

## Figs (*Ficus*, Moraceae) in Urban Hong Kong, South China<sup>1</sup>

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### ABSTRACT

Hong Kong (22°N) is on the northern margins of the Asian tropics and has a native fig flora of 24 species. A total of 3.4 km<sup>2</sup> of the urban area on Hong Kong Island was surveyed for spontaneous and planted fig plants of reproductive size. The 1124 individuals included 14 species in four subgenera: seven native species (*F. fistulosa*, *F. hirta*, *F. hispida*, *F. microcarpa*, *F. pumila*, *F. subpisocarpa*, and *F. variegata*), four of which were sometimes planted, one probably native (*F. virens*), one naturalizing species (*F. religiosa*), and five exotic species that occurred only in cultivation, two of which (*F. altissima*, *F. rumphii*) are pollinated and produce viable seeds. The native species in the two most common subgenera form distinct ecological guilds: those in subgenus *Sycomorus* bear large, many-seeded, green or yellow figs and are bat-dispersed pioneers on exposed soil; those in subgenus *Urostigma* bear small, few-seeded, dark-purple figs and are largely bird-dispersed and epilithic. The density of potentially fruiting fig plants in the study area (2.3/ha) was within the range reported for tropical forests and between them they were visited by the entire urban frugivore fauna. This study shows the importance of the urban fig flora to urban wildlife and also highlights the risk of cultivated *Ficus* species becoming invasive, despite their obligate species-specific pollinator mutualisms.

*Key words:* China; frugivory; invasive species; seed dispersal; urban ecology.

*FICUS* IS THE MOST IMPORTANT PLANT GENUS for tropical frugivores (Shanahan *et al.* 2001). In some communities, figs may be “keystone resources” that allow an area to support a higher density and/or diversity of frugivores than it could otherwise. Individual fig species, however, are not equally important for all fig eaters and throughout the tropics there are discrete guilds of fig species that differentially attract subsets of the local frugivore fauna (Shanahan *et al.* 2001). Figs, both planted and spontaneous are diverse and abundant in many tropical cities and are probably very important for urban wildlife. These urban fig communities are of considerable interest, not only because they provide an opportunity to look at the relationships between an entire fig flora and an entire frugivore fauna, but also because figs are becoming an increasing pantropical weed problem, with a potential to spread into natural communities (McKey 1989, Nadel *et al.* 1992, Beardsley 1998). Furthermore, urban areas provide a series of similar habitats replicated in different climatic zones and different biogeographical regions, thus giving an opportunity for global comparisons that is not present with more natural habitat types.

Hong Kong (22°N) is on the northern margins of the East Asian tropics, with a thermal climate similar to that of southern Florida. The temperature has fallen to 0°C only once in the last 150 years in the main urban areas around Victoria Harbour, but frosts are more frequent inland and occur most years above 700 m altitude (Dudgeon & Corlett 2004). Rainfall is also seasonal, with 77% of the mean annual total of 2214 mm falling between May and September. Despite this rather marginal climate for figs, 24 native species have been recorded in Hong Kong (Hong Kong Herbarium 2004), compared with 2 in Florida and 21 in all of Mexico, with representatives from all six currently recognized subgenera (Zhou & Gilbert 2003).

Urbanization in Hong Kong is constrained by rugged topography, so the 7 million human population is largely confined to

only 20% of the total land area of 1100 km<sup>2</sup> (Dudgeon & Corlett 2004). Most of the rest is still rural in character, although the original forest cover was cleared centuries ago and replaced by a mosaic of fire-maintained grassland, shrubland, and secondary forest. Hong Kong is thus characterized by very high urban population densities, very sharp urban/rural contrasts, and only a small area of low-density suburbs. Much of the urban area is on terraced hillsides, and the slopes between terraces are the major habitat for spontaneous urban figs. Exposed rock surfaces and stone retaining walls (Jim 1998) are favored by epiphytic species, whereas areas covered with soil support ground-rooted species. Fig trees are also widely planted in urban parks and along the few roads wide enough to accommodate them. The aims of this study were to investigate the ability of native and exotic fig species to establish in a tropical city and to assess their role in the maintenance of urban wildlife.

