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Title:

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

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

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

Introduction

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

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

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

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

Methods

Study site

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

Food web construction

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

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

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

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

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

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

Potential for apparent competition

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

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

where $\alpha_{ik}[t]$ is the strength of the link between host i and parasitoid k in the food web in generation t. The sums of k and l include all parasitoids and that of m includes all hosts. The first quantity within the square brackets represents the relative importance of parasitoid species k for host species i in generation t. The second quantity is the proportion of parasitoid species k that emerged from host species j in the previous generation t – 1. When host species i is equal to species j, hence d_{ii}, the index value indicates a fraction of parasitoids from host i developing on the same host species. The extent to which leafminer species were intergenerationally linked was conventionally represented using parasitoid overlap diagrams (Müller et al. 1999). These diagrams consist of a set of vertices, each representing a leafminer species. Two leafminer species are connected by an edge when they share at least one parasitoid species.

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

(R Development Core Team 2005).

Results

Structure of tree–leafminer–parasitoid community

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

Seasonality of leafminer–parasitoid community

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

Potential for apparent competition

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

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

Discussion

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

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

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

The asymmetric apparent competition observed in the parasitoid overlap diagrams suggests the effect of background spatial habitat structure on the dynamics in leafminer and parasitoid community, which would underpin the observed structure of the quantitative food webs. Asymmetric apparent competition may provide insights into the relationship between the horizontal spatial structure of habitats and quantitative food webs. Holt (1996) theoretically highlighted the spatial aspect of apparent competition, and Morris et al. (2005) tried to introduce spatial scale into measurements of the potential for apparent competition. Apparent competition can theoretically occur in space (Holt 1996), and spatial perspectives have been considered in recent years (e.g., Bonsall and Hassell 2000; Holt and Barfield 2003). Recently, McCann et al. (2005) also argued that the spatial structure of food webs affects their stability. If two hosts share a common parasitoid, but occur on spatially isolated plants that rarely grow in close proximity, the opportunities for apparent competition between these herbivores may be substantially diminished (Morris et al. 2005). In our system, individual trees can be regarded as habitats for leafminer–parasitoid assemblages. If asymmetric apparent competition between leafminer species occurs via a shared parasitoid, it is expected that adult parasitoids would disperse from tree species on which the predominant leafminer species feeds to other tree species. Assuming that tree species show no biased distributions in the forest, parasitism would aggregate around individual trees of species preferred by the predominant host. The spatial aggregation of ecological events like this has been called "spillover predation" (e.g., Lidicker 2000; Kristan and Boarman 2003; Power and Mitchell 2004), which is *sense lato* allochthounous input intensively studied in the context of food webs (e.g., Polis et al. 1997). The spatial aggregation of parasitism or spillover-like parasitism from predominant patches to other patches has been suggested in host–parasitoid systems (Brodmann et al. 1997; Maron and Harrison 1997).

Quantitative food webs and parasitoid overlap diagrams offer promise for future studies. Because quantitative food webs have been constructed using standardised methods based on Müller et al. (1999) in a variety of communities and climates (e.g., Rott and Godfray 2000; Valladares et al. 2001; Lewis et al. 2002), comparing these food webs would offer an opportunity to study geographic variation in the potential for apparent competition and macroecological patterns in food web structure. Furthermore, we hypothesise that parasitism would aggregate around the plant species on which each host species specialises, and in particular, around individuals of a plant species preferred by the predominant host species in the community, where there is a potential for asymmetric apparent competition to occur. The spatial pattern of parasitism in host–parasitoid communities with spatially structured habitats (e.g., tree species) with a potential for asymmetric apparent competition deserves to be investigated in detail. Approaches to link spatial perspectives to the analysis of quantitative food webs may afford new insights into food web ecology.

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Figure legends

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

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

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

Fig. 4 Quantitative parasitoid overlap diagrams. (a) June–July; (b) July–August; (c) August–September; (d) September–October. The numbered vertices show leafminer species; circle sizes indicate the contribution of the focal leafminer species as a source of its own parasitoids. Polygons between leafminer species denote shared parasitoid numbers, where the width of the link at each species represents the potential effect derived from another leafminer species as a source of parasitoids. Species code numbers are listed in Table 1.

