FICUS: A RESOURCE FOR ARTHROPODS IN THE TROPICS, WITH PARTICULAR REFERENCE TO NEW GUINEA

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19.1 INTRODUCTION

Ficus (Moraceae) represents an important component of tropical floras, in terms of both species richness and diversity of growth strategies. Estimates of species richness for *Ficus* range from 740 to 900 species (Janzen, 1979; Berg, 1989), but our survey of the primary taxonomic literature yielded a more conservative estimate of 712 (Corner, 1958, 1965; Berg and Wiebes, 1992). *Ficus* is pantropical in distribution although the Indo-Australian region is the main centre of diversity with over 500 species. A few of the approximately 105 African species are found in Asia. About 130 species are native to the Neotropics. The genus is divided into four subgenera, including the monoecious strangling-figs (subg. *Urostigma*), the monoecious free-standing figs (subg. *Pharmacosycea*), the (gyno)dioecious figs (subg. *Ficus*) and their monoecious relatives (subg. *Sycomorus*; Corner, 1958, 1962). All Neotropical *Ficus* species are monoecious, whereas in Africa a minority of species are (gyno)dioecious. The Indo-Australian region contains the broadest taxonomic distribution of *Ficus*. Each of the four subgenera is represented, numerous sections are endemic and (gyno)dioecious figs are prevalent. New Guinea and Borneo are major centres of diversity. New Guinea is particularly rich, with 135 described species (nearly 20% of the world species count) and a high degree of endemism (53% of species; Corner, 1967).

The high species richness of the genus is mirrored by the variety of growth forms and life histories (trees, shrubs, stranglers, hemiepiphytes, epiphytes, vines, rheophytic species), as well as the diversity of habitats that it occupies (coastlines, swamps, savannas, riparian, lowland and montane forests; Berg, 1989). In tropical forests, *Ficus* is a conspicuous element of both pioneer and climax vegetation. For example, in Indo-Australian secondary forests, (gyno)dioecious free-standing figs are among the most abundant tree species, whereas (gyno)dioecious climbing figs and monoecious stranglers commonly occur in primary forests. Figs may be important in reforesting areas of degraded pasture in the Neotropics (Williams-Linera and Lawton, 1995). Some species, such as *F. microcarpa*, have become invasive pest trees, particularly in Hawaii and Florida (McKey, 1989).

The key taxonomic feature of the genus is the syconium, a receptacle containing many minute flowers which is enclosed by a bract-lined opening (ostiole). This highly specialized inflorescence is pollinated by host-specific agaonid wasps (Hymenoptera: Agaonidae). Fig pollination has attracted considerable scientific interest world-

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wide and generated substantial literature, with particular reference to mutualism, antagonism, host specificity and coevolution (reviews in Janzen, 1979; Wiebes, 1979; Frank, 1989; Herre, 1989; McKey, 1989; Bronstein, 1992), but it is not our aim to treat this subject.

The interest in *Ficus* for conservation studies is equally considerable. The genus is known to attract a wide range of frugivorous animals, including many species of birds, bats, marsupials and primates. Observations of vertebrate feeding habits, the local abundance of figs and their distinctive fruiting schedules led Terborgh (1986) to hypothesize that figs are keystone species. Terborgh supposed that figs could provide a continual supply of food to frugivorous vertebrates and could be particularly important during periods of resource scarcity, due to pollination-level flowering asynchrony which results from the unique system of pollination (Janzen, 1979). However, Mills *et al.* (1993) indicated that the concept of 'keystone species' (Paine, 1969) is not accepted widely and is defined inadequately. Recently, an international workshop was organized to seek consensus on a definition of keystone species (Power and Mills, 1995). The participants re-defined a keystone species as one 'whose impact on its community or ecosystem are large, and much larger, than would be expected from its abundance' (Power and Mills, 1995).

In addition to fig crops being eaten by frugivorous vertebrates, arthropods are also conspicuous primary consumers of the syconia (= 'figs'), foliage and wood of *Ficus* trees. Arthropod consumers may be classified into four main categories, according to the type of resource and how it is used:

1. arthropods feeding on syconia, either internally or externally;
2. arthropods feeding on sap, tapping either the mesophyll, phloem or xylem;
3. insects chewing leaf tissues, either free-living, gall-making or leaf-mining;
4. insects boring into stems (living tissues) and wood (living or early decaying).

If we assume that certain *Ficus* species may be keystone for frugivorous vertebrates, it may be of particular interest to examine whether these same tree species could also be considered as keystone for the community of *Ficus*-feeding arthropods. Such fig species would be invaluable in maintaining local animal diversity.

In this chapter, information about arthropod consumers of *Ficus* is provided. Root-feeding arthropods are not treated because specific information on this guild could not be located. The standard definition of a keystone species set by the international workshop is followed and the impact of a *Ficus* species on the community of *Ficus*-feeding insects is examined in terms of the number of insect species feeding on it. More specifically, three questions are addressed:

1. Which arthropod families and genera are most likely to feed on *Ficus* and are these taxa relatively species-rich and/or host-specific?
2. Is the local composition of arthropod faunas feeding on *Ficus* in New Guinea different from elsewhere, when considered at a higher taxonomic level?
3. Can the keystone species concept be substantiated for certain *Ficus* species, with reference to the *Ficus*-feeding insect community in the Madang area, Papua New Guinea?

To answer these questions, the literature is reviewed and some preliminary data from an ongoing study of selected taxa feeding on 15 species of *Ficus* in New Guinea are presented.

19.2 ARTHROPOD PRIMARY CONSUMERS OF *FICUS*: A LITERATURE REVIEW

19.2.1 METHODS

General surveys and community studies of *Ficus*-feeding arthropods, particularly foliage feeders, are rare (e.g. Picard, 1919; Swailem and Awadallah, 1973; Ozar *et al.*, 1986; Basset *et al.*, 1996). Instead, most of the compiled literature was extracted from the CABAbstracts (1984–1994) and CABPestCD (1973–1995) databases (Centre for Agriculture and Biosciences International, Wallingford, UK). This information was supplemented by taxonomic monographs (indicated later in the text) and with various lists or catalogues providing host records (e.g. Houard, 1922; Lima, 1936; Beeson and Bhatia, 1937, 1939; Condit and

Enderud, 1956; Duffy, 1957, 1960, 1963, 1968; Guagliumi, 1966; Silva *et al.*, 1968; Avidov and Harpaz, 1969; Bruner *et al.*, 1975; Martorell, 1976; Mound and Halsey, 1978; Annecke and Moran, 1982; Bigger, 1988; Williams and Watson, 1988a,b, 1990; Zhang, 1995). Several colleagues supplied additional records and, in particular, G. Robinson and I. Kitching allowed us to extract lepidopteran records from their database 'Hosts' (The Natural History Museum, records as from August 1995). Fig wasps are included in our estimates of arthropod species richness feeding on *Ficus* but are not discussed since the literature is comprehensive (e.g. Wiebes, 1966, 1979, 1994; Hill, 1967; Ramírez, 1970; Boucek, 1988; Berg and Wiebes, 1992; Compton and Hawkins, 1992; Compton and van Noort, 1992). Arthropods feeding on fallen, or dried and stored, syconia are not treated. Arthropods feeding on syconia are treated by G.W., sap-sucking arthropods by V.N. and leaf-chewing and wood-boring insects by Y.B. The database, in which each 'record' represents a different arthropod species, is available from the authors on request.

19.2.2 LITERATURE REVIEW

(a) General patterns and limitations

In total, we found published records of 1875 species feeding on *Ficus*, including 742 species feeding on syconia, 481 sap-sucking species, 369 leaf-chewing species and 283 stem/wood-boring species. It is probable that the actual number of species feeding on *Ficus* is much higher than these figures. Arthropod records were obtained from only 286 species of *Ficus*, but these are likely to be biased towards *Ficus* species of economic importance – for example, edible and ornamental species: *F. carica* (151 arthropod records), *F. elastica* (51 records), *F. retusa* (42 records), *F. sycomorus* (35 records), *F. benghalensis* (35 records), *F. benjamina* (33 records), *F. religiosa* (29 records) – and arthropod pests.