### METHODS

Fig plants of reproductive size were identified and counted in the urban areas of northwest Hong Kong Island (from Central to Sandy Bay) in 2004. The study area of approximately 3.4 km<sup>2</sup> is on terraced hillsides and flat land reclaimed from the sea and consists largely of commercial districts and ultra-high density residential areas, with smaller areas of lower-density housing, public parks, and private gardens. Areas of semi-natural vegetation on natural topography were excluded. The cut-off for minimum reproductive size in the *Urostigma* species was the estimated crown volumes of the smallest trees that regularly reproduced. Height and the presence of fruiting scars were used for the dioecious trees and shrubs, and the overall size for *F. pumila*. However, plants above these minima do not necessarily reproduce. Each plant was identified as spontaneous or planted, although this was often not clear for *Ficus microcarpa* and *F. virens*, in which individuals planted in the soil may engulf surrounding artificial structures and *vice versa*.

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For each species, at least 20 large individuals (or all accessible individuals if fewer) were kept under regular observation to determine if they initiated syconia, if these were pollinated, and which animals ate the ripe syconia. Frugivory observations included a total of at least 2 h of nocturnal observations and 6 h of diurnal observations at ripe crops on at least five individuals of each species, for all except the rare or rarely fruiting *F. altissima*, *F. rumphii*, *F. hirta*, and *F. pumila*. I have also made use of 16 years of informal, but systematically recorded, observations in the same area, so that infrequent fig crops, rare pollinators, and unusual frugivores are unlikely to have been missed. This extended study period also allowed detection of trends in the abundance of individual fig species. Additional time depth is provided by a comprehensive nineteenth century flora of Hong Kong Island (Bentham 1861), a survey of the figs of Hong Kong, based in the study area, in 1962–1964 (Hill 1967), a survey of wall plants, largely in the study area, in 1985–1987 (Chan 1992), and a survey of wall trees on Hong Kong Island in 1996 (Jim 1998).

## RESULTS

A total of 1124 fig plants of potential reproductive size were identified in the study area. This included 14 species in four subgenera

(Table 1, 2): seven native species, four of which were sometimes planted, one species of uncertain status (*F. virens*), one apparently naturalizing species (*F. religiosa*), and five exotic species that occurred only in cultivation. An additional four exotic species (*F. benghalensis* L., *F. binnendijkii* Miq., *F. lyrata* Warb., and *F. triangularis* Warb.) were represented only by immature plantings. Eleven species in the study area—the natives (including *F. virens*), *F. religiosa*, and the planted exotics *F. altissima* and *F. rumphii*—produced syconia that were pollinated and developed into normal ripe figs. The syconia of *F. drupacea* were not pollinated, but developed to their reported natural mature size and color. The syconia of *F. elastica* softened and turned red, but did not expand, whereas those of *F. benjamina* were shed when hard and green. An additional 16 fig species are native to Hong Kong (*F. concinna* Miq., *F. erecta* Thunb., *F. esquiroliana* Lévl., *F. formosana* Maxim., *F. hederacea* Roxb., *F. langkokensis* Drake, *F. nervosa* Roth., *F. pandurata* Hance, *F. pyriformis* Hook. & Arn., *F. sagittata* Vahl, *F. sarmentosa* Sm., *F. subulata* Bl., *F. simplicissima* Lour., *F. tinctoria* G. Forst., *F. variolosa* Benth., *F. vasculosa* Miq.; Hong Kong Herbarium 2004), but were not found in the urban study area.