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

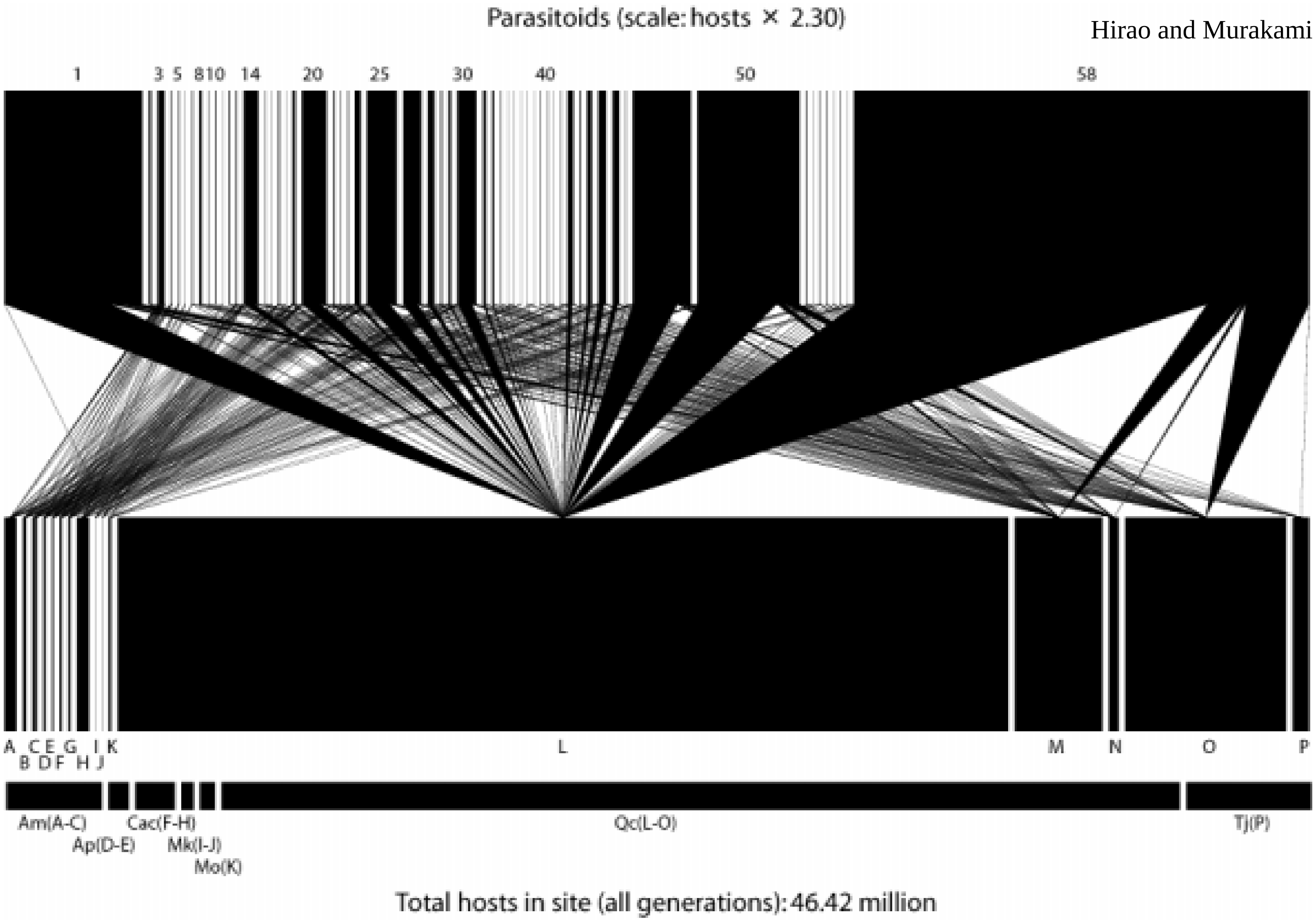
			Am			Ap		Cac			Mk		Mo	Qc				Tj	
			A. *Phyllonorycter jezoniella* (Matsumura)	B. *Caloptilia sp.1*	C. *Stigmella sp.*	D. *Phyllonorycter orientalis* (Kumata)	E. *Cameraria niphonica* Kumata	F. *Phyllonorycter sp.2*	G. *Phyllonorycter turugisana* (Kumata)	H. *Phyllonorycter sp.1*	I. *Caloptilia sp.2*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