The 20 most speciose arthropod families (Table 19.1), accounting for about 80% of arthropod records, include:

- some polyphagous pests prominent in the literature, such as certain Cerambycidae, Aleyrodidae, Coccidae, Pseudococcidae, Diaspididae, Bostrichidae, Lymantriidae and Noctuidae;
- some specialized and often speciose taxa that exploit particular resources, such as in certain Agaonidae, Drosophilidae, Curculionidae and Tephritidae, feeding internally on syconia; Homotomidae feeding on phloem; certain Phlaeothripidae feeding on mesophyll; and certain Nymphalidae, Crambidae, Bombycidae and Noctuidae, feeding on leaf tissues.

Although these patterns are more conspicuous when examined at generic level (Table 19.2), it should be noted that the number of congeneric species may depend on the availability of recent taxonomic revisions.

Considering broad biogeographic areas, the database included 892 species records for the Indo-Australian region, 331 Afrotropical, 310 Neotropical, 91 Palaearctic, 33 Nearctic and 76 cosmopolitan records. It is probable that Palaearctic records are inflated by arthropods feeding on cultivated figs (*F. carica* and *F. sycomorus*) and that the numbers of Neotropical and cosmopolitan species are underestimated. In particular, for the former, a compilation of Neotropical Agaoninae was not available. Approximately 5% of arthropod records came from New Guinea, in comparison with New Guinean species of *Ficus* contributing nearly 20% of the total. This suggests that arthropods feeding on *Ficus* in New Guinea may have been undersampled.

(b) Arthropods feeding on syconia

Internal feeders

The fig wasps (Agaonidae) are the largest group of internal feeders (Tables 19.1 and 19.2), consisting of pollinating wasps (335 records; all in Agaoninae), and 'parasitoids' (186 records). Many of the so-called parasitoid fig wasps are phytophagous, feeding on the seed contents of galled fig flowers, but the life history of many species is not well understood (e.g. Boucek, 1988; Compton and van Noort, 1992; Compton *et al.*, 1994). For example, some species are capable of galling fig flowers in the absence of wasp larvae (i.e.

Table 19.1 The 20 most speciose arthropod familes feeding on *Ficus*, recorded from review of literature

Family	*No. species*	*Family*	*No. species*
1. Agaonidae (Hym.)	529	11. Diaspididae (Hem.)	31
2. Cerambycidae (Col.)	225	12. Nymphalidae (Lep.)	31
3. Aleyrodidae (Hem.)	82	13. Phlaeothripidae (Thys.)	30
4. Drosophilidae (Dipt.)	73	14. Triozidae (Hem.)	28
5. Curculionidae (Col.)	61	15. Aphididae (Hem.)	28
6. Noctuidae (Lep.)	52	16. Eriophyidae (Ac.)	27
7. Homotomidae (Hem.)	49	17. Chrysomelidae (Col.)	25
8. Coccidae (Hem.)	42	18. Tephritidae (Dipt.)	24
9. Crambidae (Lep.)	41	19. Bostrichidae (Col.)	22
10. Pseudococcidae (Hem.)	31	20. Lymantriidae (Lep.)	21

Apocryptophagus: Godfray, 1988; G.W., personal observation). It is accepted that each *Ficus* species has a host-specific pollinator (Wiebes, 1987; but exceptions were noted in Ramírez, 1970; Compton, 1990; Wiebes, 1994) but, as yet, wasps are known from only one-third of all *Ficus* species (Wiebes, 1994). 'Parasitoid' fig wasps appear to be less host specific than the pollinators (Compton and van Noort, 1992).

Many other arthropods feed internally on syconia, mostly in the Coleoptera, Diptera and Lepidoptera. Perrin (1992) reported that 35 African species of *Curculio* (Curculionidae) are specialists feeding on syconia, whilst others feed on Fagales. In Australia, some species also feed on syconia, but *C. bicruciatus* breed in the fruits of *Syzygium* (A. Howden, personal communication). Other weevil species also feed within syconia, such as African species of *Omophorus* and Neotropical species of *Ceratopus*, and, perhaps, of *Geraeus* (A. Howden, personal communication). One species of the former is reported to be a pest of cultivated figs in

Table 19.2 The 36 most speciose arthropod genera feeding on *Ficus*, recorded from review of literature

Genus	*No. species*	*Genus*	*No. species*
1. *Ceratosolen* (Agaonidae) *	62	19. *Euploea* (Nymphalidae)	14
2. *Pegoscaphus* (Agaonidae) *	45	20. *Asota* (Noctuidae)	14
3. *Drosophila* (Drosophilidae)	40	21. *Elisabethiella* (Agaonidae) *	14
4. *Curculio* (Curculionidae)	35	22. *Pleistodontes* (Agaonidae) *	14
5. *Apocrypta* (Agaonidae)	35	23. *Lissocephala* (Drosophilidae)	14
6. *Apocryptophagus* (Agaonidae)	30	24. *Courtella* (Agaonidae) *	13
7. *Blastophaga* (Agaonidae) *	29	25. *Eupristina* (Agaonidae) *	12
8. *Krabidia* (Agaonidae) *	23	26. *Macrohomotoma* (Homotomidae)	11
9. *Pauropsylla* (Triozidae)	22	27. *Aleuroplatus* (Aleyrodidae)	11
10. *Homotoma* (Homotomidae)	20	28. *Zaprionus* (Drosophilidae)	10
11. *Dialeurodes* (Aleyrodidae)	20	29. *Choreutis* (Choreutidae)	9
12. *Agaon* (Agaonidae) *	19	30. *Glyphodes* (Crambidae)	9
13. *Wiebesia* (Agaonidae) *	18	31. *Dolichoris* (Agaonidae) *	9
14. *Waterstoniella* (Agaonidae) *	17	32. *Ceroplastes* (Coccidae)	8
15. *Liporrhopalum* (Agaonidae) *	16	33. *Camarothorax* (Agaonidae)	8
16. *Platyscapa* (Agaonidae) *	15	34. *Aceria* (Eriophyidae)	7
17. *Gynaikothrips* (Phlaeothripidae)	14	35. *Stathmopoda* (Oecophoridae)	7
18. *Clusiosoma* (Tephritidae)	14	36. *Alfonsiella* (Agaonidae) *	7

* Pollinators

South Africa (Annecke and Moran, 1982). However, many fig species have yet to be examined for Curculionidae, particularly in Australasia.

In Diptera, records of Cecidomyiidae include several Indo-Australian genera and Nearctic species of *Ficiomyia*. Records of Lonchaeidae include several Palaearctic and Indo-Australian species, including some in *Lonchaea*. In Tephritidae, in addition to several rather polyphagous and cosmopolitan species, at least the genus *Clusiosoma* in New Guinea appears to be species-rich and specialized on *Ficus* (Hardy, 1986). Many Drosophilidae feed on syconia, but most records are Afrotropical. *Lissocephala* are obligate fig-breeders, with some species being restricted to a single species of *Ficus*. However, *Zapronius* and *Drosophila* appear to be feeding facultatively on yeast growing in the decaying syconia. Adults of *Lissocephala* lay eggs in and around the ostiole, through which first instar larvae enter the syconium cavity. Second and third instars feed inside the syconia and then emerge to pupate in the ground. Cohabiting *Lissocephala* species have slightly different oviposition sites, suggestive of niche partitioning. Temporal separation of niche was invoked to account for the succession of *Lissocephala*, *Zapronius* and *Drosophila* species feeding in the same syconia (Lachaise, 1977; Lachaise *et al.*, 1982; Couturier *et al.*, 1986). There are records of Phoridae reared from syconia, but larvae may feed mostly on dead fig wasps (Compton and Disney, 1991).

In Lepidoptera, families Crambidae, Oecophoridae and Pyralidae are also known to feed internally on syconia. Notably, many crambid records involve Indo-Australian species of *Cirrhochrista*, whereas oecophorid records include several Indo-Australian species of *Stathmopoda*.

