Frugivory, seed dispersal and gene flow of riparian figs in western Thailand

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The candidate confirms that the work submitted is his/her own and that appropriate credit has been given where reference has been made to the work of others.

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Thanate Kerdkaew

Abstract

Fig trees (*Ficus* spp., Moraceae) are widely known as one of the most important plant genera in terms of providing food resources for wildlife. They also have an obligatory mutualism with fig wasps (Agaonidae), which makes fig trees a good subject to investigate coevolution between plants and animals. Many fig tree species are found in high humidity riparian areas, where some display adaptations for seed dispersal by water. However, the majority of research on fig tree seed dispersal has focused on big monoecious strangler fig tree species (Subgenus *Urostigma*), with few studies of smaller shrubby dioecious fig trees. This thesis aims to examine the vegetative and reproductive phenology of riparian fig tree species in Kanchanaburi Province, western Thailand including their interactions with terrestrial and aquatic frugivores, the function of a jelly-like substance produced by one species, and how gene flow has influenced the genetic structure of a second riparian fig tree. Also, current knowledge about global fig tree species and their interactions with vertebrate frugivores, based on published articles, is updated.

The four riparian fig tree species studied are all evergreen. Figs of the dioecious *F. oligodon, F. ischnopoda* and *F. montana* were produced seasonally, with less seasonality of fig production in the monoecious *F. racemosa*. Fig production was likely to be influenced by temperature. Figs of *F. racemosa* were mostly produced towards the canopy level (more than 5 m above the ground), but the other three species tended to produce figs near to ground level. Most fig crops of the three dioecious species, which produced relatively smaller crop sizes than *F. racemosa*, were not visited by any frugivores during observation periods, and uneaten figs mainly fell to the ground or water. Where crops were visited, bulbuls (Pycnonotidae) were the most frequent frugivores visiting the small shrubs *F.*

ischnopoda and *F. montana* and the Grey-bellied squirrel (*Callosciurus caniceps*, Sciuridae) were frequent visitors to the larger fig tree species (*F. oligodon* and *F. racemosa*).

Figs that fell onto the water were consumed quickly by a fish, Blue mahseer (*Neolissochilus stracheyi*, Cyprinidae). However, seeds of *F. montana* ingested by this and another cyprinid fish (*Barbonymus altus*) were mostly destroyed, suggesting their roles are as seed predators rather than dispersers. A mucilaginous jelly covering *F. oligodon* seeds did not attract any ant species. Seeds covered with this jelly did not germinate, but could germinate rapidly once it was removed, suggesting its function is seed germination suppression and probably to protect the seeds from pathogens. Most genetic variation was within rather than between populations of *F. montana*, but extensive gene flow between populations was detected, generated mostly by pollen flow, because gene flow by seed dispersal was limited. This is consistent with the observations that very few frugivores interacted with this fig tree species.

The global review of interactions between vertebrate frugivores and fig trees, which included data from this thesis, showed that the major frugivorous bird families that interact with fig trees are mynahs (Sturnidae), pigeons (Columbidae), bulbuls (Pycnonotidae) and parrots (Psittasidae), and the major families of frugivorous mammals were Old World monkeys (Cercopithecidae), Old World fruit bats (Pteropodidae) and New World fruit bats (Phyllostomidae). Strangler figs had the highest number records of frugivore species interactions, and few small dioecious species had any records of what eats their fruits. The limitations of the relevant literature outlined in an earlier (2001) review are unchanged, with recent records adding to the number of species records, but generally failing to add to a detailed understanding of how fig trees interact with frugivores.

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Chapter 1 General Introduction

1.1 Mutualisms: positive interactions between living organisms

Living organisms have several ways to interact positively with one another (West et al., 2007; Ezoe, 2012), and these interactions often reflect coevolution and coadaption through time among the interacting species (Janzen, 1980). The general definition of mutualism can be stated as the cooperation between two organisms of different species, and each organism gains some benefits from maintaining the interaction (Boucher, 1985; Bronstein, 1994; Connor, 1995). Boucher et al. (1982) proposed that benefits gaining through the interactions can be identified as four major types: nutrition, energy, protection and transportation. Nutrients or other essential factors for growth gained from mutualistic symbionts may be directly absorbed from cooperative partners or transferred among partner pairs, as for example, the nitrogen fixation provided by mycorrhizal fungi to their host plants, while the host plant supplies nutrients produced by photosynthesis to those fungi (Johnson et al., 1997). In addition, the energy produced by mutualist partners can be made available to benefit another, for example, corals can gain energy produced by the photosynthetic algae they contain (Muscatine & Porter, 1977). Another benefit of living together can be protection. The classic example of a protective mutualism is the ant-mealybug association, where ants protect mealybugs from natural enemies by showing their aggressive guarding behavior, and ants get sugar-rich honeydew droplets from mealybugs in return (Rico-Gray & Thien, 1989; Cheng et al., 2015; Zhou et al., 2017). Transportation mutualisms involve the movement of plant pollen (pollination) and seeds (seed dispersal) assisted by animal mutualists (Morin, 2011). Because plants are sessile organisms which have little or no ability to move by themselves, plants needs external vectors that assist them to transfer their genes

(Barrett & Eckert, 1990). Usually dispersal and pollination are mutualistic, because the plants provide rewards to the vectors (usually food).