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

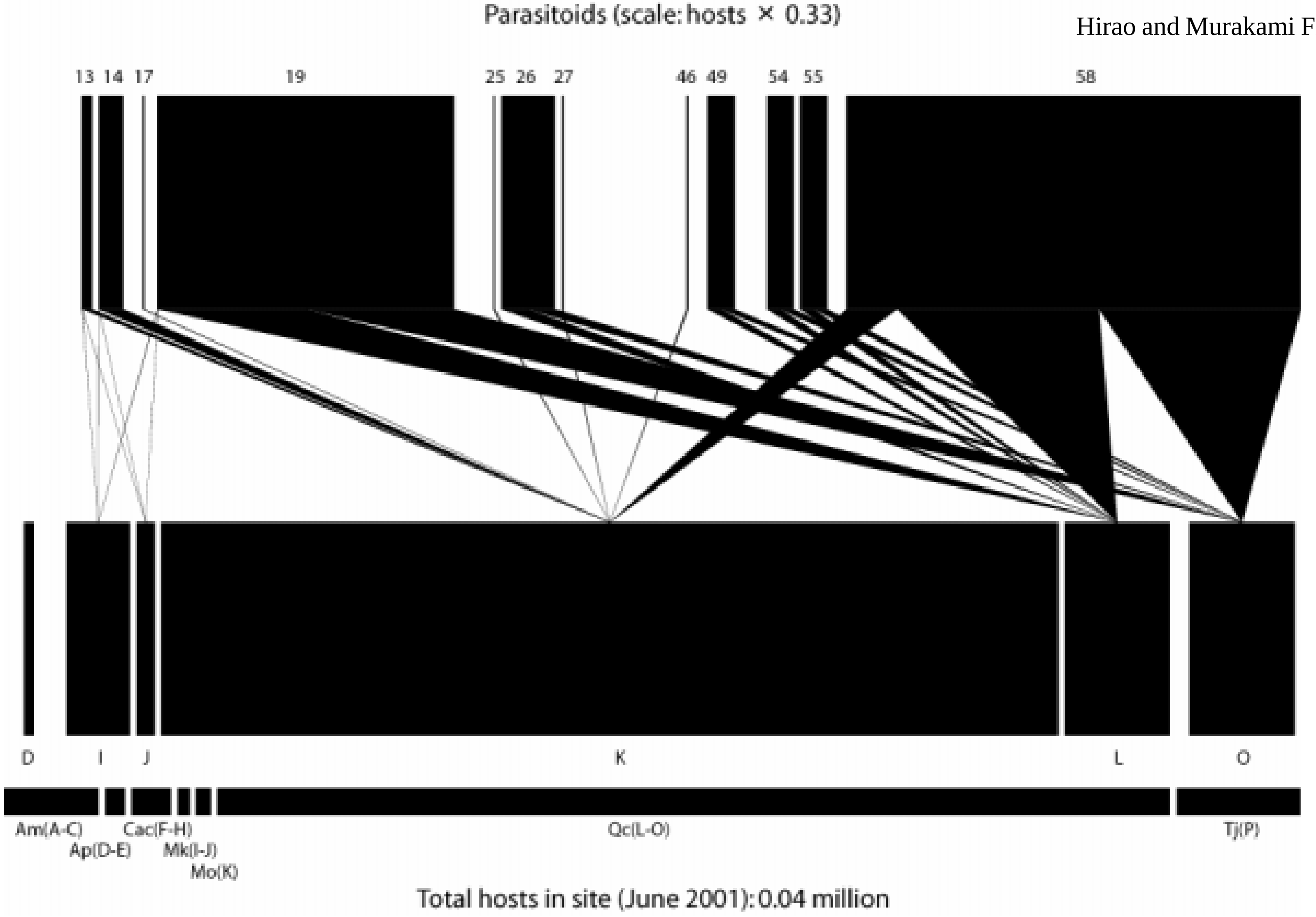
	Pnigalio sp.5					+			57
	Pnigalio sp.6					+			47
	Eulophinae sp.1					+	+		42
Entedontinae									
	Achrysocharoides sp.1					+	+		1
	Achrysocharoides sp.2						+		2
	Achrysocharoides sp.3	+	+	+					3
	Achrysocharoides sp.4	+	+						4
	Achrysocharoides sp.5			+					5
	Achrysocharoides sp.6			+			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