External feeders

In comparison with internal feeders, there are relatively few records of arthropods that feed externally (only 35 out of 742 records) and a conspicuous part of this is species of Lygaeidae (Hemiptera). Many arboreal records are Afrotropical, including species of *Dinomachus* and *Appolonius*, the latter also known from Australia (Slater, 1972). Several polyphagous species of *Cotinis* (Coleoptera: Scarabaeidae: peach beetle) feed on cultivated figs in the United States (Ebeling, 1959). Several species of fruit-piercing moths in the Noctuidae also feed on syconia.

(c) Sap-sucking arthropods

Species feeding on *Ficus* are found within Acari, Hemiptera and Thysanoptera. All Acari and Thysanoptera are mesophyll feeders, whereas Hemiptera include phloem feeders (Stenorrhyncha: Coccoidea, Aleyrodoidea, Psylloidea and Aphidoidea; and most Auchenorrhyncha), mesophyll feeders (Heteroptera and Auchenorrhyncha: Typhlocybinae) and xylem feeders (Auchenorrhyncha: Cicadellinae, Cicadidae and Cercopidae).

Acari and Thysanoptera account for about 90% of all mesophyll-feeding records. The most species-rich families are gall-making thrips (Phlaeothripidae) and mites (Eriophyidae; Table 19.1). *Ficus* represents one of the most important host plant groups for the Phlaeothripidae (Ananthakrishnan, 1978). At least six genera contain *Ficus*-feeding species, including the species-rich, mainly Indo-Australian *Gynaikothrips*. One species, *G. ficorum*, has become a pest on ornamental *F. retusa* and *F. microcarpa* (Loche *et al.*, 1984; Paine, 1992). Gall-making thrips exhibit complex interspecific interactions, with only some species capable of gall induction, and others living in these galls as inquilines. In contrast with the Acari and Thysanoptera, only a few records of mesophyll-feeding hemipterans are available, namely Tingidae, Coreidae, Miridae and Cydnidae (Heteroptera), as well as several species of Typhlocybinae (Cicadellidae).

Phloem feeders are the most species-rich guild of sap-sucking herbivores on *Ficus*. They are dominated by three stenorrhynchous groups: Aleyrodoidea, Psylloidea and Coccoidea, while Aphidoidea and Auchenorrhyncha are poorly represented. In particular, three psyllid families – Psyllidae, Triozidae and Homotomidae – feed on *Ficus*, the latter family being limited almost exclusively to *Ficus*. Most of the homotomids are found in the Indo-Australian region (*Macrohomotoma*, *Mycopsylla*, *Homotoma* in part), though some are distributed also in the Afrotropical (e.g. *Pseudoeriopsylla*) and Neotropical (*Synoza*) regions. In Triozidae, the gall-making genus *Pauropsylla* is restricted to *Ficus* in the Old World tropics (Hollis and Broomfield, 1989). In general, psyllids exhibit narrow host specificity, and some genera are restricted to a single subgenus or section of *Ficus* (Hollis and Broomfield, 1989).

In contrast with generally host-specific psyllids, a large number of the scale insects and aleyrodids reported from *Ficus* include many polyphagous, often pest, species (e.g., *Ceroplastes rubens*, *Coccus viridis*, *Rastrococcus invadens*, *Dialeurodes citrifolii*; Mound and Halsey, 1978; Williams and Watson, 1988a,b, 1990). Polyphagous pests are numerous among the aphid species reported from *Ficus* (e.g. *Aphis craccivora*, *A. gossypii*, *A. fabae*, *Myzus persicae*; Blackman and Eastop, 1994). Although global species richness of phloem-feeding Auchenorrhyncha and Stenorrhyncha are similar, there are only 32 species of Auchenorrhyncha recorded from *Ficus*, in contrast with about 300 species of Stenorrhyncha. Eleven families of Auchenorrhyncha are represented, Cicadellidae being the most species-rich. Xylem-feeding groups are represented in the database by seven species on *Ficus*.

(d) Leaf-chewing insects

Free-living insects

Only one record of Orthoptera (Tettigoniidae) feeding on *Ficus* exists in the database. In Coleoptera, leaf-feeding records appear rather scattered, such as those of Melolonthinae (Scarabaeidae). Several species of Lamiinae (Cerambycidae) which bore the wood of *Ficus* perform maturation feeding by gnawing twigs and young leaves of *Ficus* (e.g. Basset *et al.*, 1996). To date, these records include mostly Indo-Australian species in the genera *Acololepta*, *Epepeotes*, *Olenecamptus* and *Rosenbergia*, but many other examples may exist. Records of Chrysomelidae are surprisingly few and include some rather host-specific Indo-Australian Galerucinae (within the genera *Atysa* and *Poneridia*, for example) and some Neotropical Alticinae (within the genus *Epitrix*). Several other chrysomelids (Eumolpinae: genera *Rhyparidella* and *Rhyparida*) feed on *Ficus*, particularly in New Guinea, but little is known about their host range. Records of Curculionidae feeding on foliage, particularly host-specific species, such as *Viticiina* (Viticiinae) from Papua New Guinea, are even rarer.

Most records of free-living insects chewing the leaves of *Ficus* involve Lepidoptera (at least 23 families and 127 genera recorded). Young leaves are tied together by Indo-Australian species of *Phycodes* (Brachodidae), *Choreutis* and *Tortyra*, and Neotropical species of *Hemerophila* and *Tortyra* (all Choreutidae). For example, *Choreutis nemorana* is considered to be a pest of cultivated figs in Crimea (Tkachuk, 1986). Most Crambidae (Pyraustinae) are leaf-rollers, such as Indo-Australian species of *Glyphodes* and *Talanga* and Afrotropical and Neotropical species of *Margaronia*. Skeletonizing occurs in Indo-Australian species of *Brenthia* (Choreutidae) which often exploit mature leaves by spinning a small web on the underside of leaves and chewing a hole to retreat rapidly to the adaxial surface in case of danger (Y.B., personal observation). Other skeletonizing species occur in Zygaenidae, particularly in Indo-Australian species of *Phauda* (Nageshchandra *et al.*, 1972). All Lycaenidae feeding on *Ficus* are within the subfamily Lycaeninae, which are not obligate myrmecophiles (Fiedler, 1991). Most records involve the genera *Myrina* (Africa), *Iraota* (Malaysia) and *Philiris* (New Guinea and Australia). In this last, the larvae feed on the tissue of the lower surface of leaves, leaving the upper epidermis intact (Parsons, 1984).

Most other lepidopterans eat the margin of leaves. In the Nymphalidae (Ackery, 1988), most records occur in the Limenitinae (Indo-Australian and Afrotropical species of *Cyrestis*, Neotropical species of *Marpesia*), Nymphalinae (*Hypolimnas*, Afrotropical) and, particularly, Danainae (*Euploea*, Indo-Australian, and *Lycorea*, Neotropical). Records of Bombycidae are mostly in the Indo-

Australian Bombycinae (*Gunda* and the '*Ocinara* group'). Several records of Saturniidae exist, but no genera appear to be particularly species-rich on *Ficus*. Records of *Ficus*-feeding Sphingidae are mostly Neotropical and Afrotropical (*Pseudoclanis*). Several polyphagous species in Lymantriidae, mostly in the genera *Euproctis*, *Lymantria* (Indo-Australian records) and *Dasychira* (Afrotropical and Indo-Australian records) feed on *Ficus* (e.g. Verma *et al.*, 1989). Arctiidae feeding on *Ficus* include mostly Neotropical species of *Ammalo* (Arctiinae) and New World species of *Lymire* (Ctenuchinae). Many Noctuidae are recorded from *Ficus* and the Indo-Australian and Afrotropical species of *Asota* appear particularly host-specific (Aganainae; placement of this subfamily follows Holloway, 1988). No other noctuid genera, particularly in the Catocalinae and Ophiderinae, appear particularly speciose and many records involve polyphagous species, like the pest *Achaea janata* in India (Prasad and Singh, 1984). Other lepidopteran records occur in families Psychidae, Oecophoridae, Blastobasidae, Gelechiidae, Metarbelidae, Megalopygidae, Limacodidae, Immidae, Pyralidae, Riodinidae, Lasiocampidae and Notodontidae. Surprisingly, there are very few records of Tortricidae and Geometridae (most Indo-Australian, some polyphagous species).