Four species in subgenus *Urostigma* were represented by spontaneous plants in the study area (Table 1). All four are monoecious lithophytes or epiphytes and do not usually establish on the ground, although they grow well if planted. They all bear small, few-seeded

TABLE 1. Native and exotic fig species established in urban Hong Kong: sexual system (monoecious or dioecious), local status, distance to nearest native population (from the literature), presence of the species-specific pollinator, presence of spontaneous seedlings, substrate(s) on which it grows spontaneously in Hong Kong, maximum height in Hong Kong.

Species	Sexual system	Status in HK	Nearest native (km)	Pollinator present?	Seedlings present?	Substrate	Plant height (m)
Subgenus <i>Urostigma</i>							
<i>F. altissima</i> Blume	Mono.	Cultivated	400	Yes	No	—	(25) <sup>a</sup>
<i>F. benjamina</i> Linn.	Mono.	Cultivated	300	No	No	—	(20) <sup>a</sup>
<i>F. drupacea</i> Thunberg	Mono.	Cultivated	450	No	No	—	15
<i>F. elastica</i> Roxb.	Mono.	Cultivated	1500	No	No	—	20
<i>F. microcarpa</i> Linn.f.	Mono.	Native	—	Yes	Yes	Hard <sup>b</sup>	20
<i>F. religiosa</i> Linn.	Mono.	Naturalizing	2500	Yes	Yes	Hard	15
<i>F. rumphii</i> Blume	Mono.	Cultivated	1500	Yes	No	—	18
<i>F. subpicarpa</i> Gagnep.	Mono.	Native	—	Yes	Yes	Hard, trees	8
<i>F. virens</i> Aiton	Mono.	Native?	?	Yes	Yes	Hard	25
Subgenus <i>Sycomorus</i>							
<i>F. fistulosa</i> Blume	Dioec.	Native	—	Yes	Yes	Soil	4
<i>F. hispida</i> Linn.f.	Dioec.	Native	—	Yes	Yes	Soil	5
<i>F. variegata</i> Blume	Dioec.	Native	—	Yes	Yes	Soil	15
Subgenus <i>Ficus</i>							
<i>F. hirta</i> Vahl	Dioec.	Native	—	Yes	Yes	Soil	3
Subgenus <i>Synoecia</i>							
<i>F. pumila</i> Linn.	Dioec.	Native	—	Yes	Yes	Soil	Climb.

<sup>a</sup>In the region, none yet mature in Hong Kong.

<sup>b</sup>Walls, rocks, and other hard surfaces.

TABLE 2. *Fig species as a resource for wildlife in urban Hong Kong: number of individuals of reproductive size (spontaneous and cultivated), ripe fig diameter, seed number, color, consumption by birds and bats, and maximum number of fig crops per year (for female plants in the dioecious species).*

Species	No. of plants		Fig diam. (mm)	Mean seed no.	Ripe fig colors	Consumed by		Maximum no. crops year <sup>-1</sup>
	Spont.	Cult.				Birds	Bats	
Subgenus <i>Urostigma</i>								
<i>F. altissima</i>	0	31	24	268	Dark red	?	?	?
<i>F. benjamina</i>	0	83	—	—	—	—	—	—
<i>F. drupacea</i>	0	1	(20) <sup>a</sup>	0	Orange <sup>a</sup>	Yes	Yes	3
<i>F. elastica</i>	0	19	(6) <sup>a</sup>	0	Red <sup>a</sup>	Yes	No	—
<i>F. microcarpa</i>	353	62	11	12	Pink-black	Yes	Yes	4
<i>F. religiosa</i>	0	14	12	35	Pink-purple	Yes	No	2
<i>F. rumphii</i>	0	2	11	?	Pink-purple	Yes	?	3
<i>F. subpisocarpa</i>	66	2	12	20	Pink-black	Yes	Yes	4
<i>F. virens</i>	47	8	11	67	Pink-black	Yes	Once	2
Subgenus <i>Sycomorus</i>								
<i>F. fistulosa</i>	19	0	20	745	Green-yellow	no	Yes	4
<i>F. hispida</i>	299	0	26	1092	Yellow	no	Yes	Continuous
<i>F. variegata</i>	94	0	25	700	Green-yellow	no	Yes	4
Subgenus <i>Ficus</i>								
<i>F. hirta</i>	17	0	15	305	Dark red	Yes <sup>b</sup>	No	Continuous
Subgenus <i>Synoecia</i>								
<i>F. pumila</i>	2	6	60	?	Purple	No	Yes <sup>b</sup>	2