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

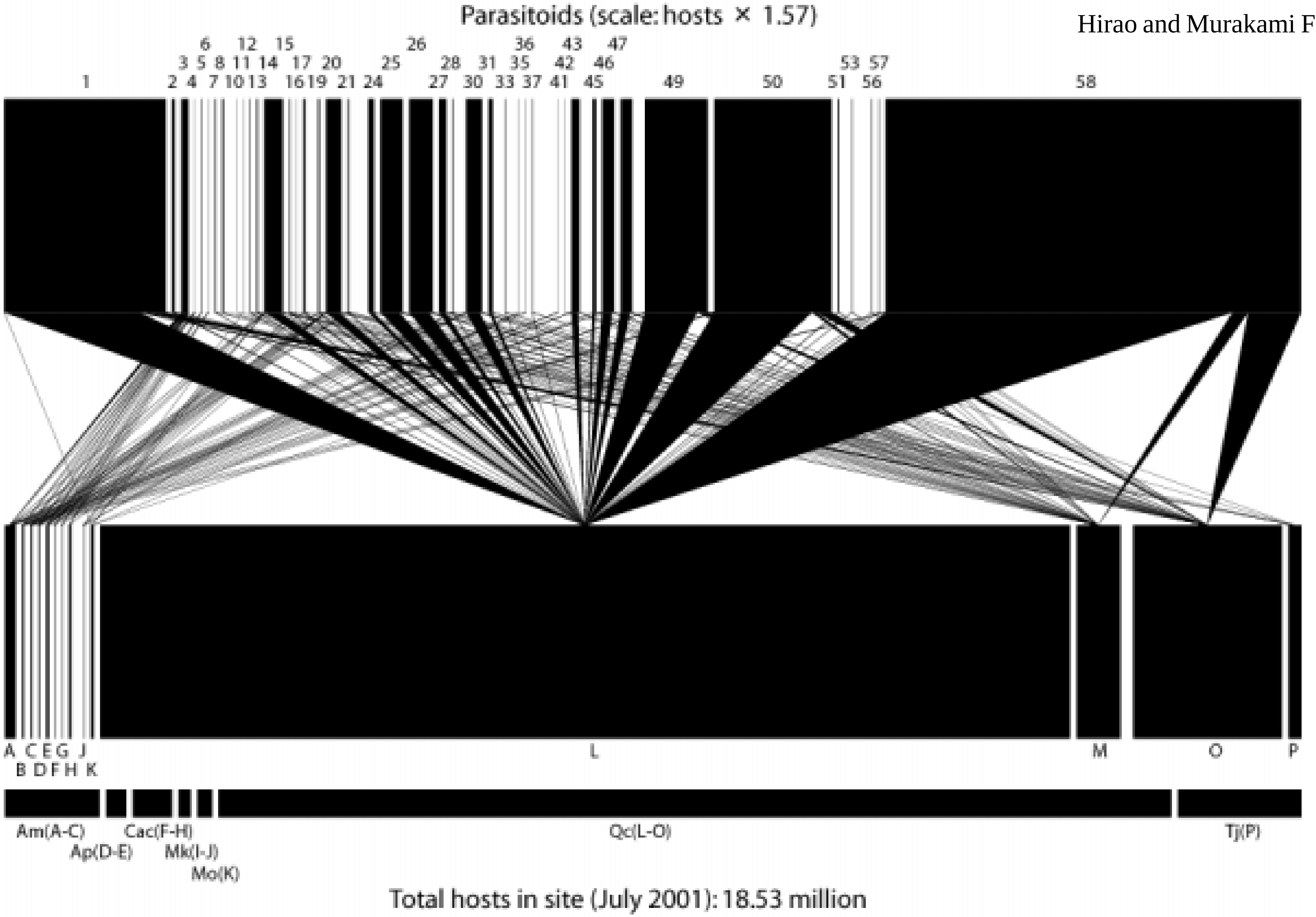