Several lepidopteran species deactivate the lactifers by chewing a narrow groove across the leaf lamina and mid-vein and then feeding on the distal portion of the leaves, thus avoiding contact with latex (Compton, 1989). This behaviour, known also as trenching (Dussourd and Denno, 1994), has been observed in African and Indonesian species of Sphingidae (*Pseudoclanis*) and Noctuidae (*Asota* and *Chrysodeixis*; Compton, 1989; S. Compton, personal communication). It may occur in some Danainae (Dussourd and Denno, 1994).

Gallers and leaf-miners

Records of leaf galls on *Ficus* are scarce and include mostly Cecidomyiidae, particularly some Indo-Australian species of *Horidiplosis* and *Pipaldiplosis*, as well as some Neotropical species of *Johnsonomya* (Barnes, 1948; Bruner *et al.*, 1975). One species of *Diplonearcha* (Tortricidae) has been recorded as a gall-maker on *Ficus* sp.

Leaf-mining insects are rather scarce on *Ficus*. One species of *Leiopleura* (Buprestidae) may be mining leaves of *Ficus* in Venezuela (Guagliumi, 1966). Other records include *Opostega* (Tineidae) on *F. carica* and *Opogona* (Lyonetiidae) on *F. elastica* in the Palaearctic region, and, most notably, several Indo-Australian species of *Acrocercops* (Gracillariidae).

(e) Stem- and wood-boring insects

Stem-borers

Several lepidopteran species bore into aerial roots, such as Indo-Australian species of *Scalmatica* and *Trachytyla* (Tineidae), as well as some species of *Meteoristis* (Gelechiidae). Records of stem- or twig-boring insects include several lepidopteran families. One species of *Paropta* (Cossidae) bores into the branches of *F. carica* in Israel (Avidoz and Harpaz, 1969). Indo-Australian species of *Indarbela* (Metarbelidae), *Copromorpha* and *Phycomorpha* (Copromorphidae), as well as Neotropical species of *Azochis* (Crambidae), are recorded in the database. Several records are from Sesiidae including some Indo-Australian species of *Carmenta* and *Tinthia*, as well as one Neotropical species of *Ficivora* (Gallego, 1971).

Wood-borers

Wood-borers are often less host specific than foliage-feeding arthropods and many records from the soft, easily rotted wood of *Ficus* (cf. Corner, 1967) include polyphagous species. All the available records are of Coleoptera, such as Buprestidae (some Neotropical species of *Colobogaster*). There are more records of Bostrichidae, particularly in the genera *Sinoxylon* (cosmopolitan) and *Dinoderus* (Indo-Australian). However, most wood-boring records include Cerambycidae. There are few records of Prioninae (Neotropical species of *Parandra*), whereas those of Cerambycinae are more common and include Neotropical species of

Cyllene, Indo-Australian species of *Xylotrechus*, and Palaearctic species of *Hesperophanes* and *Trichoferus*.

Lamiinae are the dominant wood-boring group on *Ficus*. Many species of *Acalolepta*, *Batocera*, *Cotops*, *Dihammus*, *Epepeotes* and *Rosenbergia* are recorded from the Indo-Australian region. Species of *Anisopodus*, *Oncideres*, *Taeniotes* and *Trachyderes* are recorded from the Neotropical region, whereas records in Africa include the genera *Phryneta*, *Phrynetopsis* and *Sternotomis*. Notorious pest species also include some Lamiinae, such as *Psacothea hilaris* in Japan (Fukuda, 1992), *Batocera rufomaculata* in India (Mallikarjuna Rao and Mohan Rao, 1991) and *Phryneta spinator* in South Africa (Annecke and Moran, 1982).

Records of Scolytidae are rare and include several Indo-Australian and cosmopolitan species of *Xyleborus*. *Hypoborus ficus* is a relatively host-specific pest of cultivated figs in Israel and Turkey (Avidov and Harpaz, 1969). Other wood-boring species are scattered in the families Mordellidae, Curculionidae and Platypodidae.

19.3 HERBIVORES FEEDING ON SELECTED *FICUS* SPECIES IN THE MADANG AREA: PRELIMINARY DATA

19.3.1 METHODS

Our field work took place in the Madang area, particularly in primary and secondary forests near Baitabag (145°47' E, 5°8' S, *c.* 100 m) and Ohu (145°41' E, 5°14' S, *c.* 200 m) villages, as well as in coastal areas nearby and on islands close to the mainland. We chose 15 species of *Ficus* trees (Table 19.3), which were locally abundant and easy to recognize in the field, as in most cases insects were collected from infertile saplings or from trees devoid of mature figs. These species include trees of various architectures and which grow in different habitats.

Our collections targeted (a) fig wasps; (b) sap-sucking Auchenorrhyncha (hereafter 'leafhoppers'); and (c) leaf-chewing insects. For each *Ficus* species, we attempted to rear fig wasps from 10 individual trees. Syconia were collected when ripe, but prior to the emergence of the agaonids ('D' phase, according to the developmental series of Galil and Eisikowitch, 1968). Samples ranged from one to 20 syconia (depending on the size of the fig crop) and were stored in sealed plastic bags, where elevated CO_2 levels apparently hasten the emergence of the wasps. After 24–48 hours, wasps were removed, mounted and sorted to morphospecies.

Sap-sucking and leaf-chewing insects were collected by hand collection and beating. Since most tree species are small (< 10 m), trees were climbed or sampled from the ground. Larger trees were accessed with the single rope technique (Perry, 1978). Leafhoppers were collected during day-time from June to September 1995, whereas leaf-chewing insects were collected during both day and night, and from July 1994 to September 1995. Collecting effort was similar for each tree species and amounted, in average and for each *Ficus* species, to 1.5 hours spent in inspecting the foliage and 29 tree-inspections for sap-sucking insects (total 437 tree-inspections for all species), and to 10.9 hours and 165 tree-inspections for leaf-chewing insects (total 2472 tree-inspections for all species). Leaf-chewing species collected in the field were provided with fresh *Ficus* foliage in the laboratory to ensure that these species feed on the *Ficus* species from which they were collected. Leaf-chewing insects were raised to adults whenever possible. Collecting, rearing, mounting and sorting to morphospecies involved the authors, seven technical assistants and 12 collectors. The sampling programme, which surveyed individual trees in a variety of age classes and growing in various habitats, was optimized towards a better estimation of the total number of insect species feeding on the *Ficus* species studied. Assignment to morphospecies (hereafter 'species' for sake of brevity) was verified by various taxonomists.

The abundance of resource available to leaf-feeding insects was estimated as the standing volume of compact foliage per unit area (foliage volume in m^3 per hectare of forest). It was calculated for each of the 15 *Ficus* species as a product of (tree density, estimated from 167 surveys, each represented by a 20-minute walk covering an appro

Table 19.3 Species of *Ficus* on which insect collections were made and their taxonomic placement, architecture, preferred habitats (Hab), leaf texture (Leaf), mode of reproduction (Rep), size of syconia (Syc) and abundance within the study area (Ab)

Ficus species	*Ficus section*	*Habitus*	*Hab*[(a)]	*Leaf*[(b)]	*Rep*[(c)]	*Syc*	*Ab*[(d)]
F. bernaysii King	Sycocarpus	Small evergreen	F	1	Di	Medium	62
F. botryocarpa Miq.	Sycocarpus	Medium evergreen	R	1	Di	Medium	90
F. conocephalifolia Ridley	Sycidium	Small evergreen	F	1	Di	Medium	140
F. copiosa Steud.	Sycidium	Medium evergreen	R	1	Di	Large	41
F. dammaropsis Diels	Sycocarpus	Small evergreen	R	2	Di	Large	81
F. hispidioides S. Moore	Sycocarpus	Medium evergreen	R	1	Di	Large	95
F. microcarpa L.	Conosycea	Large evergreen	C	2	Mo	Small	< 1
F. nodosa Teysm. & Binn.	Neomorphe	Large deciduous	R	2	Di	Large	67
F. phaeosyce Laut. & K. Schum.	Sycidium	Small evergreen	F	1	Di	Small	106
F. pungens Reinw. ex Bl.	Sycidium	Medium evergreen	R	1	Di	Small	185
F. septica Burm.	Sycocarpus	Small evergreen	R, C	2	Di	Medium	56
F. tinctoria Forst.	Sycidium	Medium evergreen	C	2	Di	Small	25
F. trachypison K. Schum.	Sycidium	Medium evergreen	R	1	Di	Small	66
F. variegata Bl.	Neomorphe	Large deciduous	F, R	2	Di	Large	835
F. wassa Roxb.	Sycidium	Small evergreen	F, R, C	1	Di	Small	290

[(a)] F = forest; R = regrowth; C = coastal. [(b)] 1 = scabrid; 2 = smooth. [(c)] Di = dioecious; Mo = monoecious. [(d)] Estimations of volume of foliage (m^3) per ha of forest (see text).

imate area of 380 × 4 m, during which all trees taller than 1 m were counted; and (b) tree size, measured during 25 such surveys. The area surveyed included all main sampling sites, amounting to about 25.4 ha, in which about 7200 trees were recorded.