<sup>a</sup>Soft but seedless.<sup>b</sup>Nonurban observations.

figs on the twigs and branches, which ripen to pink then dark purple or black. *F. virens* is largely confined to urban and village areas in Hong Kong and is possibly an introduction, although it was recorded here in the nineteenth century (Bentham 1861), is native in the region, and occurs in apparently natural habitats in adjacent parts of China. *F. religiosa* is a long way outside its natural range in northern India and was not planted widely until recently, but seedlings and saplings are now very common on walls and other suitable substrates in urban areas. It appears to be in the process of naturalization, but none of the spontaneous individuals in the study area were large enough to reproduce. The species in the other three subgenera are all dioecious and establish in soil. All three species in subgenus *Sycomorus* bear large, many-seeded figs that ripen to green or yellow. *F. hispida* is commonest and can start producing a few syconia when less than 1 m tall. *F. fistulosa* is rare in urban areas, being largely confined to shaded, damp sites near the urban fringes. In the other two dioecious subgenera, *F. hirta* is a shrub with bristly dark red seed figs, found only in three, densely wooded sites, whereas *F. pumila* is a climber with huge purple seed figs.

The density of potentially fruiting fig plants within the study area, including all native and naturalized *Urostigma* species (1.6/ha) and half the plants of the dioecious species (*i.e.*, assuming half are male), was approximately 2.3/ha. Fig phenology was not quantified during this study, but ripe figs of all the native or naturalizing species, except *F. fistulosa*, *F. pumila*, *F. religiosa*, and *F. virens*, could

be found in every month in 2003–2004. The gaps for most of these species probably reflect only their smaller sample sizes, but there were periods of several months when no syconia of *F. religiosa* were seen in or out of the study area. Crop sizes ranged from one to a few ripe syconia at a time over a long period in *F. hispida* and *F. hirta*, to tens of thousands of syconia ripening over 1–3 weeks on large individuals of *F. microcarpa* and *F. subpisocarpa*.

Only fruit bats (and occasionally squirrels, see below) were observed taking seed figs from the three *Sycomorus* species, *F. fistulosa*, *F. hispida*, and *F. variegata*. Most of the bat visitors were *Cynopterus sphinx*, but some larger individuals may have been the only other fruit bat in Hong Kong, *Rousettus leschenaulti*. Fruit bats were also common nocturnal visitors to large crops of the *Urostigma* species, *F. microcarpa* and *F. subpisocarpa*, but were only recorded once at *F. virens* and never at *F. religiosa*. However, *C. sphinx* eats *F. religiosa* in India (Bhat 1994). Bats also took the ripe but seedless syconia of *F. drupacea*. The “steady-state” fruiting of *F. hispida* attracted solitary bats whereas the “big-bang” fruiting of the *Urostigma* species attracted small groups. The bats flew off with single large figs from the dioecious species, but apparently harvested several small figs at a time from the *Urostigma* species. Fruit bats were less active on moonlit nights, but regularly visited fig trees along brightly lit urban roads. Fruit processing by bats was not observed, but *C. sphinx* typically shuttles between fruiting trees and a nearby feeding roost where fruit is processed (Corlett 1998). However, fibrous pellets

containing some seeds were occasionally seen under isolated trees of *F. microcarpa* in quiet localities, where the bats had apparently processed the syconia before leaving the fruiting tree.