Hirao and Murakami Fig. 1



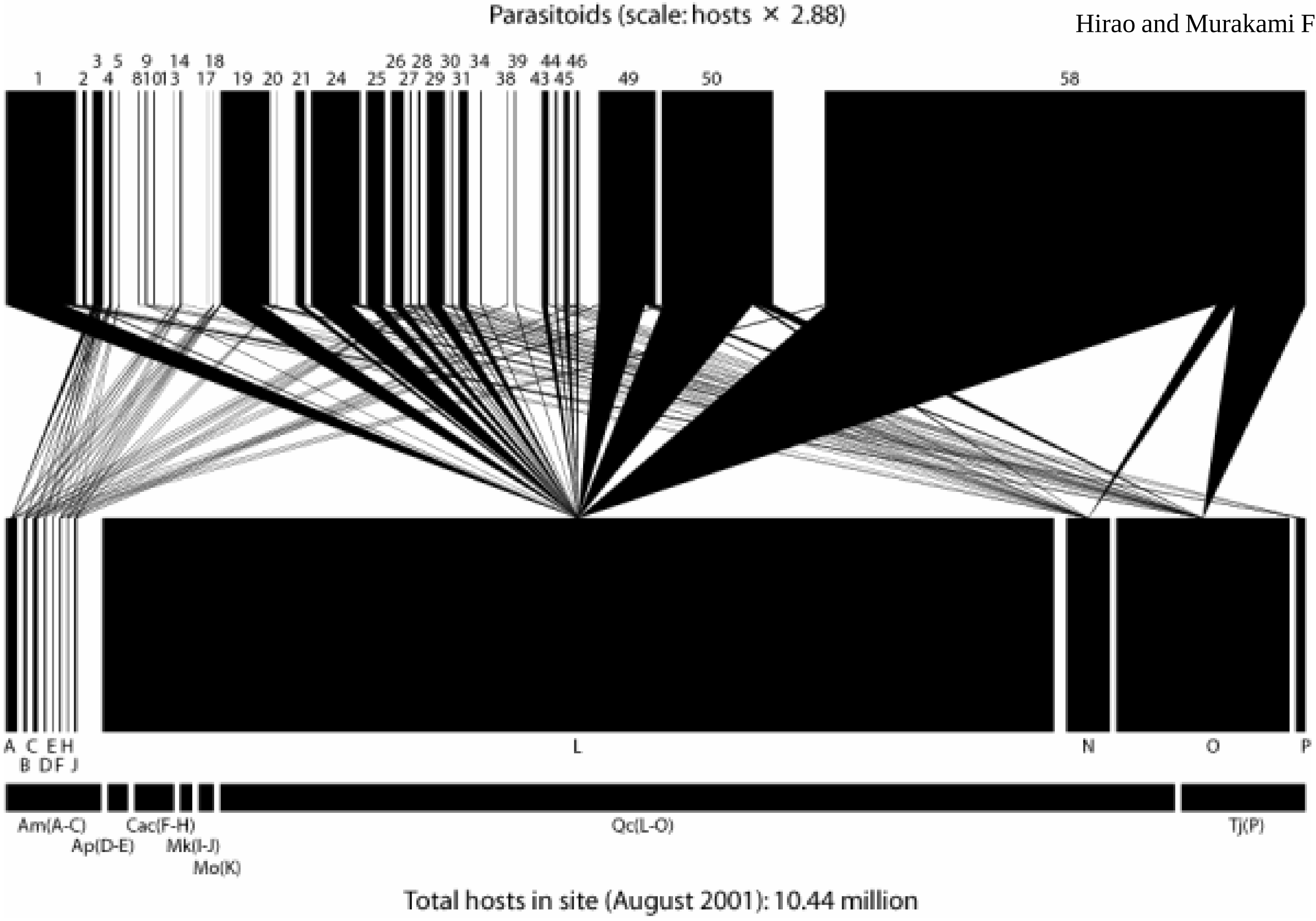
Hirao and Murakami Fig. 2a