19.3.2 RESULTS

(a) Fig wasps

During April to September 1995, 65% of the fig wasp sampling programme was completed (97 of 150 samples) and material from 14 *Ficus* species was obtained. Counts were based on the examination of a single collection representing each fig species and wasp species have not yet been compared among fig taxa. Surprisingly, few wasp species were found, ranging from two to four per fig species (Table 19.7 in section 19.5). It is probable that these data underestimate the richness of the local fig wasp fauna. However, Compton and Hawkins (1992), from species accumulation curves, showed that most (over 50%) wasp species could be obtained from a single collection of syconia. Table 19.4 lists the published records of the fig wasp associations for the 15 *Ficus* species, though these associations require confirmation in the Madang area. Anecdotal observations showed that, among other insects reared from syconia, Curculionidae, Cecidomyiidae, Phoridae and Crambidae are also present in the Madang area.

(b) Leafhoppers

In total, 5035 specimens of Auchenorrhyncha, representing 166 species from 18 families, were collected from the foliage of the 15 *Ficus* species. This figure does not include all the species feeding on these various *Ficus*, as new species were still being found at a high rate. In addition, it includes transient species, as no feeding experiments were performed. The Cicadellidae and Derbidae were the most species-rich families, while Aphrophoridae was the most abundant one (Table 19.5). Phloem feeders were by far the most species-rich guild (122 species from 15 families), followed by xylem feeders (23 species of Aphrophoridae, Cercopidae, Cicadidae and Cicadellinae) and mesophyll feeders (21 species of

Table 19.4 Fig wasps reported in the literature to be associated with the *Ficus* species studied in the Madang area (Ulenberg, 1985; Boucek, 1988; Wiebes, 1994)

Ficus species	*Pollinator*	*'Parasitoids'*
F. bernaysii	*Ceratosolen hooglandi* Wiebes	*Apocrypata meromassa* Ulenberg
F. botryocarpa	*Ceratosolen corneri* Wiebes	?
F. conocephalifolia	*Kradibia jacobsi* (Wiebes)	*Sycoscapter conocephalus* Wiebes
F. copiosa	*Kradibia copiosae* (Wiebes)	*Grandiana armadillo* Boucek
F. dammaropsis	*Ceratosolen abnormis* Wiebes	*Tenka percaudata* Boucek
F. hispidioides	*Ceratosolen dentifer* Wiebes	*Apocrypta mega* sp.
F. microcarpa	*Eupristina verticillata* Waterson	*Acophila* sp., *Epichrysomalla* sp., *Walkerella 'kurandensis'* Boucek, *Odontofroggatia corneri* Wiebes *O. galili* Wiebes, *O. ishii* Wiebes
F. nodosa	*Ceratosolen nexilis* Wiebes	?
F. phaeosyce	?	?
F. pungens	*Ceratosolen nanus* Wiebes	*Sycoscapter* spp.
F. septica	*Ceratosolen bisulcatus* (Mayr)	?
F. tinctoria	*Liporrhopalum gibbosa* Hill	*Neosycophila* sp.
F. trachypison	?	?
F. variegata	*Ceratosolen appendiculatus* (Mayr)	*Apocrypta caudata* (Girault)
F.wassa	*Kradibia wassae* (Wiebes)	*Epichrysomalla 'atricorpus'* Girault *Grandiana wassae* Wiebes

Typhlocybinae). Xylem feeders however dominated in terms of abundance.

Approximately half of the leafhopper species were collected from a single *Ficus* species, but this included many species found as singletons which could not be used in analysis of host preferences (Figure 19.1a). Even after the exclusion of singletons from the analysis, there was a strong correlation between the number of individuals collected (log transformed) and the number of fig hosts (Figure 19.1b; regression calculated by Bartlett's three group method, as the error of both the *X* and *Y* variables is unknown and the data are non-normal; Sokal and Rohlf, 1981). This regression predicted that a sample of only three individuals was needed in order to collect a species from two *Ficus* host species. In fact, all species collected in more than five individuals were found on at least two *Ficus* hosts (Figure 19.1b). On average, xylem feeders have a wider host plant range (7.7 *Ficus* spp. per species; singletons excluded from the analysis) than mesophyll and phloem feeders (3.8 and 4.6 *Ficus* spp. per species, respectively; host range differs significantly between feeding modes; Kruskal-Wallis test, $P < 0.05$; Figure 19.2).

Table 19.5 Species richness and abundance of the most important families and guilds of leafhoppers (Auchenorrhycha) collected in the Madang area

Family/guild	*No. of species*	*No. of individuals*
Cicadellidae	48	1267
Derbidae	33	170
Flatidae	18	270
Aphrophoridae	15	2474
Meenoplidae	10	97
Ricaniidae	10	410
Issidae	9	151
Phloem-feeders	122	1426
Xylem-feeders	23	3245
Mesophyll-feeders	21	364

Auchenorrhyncha were the only sap-sucking herbivores sampled systematically, but some attention was also paid to the aphids and psyllids. Despite a considerable sampling effort, no aphids and only seven psyllid species were found on the 15 *Ficus* species in the Madang area. However, we

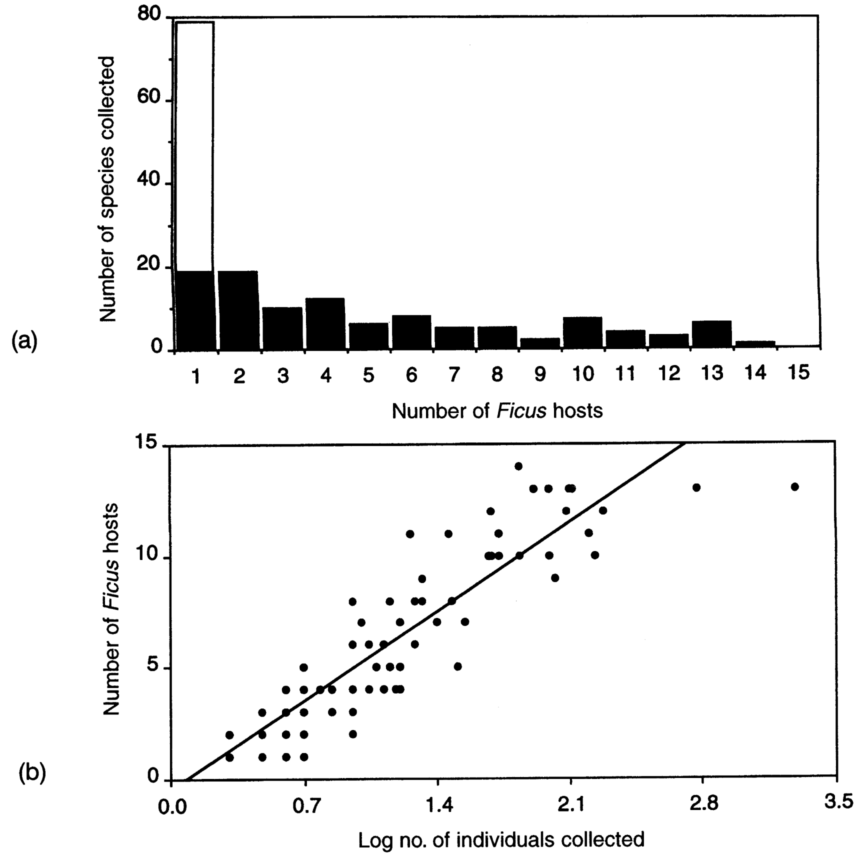

Figure 19.1 Host specificity of leafhoppers in the Madang area. (a) Number of species collected on particular number of *Ficus* species (for single *Ficus* records, empty bar shows number of singleton species). (b) Regression of log number of individuals collected against number of *Ficus* species on which they were collected (Bartlett's three group method: $y = 0.20 + 3.49x$; SE slope = 0.29).