All the native and naturalizing *Urostigma* species were also consumed by birds, which probably remove many more ripe syconia than do bats. Five passerine frugivores (*Pycnonotus jocosus*, *P. sinensis*, *Zosterops japonica*, *Acridotheres cristatellus*, and *Sturnus nigricollis*) and one non-passerine (*Eudynamis scolopacea*) were seen consuming all four species. By far the most common consumers were the bulbuls, *P. jocosus*, and *P. sinensis*, followed by the Japanese white-eye, *Z. japonica*, all of which visited fruiting trees in all urban habitats. Mynahs (*A. cristatellus*) usually foraged in flocks and only visited the largest crops. All the other frugivorous or partly frugivorous birds recorded in urban areas were seen consuming at least *F. microcarpa* and/or *F. subpisocarpa*, and sometimes the other two *Urostigma* species. The same bird species also ate the soft but unexpanded syconia of *F. elastica* and most of them also pecked pieces from the larger seedless syconia of *F. drupacea*. No consumption of either *F. hirta* or *F. pumila* was seen in the study area, but ripe figs of *F. hirta* are eaten by a variety of birds in rural areas and those of *F. pumila* are taken by fruit bats.

The tree squirrel, *Callosciurus erythraeus*, introduced to Hong Kong Island around 30 years ago (Dudgeon & Corlett 2004), was occasionally seen consuming all the common urban fig species, usually before they were ripe enough for bats or birds, but only *F. variegata* seems to form a significant component of its diet. The masked palm civet, *Paguma larvata*, enters the outer fringes of urban areas in Hong Kong. I have second-hand reports of these civets feeding in trees of *F. variegata* and *F. virens* at urban fringe sites and *F. microcarpa* and *F. subpisocarpa* at rural sites.

## DISCUSSION

**URBAN FIG GUILDS.**—The native species of the two most important subgenera form distinct ecological guilds in urban Hong Kong. Species in subgenus *Sycomorus* are bat-dispersed pioneers on exposed soil, whereas the *Urostigma* figs are largely bird-dispersed and largely epilithic. There is a degree of overlap, particularly on soil-backed retaining walls, where *F. hispida* may share a crack with a *Urostigma* fig and both be visited by bats; but in general the differences are as great as the similarities that come from shared membership of a highly distinctive genus. Shanahan and Compton (2001) recognized six seed dispersal guilds among 34 *Ficus* species in lowland rain forest at Lambir, Sarawak, including "fruit bat figs" and "mixed bird figs," with fig characters similar to the two guilds in urban Hong Kong. The much larger data set on fig consumption accumulated by Shanahan *et al.* (2001) shows that, whereas the observations in urban Hong Kong are typical for the same species studied in other habitats, other species in the same subgenera attract a different range of dispersal agents, so dispersal biology is not entirely confounded with phylogeny.

Fruit bats are probably excellent dispersal agents for figs because the seeds are small enough for many to be swallowed and defecated in flight (Corlett 1998). Although normal gut passage times are

very short (10–15 min), *C. sphinx* has been shown to retain some fig seeds in the gut for over 12 h (Shilton *et al.* 1999), so maximum dispersal distances will be constrained only by the home range of the bat. The major avian fig consumers are all effective seed dispersal agents (Corlett 1998, 2002). White-eyes have small gaps and ate the syconia piecemeal, whereas the others usually ate whole syconia, after a varying amount of manipulation. Spotted doves (*Streptopelia chinensis*) ate fallen figs of all the *Urostigma* species off the ground, but probably destroyed most or all of the seeds in their muscular gizzards. The squirrels are also assumed to be seed predators, although this assumption needs testing. Dispersal by birds and bats would be expected to result in very different seed shadows, because birds usually defecate only from perches (McClanahan & Wolfe 1993, Corlett 1998). Most fig seedlings were at sites where the seed could equally well have been deposited by a perching bird or flying bat, but only the bat-dispersed dioecious species establish on bare soil in open sites, where bat dispersal would be an obvious advantage.