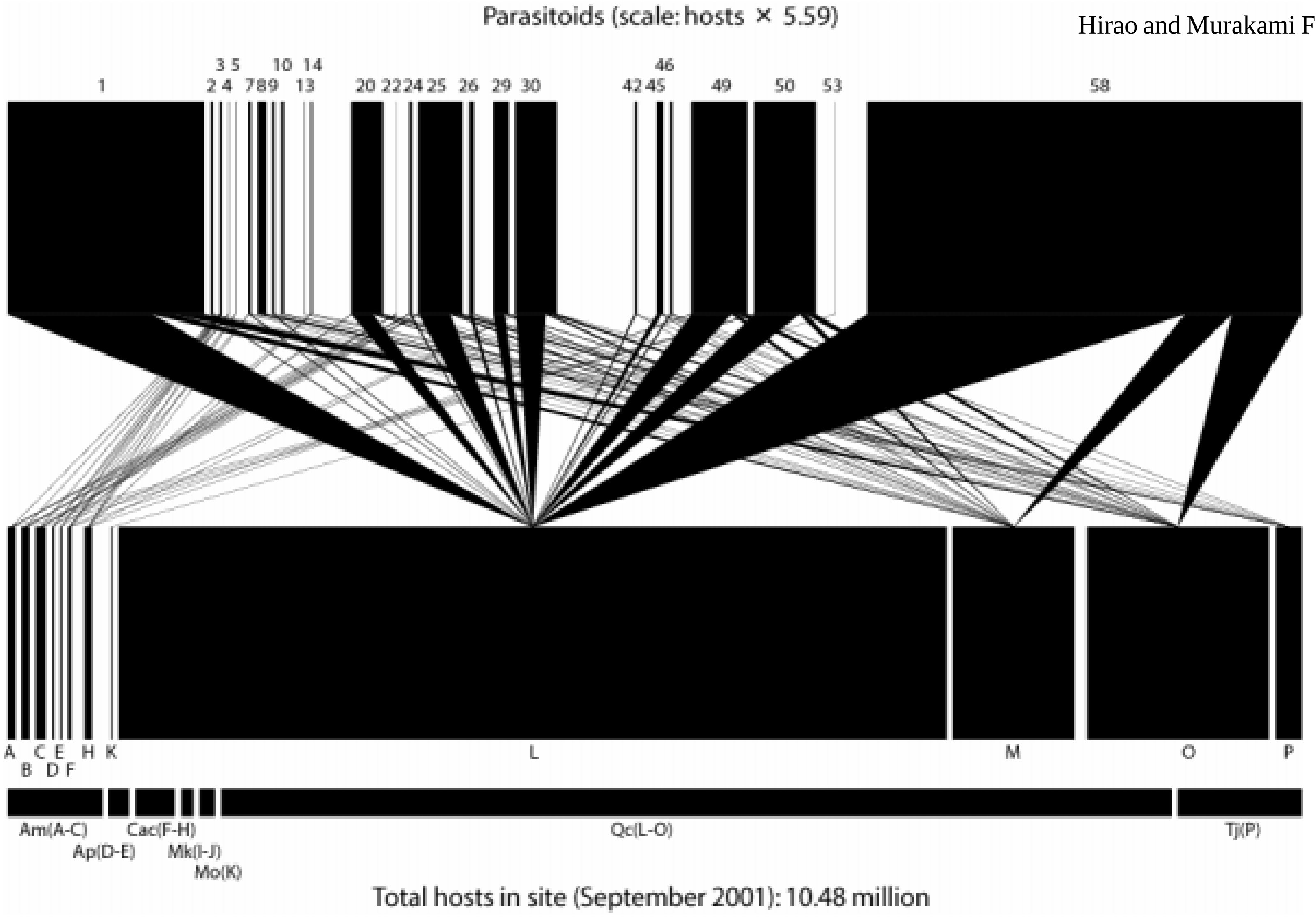
Hirao and Murakami Fig. 2b



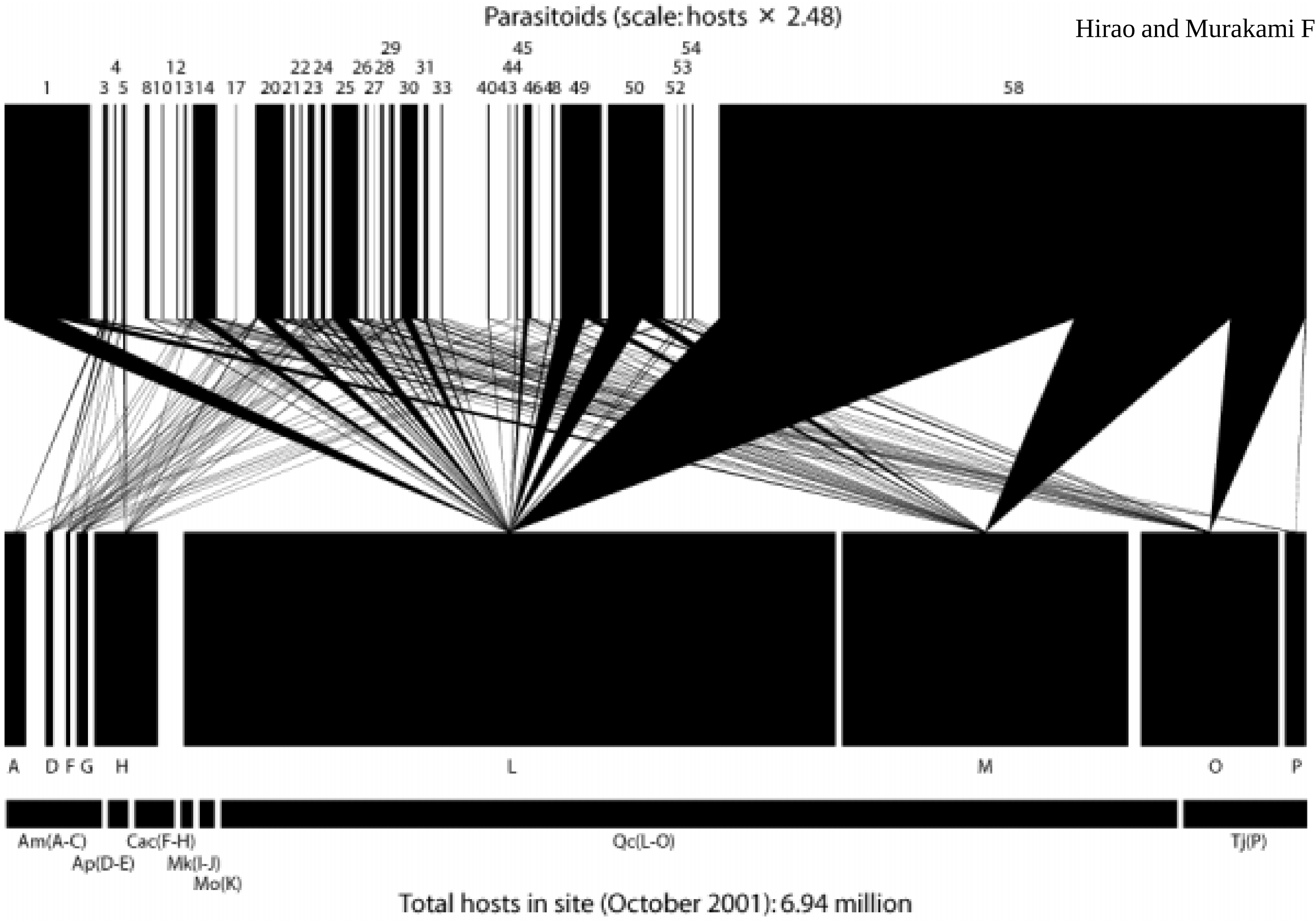