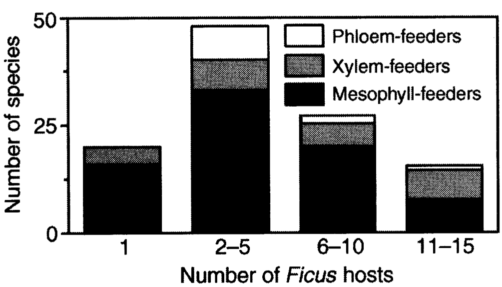

Figure 19.2 Host specificity of phloem-, xylem- and mesophyll-feeding Auchenorrhyncha on *Ficus* species in Madang area (singletons excluded).

recorded aphids feeding on these *Ficus* species in other locations in Papua New Guinea.

(c) Leaf-chewing insects

Overall, 6280 individuals representing 234 species from 21 families of leaf-chewing insects were collected from the 15 *Ficus* species in the Madang area. Despite the extensive sampling effort, the species accumulation curve showed that the number of new species collected grew steadily (Figure 19.3a; leaf-mining species excluded from these data). One explanation for this is that many species collected as singletons may feed only occasionally on *Ficus* (for example, most of the Cerambycidae involved in maturation feeding). In other terms, all the polyphagous species in the different locations visited may not have been sampled yet. However, when the species accumulation curve was plotted for species collected as five or more individuals only, the curve levelled out at about 80 species (Figure 19.3b).

The most important families, as well as the generic identity of some species, are summarized in Table 19.6. Chrysomelidae, Choreutidae, Crambidae (Pyraustinae) and, to a lesser extent, Cerambycidae dominated the samples. The species richness of different subguilds, with regard to the type of foliar damage, was distributed as follows: 66 species 'holing' leaves (chrysomelids, etc.), 58 spp. eating the leaf-margin (various lepidopteran families), 41 spp. gnawing leaves and twigs (cerambycids), 37 spp. tying leaves (choreutids and tortricids), 15 spp. rolling leaves (crambids), 6 spp. mining leaves (gracillariids, etc.) and 5 spp. skeletonizing leaves (choreutids and lycaenids). Many choreutids combined leaf-tying with skeletonizing. No galling insects were recorded.

Many leaf-chewing species were collected from a single species of *Ficus* (Figure 19.4a). However, many of these species were collected as singletons and nothing could be inferred from their host preferences. About half of the species were collected from and fed in the laboratory upon more than one *Ficus* species. On average, each species was feeding on 3.5 *Ficus* hosts (singletons excluded). For example, *Rhyparidella sobrina* (Bryant) and *Choreutis* sp. (an undescribed species: S.E. Miller, personal communication) were recorded on 14 and 13 out of the 15 *Ficus* species studied, respectively.

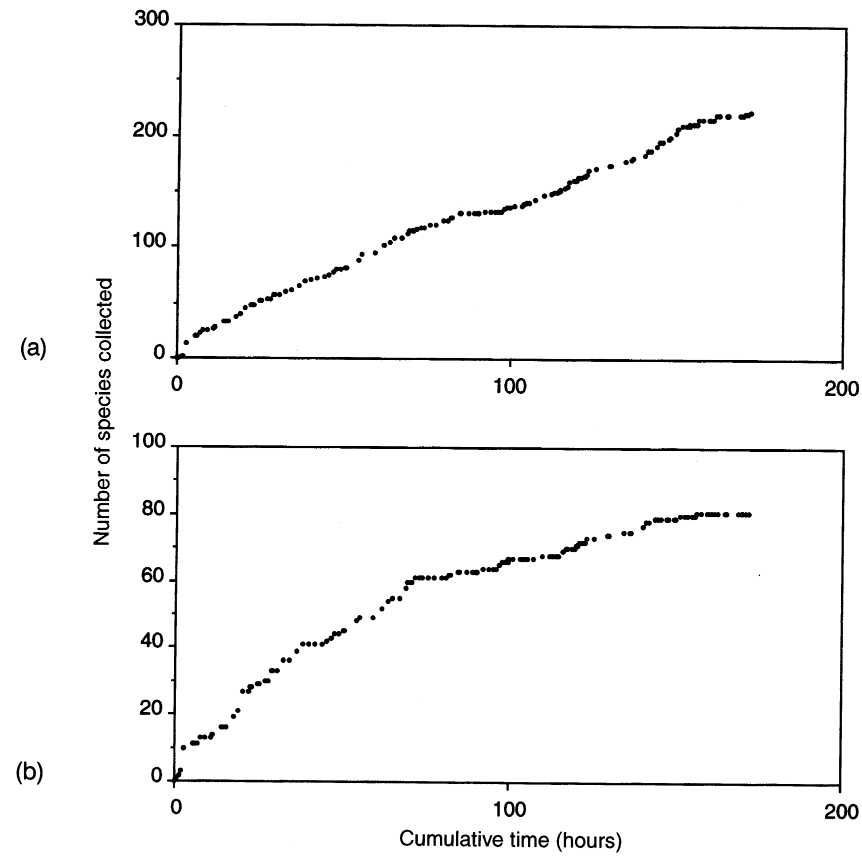

Figure 19.3 Species accumulation curves for leaf-chewing insects with regard to (a) all species collected and (b) species collected as five or more individuals.

Table 19.6 The most important families and guilds of leaf-chewing and stem-boring insects collected in the Madang area, their species richness, abundance and some representative genera identified to date

Family/guild	*No. of species*	*No. of individuals*	*Genera*
Chrysomelidae	50	2864	*Rhyparida, Rhyparidella, Atysa, Sastra*
Cerambycidae	40	149	*Rosenbergia, Epepeotes, Prosoplus*
Choreutidae	23	1793	*Choreutis, Brenthia, Saptha*
Tettigoniidae	16	57	*Sasima, Phyllophora*
Crambidae	15	853	*Talanga, Glyphodes, Parotis*
Tortricidae	14	38	*Adoxophyes*
Curculionidae	13	193	*Apirocalus, Oribius, Rhinoscapha*
Noctuidae	11	82	*Asota, Caryatis*
Phasmatidae	6	19	?
Lymantriidae	6	14	*Euproctis*
Acrididae	5	8	?
Nymphalidae	4	89	*Euploea, Cyrestis*
Pyrgomorphidae	3	21	?
Lycaenidae	2	43	*Philiris*
Eumastacidae	2	5	*?Mnesicles*
Stem-borers	7	15	?
Leaf-miners	6	15	?

Bartlett's three group regression between the number of individuals collected (log transformed, singletons excluded) and the number of *Ficus* hosts predicts that a minimum sample size of four individuals would be needed to collect a particular species from two *Ficus* hosts (Figure 19.4b). Thus, of the 126 species collected from a single *Ficus* species, only 17 species (collected as four or more individuals) were more likely to be monophagous. A further four species were unlikely to be very host specific, since they belong to distinctly polyphagous groups such as Acrididae and Limacodidae. Thus, 13 species (11% of the total number of species, excluding singletons) may be expected to be monophagous. It is probable that this figure is inflated since insects were collected from only 15 *Ficus* species, out of a conservative 40 *Ficus* species found in the Madang area.

19.4 FAUNAL COMPOSITION AND USE OF RESOURCES ON *FICUS*

New field data presented here show unequivocally that many families feeding on the foliage have been overlooked in the literature, namely Derbidae, Flatidae, Aphrophoridae, Chrysomelidae, Tettigoniidae and Tortricidae. This observation is supported by a field study of the insect fauna of *F. nodosa* at a different location (Wau, Papua New Guinea, 1200 m altitude) with different sampling methods (Basset *et al.*, 1996). This disparity between field data and published records is common in the tropics, unlike in countries where the insect fauna is well known (e.g. Southwood *et al.*, 1982, in the UK).

