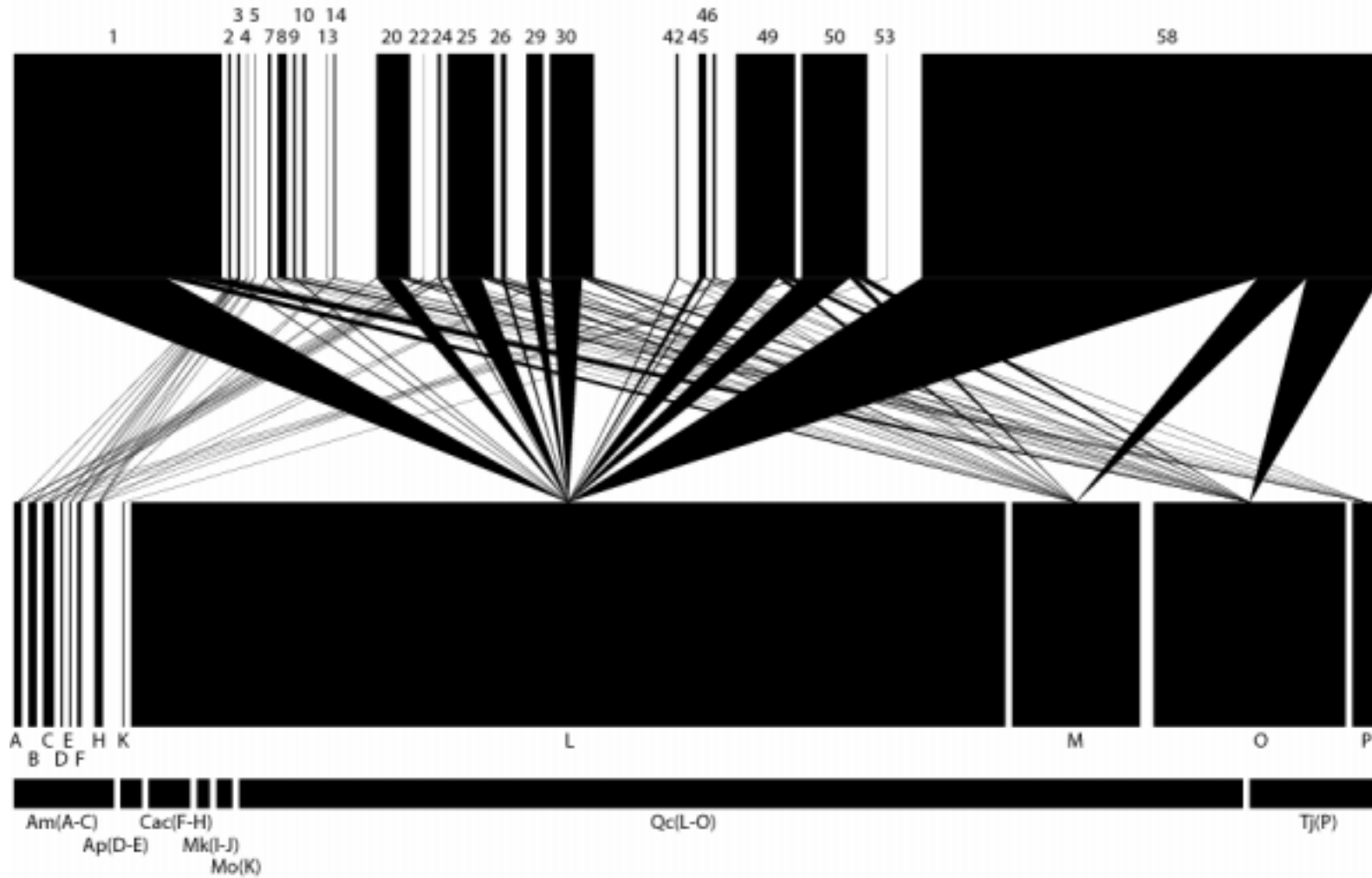
Hirao and Murakami Fig. 2c



Total hosts in site (August 2001): 10.44 million

Parasitoids (scale: hosts × 5.59)

Hirao and Murakami Fig. 2d



Total hosts in site (September 2001): 10.48 million