**FIGS AND URBAN WILDLIFE.**—Fig densities in the urban study area are within the range of 1–14 *Ficus*/ha reported from a variety of tropical forests (McPherson 1999), highlighting their potential importance for urban wildlife. The density in the study area is at the upper end of fig densities in urban Hong Kong, particularly for spontaneous *Urostigma* figs, but the same species are present in all urban areas visited. Fig trees in urban Hong Kong fruit all year round and between them attract the entire urban frugivore fauna. As Shanahan *et al.* (2001) point out, however, before urban figs can be considered a keystone resource, it is necessary to show that non-fig food is in limited supply for at least part of the year. In semi-natural communities in Hong Kong, there is an annual February–April trough in fruit production (Corlett 1993), the earlier part of which coincides with a trough in insect availability (Kwok & Corlett 2002). However, in urban areas, cultivated and naturalized exotics partly fill the fruit gap (Corlett, pers. obs.) and artificial irrigation may partly ameliorate the insect shortage. Although no other urban plant species attracts as many birds and bats as a large *Urostigma* fig, all fig trees in the study area were less than 1.3 km from nonurban habitats, which is well within the normal foraging range of both bulbuls and *Cynopterus* fruit bats (J. E. S. Weir & Corlett, pers. obs.). The case for urban keystone status is strong but unproven.

Crude nutritional value data are available for the ripe figs of all species except *F. religiosa* and *F. virens* (Corlett 1996, Ko *et al.* 1998). All are pulpy (seeds <5% of syconia fresh weight) and watery (79–87%), with high total soluble carbohydrate (37–71% of dry weight) contents and low lipid (<4%) and nitrogen (<2%) contents. Compared with the median values for 153 native fruit species in Hong Kong (Corlett 1996), seeds make up a smaller percentage of ripe fig mass, and figs have a higher water content, but they are otherwise unexceptional. Figs of *F. microcarpa* and *F. subpisocarpa* contain only hexose sugars whereas those of *F. hispida* also contain sucrose (9% of dry weight), which in the Hong Kong fruit flora is associated with dispersal by mammals.

POLLINATORS AND INVASIVENESS.—Simulation models for monoecious hemiepiphytes suggest that adult populations of several hundred fig plants are needed to ensure the persistence of the species-specific wasp pollinators (Anstett *et al.* 1997), although the mobility of the wasps means that these fig populations can be spread over hundreds of squared kilometers (Nason *et al.* 1998, Harrison 2003). Much smaller populations may suffice for dioecious species, which often fruit more frequently (Kameyama *et al.* 1999), but their pollinators may not disperse as far (Harrison 2003). Small urban populations of native fig species (*e.g.*, *F. fistulosa*, *F. hirta*, and *F. pumila*) are presumably subsidized by seeds and pollen-carrying fig wasps from the more abundant rural populations. All the major urban seed dispersal agents also occupy the surrounding nonurban habitats and no point in the study area is more than 1.3 km from the secondary forest and shrubland. The availability of this subsidy makes the absence of *Ficus variolosa* (subgenus *Ficus*) from urban habitats surprising, because this shrub is very common in secondary forests and shrublands on the margins of the study area and is dispersed by the same bird species as the urban figs.