In Auchenorrhyncha, the low number of species reported as feeding on *Ficus*, in comparison with Stenorrhyncha, may be attributed to general lack of information on host plants for the former (see the recent and authoritative review by Wilson *et al.*, 1994). This is supported by the present field data, since all of the *Ficus* species were colonized by many leafhopper species, often at high population densities, whereas Stenorrhyncha were few in terms of both species and individuals. A related problem is the recording or extraction of the information on highly polyphagous taxa. For example, few or no records of Orthoptera, Phasmoptera or Aphrophoridae feeding on *Ficus* were found in the literature, but they are relatively common feeders on *Ficus* in the Madang area.

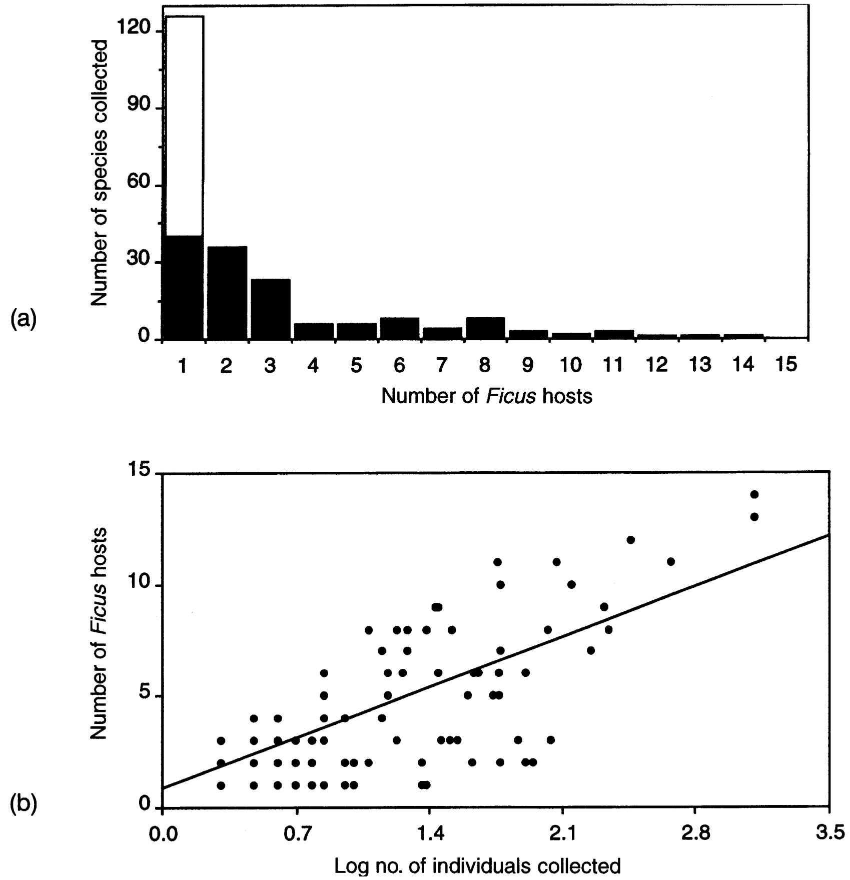

Figure 19.4 Host specificity of leaf-chewing insects in Madang area. (a) Number of species collected on particular number of *Ficus* species (for single *Ficus* records, empty bar shows number of singleton species). (b) Regression of log number of individuals collected against number of *Ficus* species on which they were collected (Bartlett's three group method: $y = -0.75 + 5.94x$; SE slope = 0.26).

Conversely, some groups, such as Psylloidea and Bombycidae, appeared under-represented or absent in the present samples, but relatively species-rich in the database, particularly in the Indo-Australian region. We do not have an explanation for this discrepancy, but Bombycidae appear to be rare in New Guinea (J.D. Holloway, personal communication). Some notably speciose phytophagous groups, such as Aphididae, leaf-feeding Curculionidae and Geometridae, appear to be rare on *Ficus*, as indicated by both the present samples and the database. Unlike psyllids, aphids do not appear to be diverse on *Ficus*. This may be a consequence of the tropical distribution of this genus and of the low species diversity of aphids in the tropics. Aphids appear to be relatively inefficient at finding their host plants in diverse tropical vegetation (Dixon *et al.*, 1987). As for the relative scarcity of the other groups, we cannot offer an explanation.

All resources provided by *Ficus* trees appear to be exploited by arthropods. We could not find specific information about root-feeding arthropods (other than some Tineidae and Gelechiidae feeding on aerial roots), but they exist (see discussion below about Eumolpinae). Perhaps the most distinctive feature of *Ficus* for its primary consumers, in comparison with other tropical trees, is the agglomeration of flowers, fruits and seeds into a single structure, the syconium, which is available throughout the year within local *Ficus* populations. This may account for the diversity of certain taxa consuming syconia, such as Agaonidae, Curculionidae, Drosophilidae and Tephritidae. Most leaf-gallers on *Ficus* are sap-sucking insects and, notably, galling thrips of the family Phlaeothripidae are exceptionally species-rich (Ananthakrishnan, 1978). Leaf-mining species appeared to be scarce, this being confirmed by both literature and field data. This may be related to the presence of lactifers and the probable inefficiency of the trenching strategy for a leaf-miner.

Although segregation of resources appears to prevail among arthropods feeding on *Ficus*, a few species are able to exploit several resources. For example, some sap-suckers, both as adults and larvae, feed on both leaves and syconia (*Acerias*, Eriophyidae, and *Oxycarenus*, Lygaeidae, notably); many Cerambycidae feed on wood as larvae and perform maturation feeding on leaves as adults; some crambid larvae (*Azochis*) feed both in syconia and inside stems; and some choreutid larvae (*Tortyra*) feed both on leaves and inside twigs. In addition, it is probable that many chrysomelids – particularly in the Eumolpinae, the dominant subfamily in the Madang samples – feed on roots as larvae and on the foliage as adults. Free-living chrysomelid larvae on *Ficus* leaves are rare and are found in *Atysa* and *Sastra* (Galerucinae).

19.5 COMPARISON OF ARTHROPOD COMMUNITIES FEEDING ON *FICUS*

19.5.1 BETWEEN ARTHROPOD GUILDS

The literature compilation indicated that arthropods feeding on syconia were much more speciose than sap-sucking and leaf-eating arthropods and, in particular, that records of fig wasps were more abundant than those of leaf-chewing insects. The preliminary field data do not support this: 40 putative fig wasp species (Table 19.7) were found as opposed to 234 leaf-chewing species (Figure 19.3a). A more probable figure may be twice as many leaf-chewing species as fig wasps (Figure 19.3b; the curve levelled out at about 80 species). These discrepancies between literature and field data may merely reflect higher scientific interest in fig wasp communities than foliage-feeding communities, or less complicated sampling procedures for the former. Whilst it is easy to define communities of arthropods feeding on syconia, it is harder to do so for communities of foliage feeders. Specifically, the minimum occurrence of a polyphagous species needed to justify its inclusion in a community of leaf-eating insects feeding on a particular species of *Ficus* is open to discussion. This is beyond the scope of this chapter (but see Basset, 1997).

In contrast with the present field data, mesophyll- and phloem-feeding leafhoppers, particularly those feeding on dicotyledoneous trees, are reported as being host-specific (Claridge and Wilson, 1981; Loye, 1992; Wilson *et al.*, 1994). However, this pattern usually emerges from a comparison of leafhopper assemblages on taxonomically distant host plants, in situations where large complexes of congeneric potential hosts either do not exist (Claridge and Wilson, 1981) or have not been studied (Loye, 1992). The broad host plant range of xylem-feeding leafhoppers on *Ficus* corroborates other data on the wide polyphagy of many xylem feeders. Xylem sap is low in nutrient and secondary metabolites (Raven, 1983) and xylem feeders appear to respond sensitively to nutrient quality of individual plants, but less so to their species identity (Novotny and Wilson, in press).