Some mutualistic interactions have a high degree of specificity, where one species relies on another and cannot survive after being separated from their cooperative partner (Morin, 2011). These are often symbiotic in nature. The relationship between fig trees (Moraceae) and their pollinators (Agaonidae), also, *Yucca* (Asparagaceae) plants and their Yucca moth pollinator are examples of extreme obligate mutualisms because these plants totally depend on one or a small number of specific pollinators to transfer their pollen to conspecifics (e.g. Pellmyr et al., 1996; Rønsted et al., 2005; Cruaud et al., 2012).

1.1.1 Seed dispersal in plants

Seed dispersal is the movement of seeds away from their source plants, usually assisted by abiotic and biotic media, for example, gravity, wind, water, ballistic mechanisms or animals (exozoochory – where seeds are transported by attaching to the outside of animals, such as, fur and skin, or endozoochory – seeds which are ingested into the animal's digestive system and dispersed after defaecation) (Janzen, 1983). Plants relying on abiotic dispersers develop specialized structures to support diaspore dispersal. For example, *Ceiba pentandra* (L.) Gaertn. (Malvaceae) seeds have a fibrous structure around their seeds which allows them to be dispersed by wind effectively (Dick et al., 2007). Also, in Dipterocarpaceae species, the seeds have twin-winged organs assisting dispersal by wind (Sinha & Davidar, 1992). Water can be an important seed dispersal medium. For example, it is suggested that coconuts, (*Cocos* spp., Arecaceae) gain advantage from seed dispersal by water because their seeds are buoyant, having air space inside and a water proof shell which allows seeds to survive while sailing in the ocean (Foale, 2003). Although some seed plants have diaspores (seeds with other structures assisting seed dispersal such as wings, fleshy fruits or elaiosomes) that are dispersed by abiotic media, many rely on animal services, for example, seeds with fleshly fruits that attract frugivorous animals (Howe & Smallwood, 1982). Seed dispersal by animals is considered to be an important process to maintain plant population structures in many habitats around the world and an understanding of seed dispersal provides better understanding about the dynamics of such populations and communities (Howe & Smallwood, 1982; Cain et al., 2000; Herrera, 2002). Globally, more than half of all plant species rely on animals to disperse their seeds (Fleming & Lips, 1991). Nutritious, soft and fleshly fruits have favourable traits that attract frugivores to feed on them and disperse the seeds they contain (Howe & Smallwood, 1982; Herrera, 1982; 1986). This leads to diffuse coevolution, in other words multiple interactions between groups of fruiting plants and several frugivorous animals (Herrera, 1982). An example is the frugivorous feeding guild associated with Melastomaceae (Stiles & Rosselli, 1993), and *Ficus* (Moraceae) (Shanahan et al., 2001). Dispersal depends on some seeds being consumed together with the fruit pulp which acts as a food reward. Then the seeds will be regurgitated or passed through the gut and defaecated. Each frugivore has a different diet, feeding behavior and sites of faecal deposition, causing various seed dispersal patterns (Howe & Westley, 1986). These seeds may be dispersed again by other dispersers, such as ants, causing secondary seed dispersal (Wang & Smith, 2002). After dispersal, seeds must land on suitable sites if they are to germinate and establish successfully. To summarise, seed dispersal consists of several processes, and it can be defined by a seed dispersal loop approach which describes the completed cycle of seed dispersal that occurs from fruit production to sapling recruitment (Wang & Smith, 2002; Fig. 1.1.).