The population of reproductive *F. religiosa* in Hong Kong appears to be too small to support a viable population of pollinators, and there were periods of several months when I could not find any syconia in or near the study area. This species was not recorded at all in the 1962–1964 survey (Hill 1967), but there were already spontaneous individuals on walls in the study area by 1985–1987 (Chan 1992) and it has increased in abundance since. It is cultivated as an ornamental all over southern China and the first individuals reaching reproductive size in Hong Kong were presumably pollinated by fig wasps from these trees. *F. rumpffii* is very rare in Hong Kong and 1500 km outside its native range, but there are numerous large, old trees in Macau, 60 km west of Hong Kong, and it is widely planted in southern China because of its resemblance to *F. religiosa*. This species was apparently not pollinated in Hong Kong in 1964 (Hill 1967), so the pollinator may have reached the Hong Kong region more recently. I have seen a few spontaneous seedlings in Macau, but none in Hong Kong. Syconia on the first individuals of *F. altissima* to reach reproductive size in the study area, in 2001, were pollinated. This species has also been cultivated for much longer in Macau, where there are a number of large spontaneous plants in the vicinity of the largest planted individuals, so the arrival of the pollinators in Hong Kong is not surprising. The large (2.5 cm diameter), dark red figs are unlike those of any native species and this species has not spread far in Macau, which has a very similar disperser fauna, suggesting it will do no better in urban Hong Kong.

So far the syconia of the other planted species are not pollinated, but it is probably only a matter of time before some of the species with large planted populations acquire their pollinators. *F. benjamina* is likely to be the first. It grows wild within a few hundred kilometers of Hong Kong and has recently been very widely planted in urban areas, in part because it does not currently produce messy ripe figs. *F. benjamina* has become naturalized in Brisbane (27°S), Australia, >1000 km south of its historic range (McPherson 1999), so Hong Kong's milder thermal climate is unlikely to be any barrier to its establishment. In equatorial Singapore, where it has become naturalized as an epiphyte on trees in urban areas, *F. benjamina* attracts the entire urban frugivore fauna (pers. obs.). *F. altissima*, *F.*

*benjamina*, *F. benghalensis*, *F. elastica*, *F. microcarpa*, and *F. religiosa*, are naturalized to varying extents in Florida (Nadel *et al.* 1992, Wunderlin 1997).

Figs, with their obligate pollination mutualism, may seem unlikely invasive weeds, but their potential has probably been underestimated. Although figs represent the most widely documented case of pollinator-mediated limitation of invasion (Richardson *et al.* 2000), the proportion of cultivated *Ficus* species that has become invasive does not appear to be lower than in genera with generalist pollinators (*e.g.*, Gardner & Early 1996, Nadel *et al.* 1992, Wunderlin 1997). Most pollinators and nonpollinating wasp associates have probably been transported in fig-bearing plant material after planting had established a large enough population of the host fig species to maintain viable wasp populations (McKey 1989). Gardner and Early (1996) suggest that seed set in *F. rubiginosa* in New Zealand may have declined following the later establishment of seed-feeding nonpollinators. *F. religiosa* and *F. virens* have a consistently higher seed set than the two native *Urostigma* figs in Hong Kong, which is consistent with the escape from species-specific seed-feeding wasps, but the cause needs further investigation. If escape from seed-feeders is a significant factor favoring fig invasions, their introduction has obvious potential as a means of control.

The absence of tropical dioecious figs from the list of exotic invaders is interesting, but may simply reflect the fact that no species is commonly cultivated. Dioecy by itself is no barrier to invasiveness, as shown by the escape of the edible fig, *Ficus carica*, from cultivation in Europe, California, Mexico, and Australia (Randall 2000). Among the monoecious figs, many *Urostigma* species, in particular, seem pre-adapted to success in human-dominated landscapes, including urban areas. Small, soft, multi-seeded fruits attract effective dispersal agents in any tropical landscape (Corlett 2002), whereas walls, buildings, and street trees provide an underexploited substrate for growth. Despite their value for urban wildlife, spontaneous fig trees can be a serious nuisance in urban areas because of damage to buildings and other structures, and the mess that ripe figs and frugivores leave on sidewalks and parked cars. Some species may then be able to use large urban populations as a springboard for invasion of natural habitats. Gardner and Early (1996) recommended that planting of the naturalizing Australian figs, *F. macrophylla* and *F. rubiginosa*, be discontinued in New Zealand, and that trees close to areas of conservation importance be eliminated. This may be too drastic a recommendation for Hong Kong, but continued vigilance is warranted.

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