Hirao and Murakami Fig. 2c



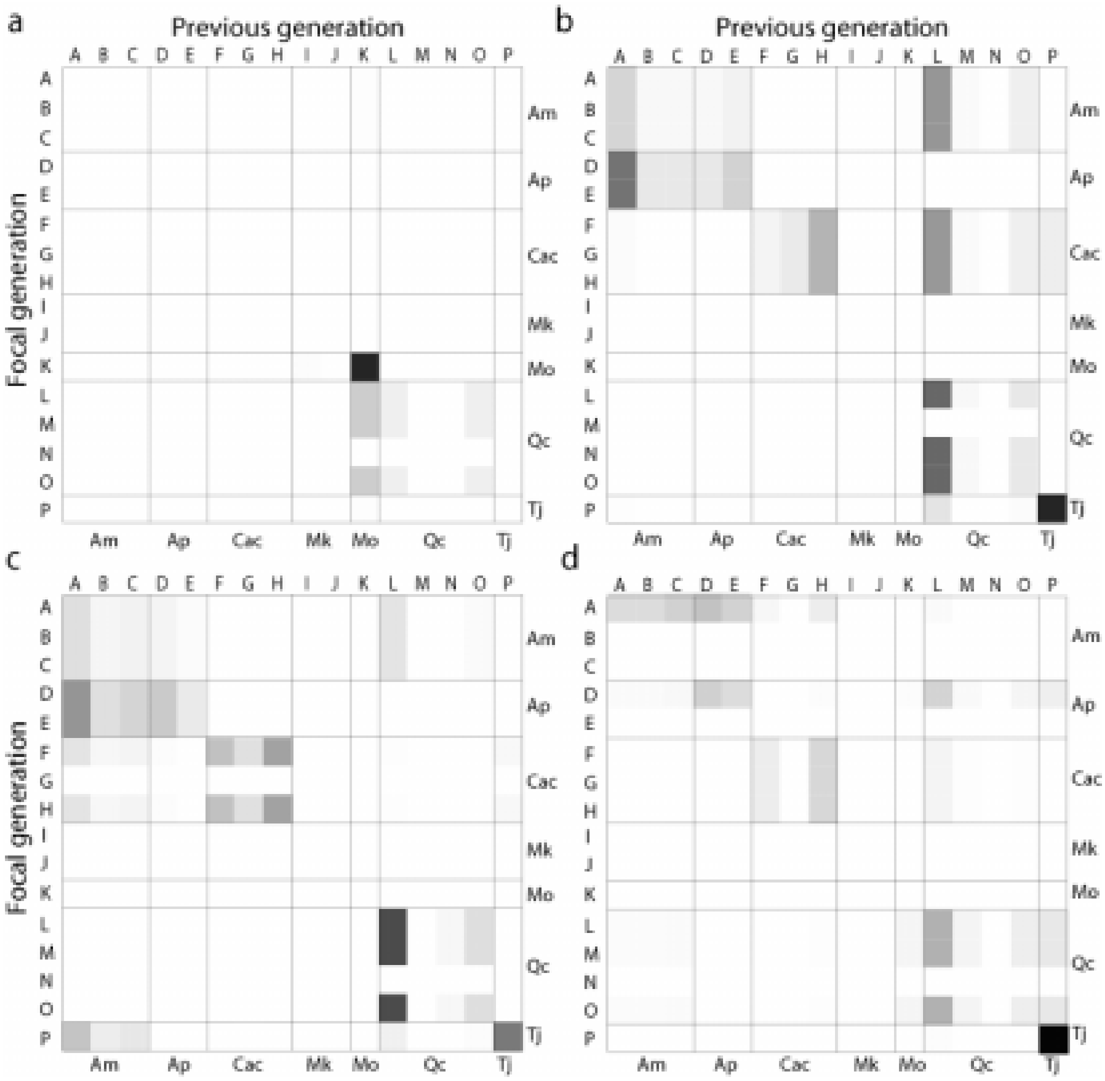
Hirao and Murakami Fig. 2d



Hirao and Murakami Fig. 2e



Hirao and Murakami Fig. 3



Hirao and Murakami Fig. 4