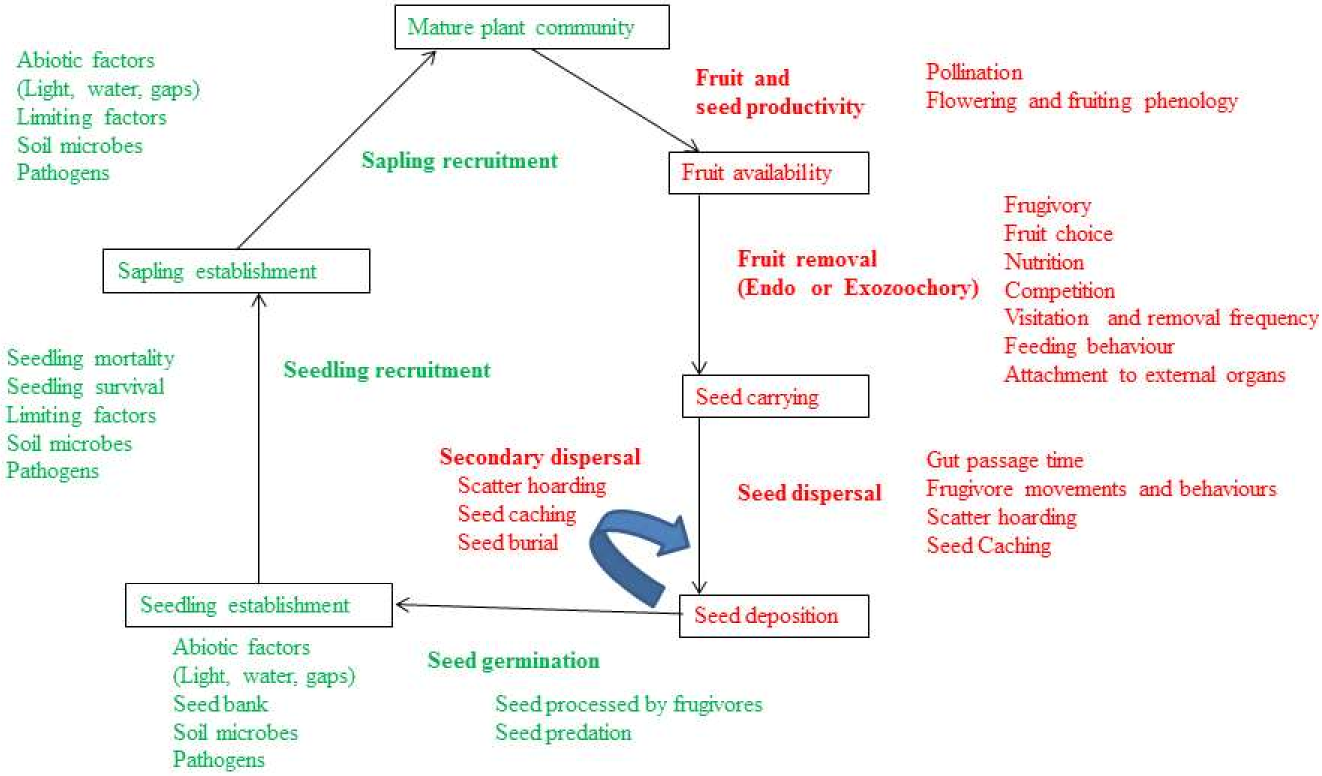

Fig. 1.1. The cycle of plant reproduction and its interactions with animal seed dispersers and biotic and abiotic factors which benefit or reduce reproductive success (Modified from Wang & Smith, 2002).

Howe & Westley (1988) proposed that the benefits of seed dispersal can be summarized by three hypotheses: Firstly, the colonization hypothesis stated that plants would benefit from dispersal into as many new areas as possible because each habitat is changing through time. Therefore, to gain maximum fitness, some plants species have adapted by producing numerous seeds to have more chance to establish on new unpredictable sites after dispersal (Howe & Westley, 1988). This hypothesis is appropriate particularly in open habitats which are in the process of succession, and in dynamic mature habitats where forest gap colonization is important (Howe & Smallwood, 1982; Howe & Westley, 1988). Augsperger (1984) tested the colonization hypothesis by comparing seedling mortality in light-gaps and shaded areas and found out that all the seedlings from nine plant species showed lower mortality rates in light-gaps, supporting the colonization hypothesis.

Secondly, the escape hypothesis, in other words the Janzen-Connell hypothesis, suggests that survival of plant seedlings occurs if they avoid distance and density dependent effects on their mortality (Howe & Smallwood, 1982). Seeds which are dispersed away from parent trees will have a higher chance to survive than undispersed seeds, because seeds which fall under their parent trees are faced with several density-dependent and distance-dependent effects, such as higher seed predation, pathogen infection and competition among seedlings (Howe & Smallwood, 1982; Levin et al., 2003). Several studies have supported this hypothesis, reporting that density-dependent and distance-dependent effects negatively impact on seedling survival (Janzen et al., 1976; Augspurger, 1983; Clark & Clark, 1984). Moreover, it was revealed that seedlings of plants in Panamanian Amazonian forest germinating near their parent trees died due to damage by soil microbiota rather than above ground natural enemies, such as mammals, foliar herbivores or pathogens (Mangan et al., 2010). However, some studies have failed to support this hypothesis. For example, predation of *Brosimum alicastrum* SW. (Moraceae) seeds in the Neotropics was negatively related to seed density (Burkey, 1994). A meta-analysis of seed and seedling predation data from 75 plant species from 147 experiments across 40 studies suggested that there was no strong evidence to support the distance-dependent effects hypothesis and only detected a small significant survival rate reduction in temperate environment (Hyatt et al., 2003). In addition, it was suggested that the hypothesis might explain patterns of seedling survivorship more than seed survivorship (Hyatt et al., 2003; Comita et al., 2014).