Although data about the host range of leaf-chewing insects outside *Ficus* are lacking, a study of *F. nodosa* in Papua New Guinea and comparison with nine other tree species belonging to different plant families (Basset *et al.*, 1996) suggests that *Ficus*-chewers are relatively specialized. Apparently more restricted host ranges of leaf-chewing than sap-sucking insects on *Ficus* (compare Figures 19.1 and 19.4, particularly the slopes of the regressions) may be explained at least in part by the different nature of each data set (that for leafhoppers includes transient species). However, mesophyll feeders and leaf-chewing insects appear to have a similar host range (average 3.8 and 3.5 *Ficus* spp., respectively) and this may reflect simi-

Table 19.7 Species of *Ficus* studied and the number of species of fig wasps, leafhoppers, leaf-chewing insects, birds and mammals that they support in the Madang area (in each of the four last taxa, the figures for the five most species-rich fig species are indicated in bold)

Ficus species	*Wasps*	*Leafhoppers*	*Chewing insects*	*Birds*	*Mammals*
F. bernaysii	3	40	30	**32**	14
F. botryocarpa	3	36	32	0	3
F. conocephalifolia	2	**49**	**52**	0	1
F. copiosa	2	**58**	**62**	2	14
F. dammaropsis	2	37	38	0	14
F. hispidioides	3	38	31	0	2
F. microcarpa	4	15	20	**39**	14
F. nodosa	2	45	44	1	**17**
F. phaeosyce	2	**49**	34	**27**	14
F. pungens	2	**48**	37	**40**	**15**
F. septica	4	32	22	0	11
F. tinctoria	4	10	23	15	**16**
F. trachypison	?	46	**45**	22	14
F. variegata	3	43	**59**	1	**16**
F.wassa	4	**67**	**57**	**32**	**15**
All *Ficus* spp	> 40	166	234	59	17

lar ecological constraints in sucking cell contents and eating leaf tissues.

19.5.2 BETWEEN GEOGRAPHICAL LOCATIONS

If groups for which literature data are certainly under-represented and those which were not targeted in field collections are excluded, the composition of the Madang samples at a higher taxonomic level appear to be similar to that of the fauna that feeds on *Ficus* elsewhere, with two major differences.

First, in Costa Rica, Janzen (1979) observed that *Ficus* does not support a rich fauna of foliage-feeding insects. In the database, Neotropical records of leaf-chewing insects represent less than a quarter of similar Indo-Australian records. In Papua New Guinea, Basset *et al.* (1996) showed that *Ficus nodosa* supports a rather rich and specialized fauna of leaf-chewing insects, in comparison with other tree species. Since *F. nodosa* is not exceptional in this respect, in comparison with other *Ficus* species (our field data), this suggests that the fauna of foliage-feeding insects on *Ficus* in New Guinea may be relatively rich and diverse compared with elsewhere. This may be a result of the considerable diversity and endemism of *Ficus* in New Guinea. One possible example of a durable association may be between *Ficus* and the Choreutidae, the latter particularly well represented in our samples. However, whether this merely indicates uneven sampling between different locations is not known. Few data on choreutids are available, presumably because they are day-flying moths and caught rarely by light trapping. An alternative or additional explanation for a rather depauperate leaf-chewing fauna on *Ficus* in the Neotropics, in comparison with the Indo-Australian region, may be related to the rather coriaceous leaves of monoecious figs, prevalent in the former region (Berg, 1989). Unfortunately, comparative data are lacking to explore this possibility.

Second, the overall richness of the fig wasp fauna for the 15 *Ficus* species in the Madang area was considerably lower than that reported for southern African species (an average of three wasp species per fig species in Madang, 11 wasp species in southern Africa: Compton and Hawkins, 1992). One explanation for this difference may involve the different mating systems within *Ficus*. All but one species of *Ficus* in the African study were monoecious, whereas all but one species in Madang were (gyno)dioecious. In contrast with monoecious figs, only male trees within (gyno)dioecious figs represent a suitable resource for wasp pollinators (Weiblen *et al.*, 1995). Overall, wasp assemblages of (gyno)dioecious figs may be rather depauperate, because many non-pollinating wasps depend on the presence of males of the pollinating species to chew exit holes (Bronstein, 1992). The only (gyno)dioecious species in the African study (*F. capreifolia*) supported only three wasp species, which is similar to our data for (gyno)dioecious figs in Madang. Furthermore, at least the published records for *F. microcarpa* (Table 19.4) suggest that this monoecious species supports a richer assemblage of fig wasps than its local (gyno)dioecious counterparts. However, it is unlikely that these considerations apply to other arthropods feeding on syconia (e.g. curculionids, drosophilids, pyralids, etc.).

19.6 KEYSTONE RESOURCES FOR *FICUS*-FEEDING INSECTS AND VERTEBRATES IN THE MADANG AREA

In Table 19.7, we presented a summary of the number of insect species supported by the 15 species of *Ficus* studied in the Madang area, as well as the number of bird and mammal species that regularly feed on the syconia of these species. The latter information was derived from discussion with villagers in Baitabag and Ohu, using the identification guides of Beehler *et al.* (1986) and Flannery (1990). These local records may be conservative and biased towards game species but, nevertheless, they suggest that the most important species for frugivorous birds are *F. pungens*, *F. microcarpa*, *F. bernaysii*, *F. wassa* and *F. phaeosyce*, whilst the most important species for frugivorous mammals are *F. nodosa*, *F. variegata*, *F. pungens*, *F. tinctoria* and *F. wassa*. No significant correlation existed between the number of bird and mammals species supported by each *Ficus* species ($r = 0.44$, $P = 0.10$). Conversely, there was strong correlation between the number of sap-sucking and leaf-chewing species supported by each *Ficus* species ($r = 0.80$, $P < 0.001$). The five most important species for foliage-feeding insects appear to be *F. wassa*, *F. copiosa*, *F. conocephalifolia*, *F. variegata* and *F. trachypison*.

Two of the important species for vertebrates (*F. microcarpa* for birds and *F. tinctoria* for mammals) appear particularly unattractive for foliage-feeding insects and two of the most important species for insects (*F. copiosa* and *F. conocephalifolia*) were not notably so for vertebrates. Further, the syconia of *F. variegata* and *F. nodosa*, while eaten by many mammals, are too big for many birds to swallow or seize. Thus, poor correlation between sap-sucking, leaf-chewing insects, birds and mammals suggests that the keystone species concept does not universally apply to all of these groups, whatever the abundance of the fig species is. In addition, the fig species supporting the highest number of consumer species of different guilds, *F. wassa,* sustains only 175 out of a total of 516 animal consumers in the system (34%, Table 19.7). *F. wassa* is a very common species in the study area (Table 19.3: it ranks second in abundance of all *Ficus* species) and its local impact on animal communities is predictable from its abundance. The present field data lead to the conclusion that the keystone concept cannot be applied across different guilds feeding on *Ficus* in the Madang area.

There are at least two further problems with the keystone concept when applied to *Ficus*. First, community-level studies in Borneo and peninsular Malaysia supported the vertebrate keystone idea (Leighton and Leighton, 1983; Lambert and Marshall, 1991), whereas other studies in Africa and India did not, as the dietary importance and seasonal availability of syconia were too low (Gautier-Hion and Michaloud, 1989; Borges, 1993). Second, the data for both herbivorous insects and vertebrate frugivores suggest substantial overlap between the faunas supported by the *Ficus* species studied (Table 19.7; compare the sum of the number of species supported by each *Ficus* with the number of species cross-checked in the last entry). Therefore, it is unlikely that any single species of *Ficus* could act as a reservoir for a specific and diverse fauna. In conclusion, we cannot confirm that any single species of *Ficus* can be considered as a keystone species for the *Ficus*-feeding insect community in the Madang area. However, whether the various species of *Ficus* could be viewed collectively as 'keystone', providing resources to a large and diverse array of consumers, remains to be considered. For example, we do not have sufficient data to discuss whether the genus *Ficus* harbours a rich and diverse insect fauna, distinct from that feeding on other speciose genera of trees in the tropics.

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