Thirdly, the directed dispersal hypothesis considers that transportation of seeds to specific microsites which are suitable for seedling establishment is important. It has generally been used to describe cases of seed dispersal services by birds and myrmecochory (seed dispersal by ants) (Howe & Westley, 1988). Plants may develop unique fruit characteristics that attract specific dispersal vectors and have special morphological structures that increase the chance that seeds will be dispersed to suitable habitats (Venable & Brown, 1993). The classic example that fit the directed dispersal hypothesis is the dispersal of Mistletoe seeds (*Loranthus* spp., Loranthaceae) by small-bodied Flowerpeckers (*Dicaeum* spp., Dicaeidae) which defaecate seeds covered with a viscid layer that sticks onto branches of host trees (Ward & Paton, 2007). Ants were reported as seed dispersers and as promoting the population growth and survival rate of *Corydalis aurea* Willd. (Papaveraceae) because seeds treated by ants germinate better. Moreover, ant mounds can provide essential nutrients for seedling development (Hanzawa et al., 1988).

Seed dispersal can be described in term of its effectiveness. Schupp et al. (2010) used the concept of seed dispersal effectiveness to compare seed dispersal processes systematically. Seed dispersal effectiveness comprises quantitative and qualitative parts. The quantity reflects how many seeds are dispersed, for example, the number of frugivore visitations at fruiting trees and amounts of seeds removed from fruiting trees per visit, and the quality represents the probability of seedling establishment from dispersed seeds. It reflects the quality of seed treatment by frugivores, including their handling of seeds and gut passage effects and also where the seeds are deposited (Schupp, 1993; Schupp et al., 2010).

1.1.2 Fruit selection by frugivores

Plant species that depend on animals for dispersal have fruits with different characteristics that attract different frugivores (Lomáscolo et al., 2010). These include fruit colour, fruit size and seed size. Janson (1983) suggested that there were two main frugivores and fruit syndromes (variation in characteristic complex of fruiting plants that evolved to attract frugivores; Fischer & Chapman, 1993) in a Peruvian rain forest, based on fruit appearance, gape required and where the fruits were located, and that these resulted in bird, bat and primate specific fruits (Table 1.1). Fruits that target birds mainly have red or black colours, and thin pericarp layers. Fruit and seed sizes of bird fruits vary, but they are usually smaller than primate-eaten fruits. Primates and other mammals feed preferentially on fruits with distinct aromas when ripe, suggesting that smell rather than colour is important for their attraction. Green and brown fruits are not likely to be eaten by birds. Primates and bats also tend to consume larger fruits than birds. This reflects the different sizes of the animals, how they feed and the relative importance of sight and smell in birds and mammals (Rybczynski & Riker, 1981; Wheelwright, 1985; Clout & Hay, 1989; Noma & Yomoto, 1997; Corlett, 1998).

In the genus *Ficus* two dispersal syndromes were described in the neotropics (Kalko et al., 1996; Korine et al., 2000). Bats predominantly consumed green or pale colour figs, whereas red or brighter colour figs are mainly eaten by birds (Kalko et al., 1996; Korine et al., 2000). Fig dispersal syndromes are more complex in Asia (Shanahan, 2000). Five dispersal guilds, comprising fruit bats, arboreal mammals, terrestrial mammals, understorey bird/arboreal mammal and canopy bird/arboreal mammals, were described in Borneo (Shanahan, 2000). It is highly likely that frugivore guilds for other plants with fleshy fruits also vary in different places.

Table 1.1. Characteristics of fruits typically eaten by birds and mammals.

Region	Fruit colour		Fruit size		Seed size		References
	Aves	Mammal	Aves	Mammal	Aves	Mammal	
Neotropics	Red, Pink, White, Black, Indigo, Mixed colour	Green, Yellow, Brown, Orange (Primate)	14 mm. or lower	> 14 mm. (Primate)	N/A	N/A	Janson, 1983
Afrotropics	Violet, Red	Orange, Red, Yellow (Monkey)	< 5 g. (Small birds)	> 5 g.	< 0.5 g.	> 0.5 g.	Gautier-Hion et al., 1985
Mediterraneans	N/A	N/A	> 1 mm.	> 3.2 mm.	N/A	N/A	Debussche & Isenmann, 1989
Various regions	Black, Indigo, Red, White, Orange	Brown, Green, White, Orange, Yellow (Primate)	<10 mm.	N/A	N/A	N/A	Howe & Westley, 1988
Various regions	N/A	N/A	11.88 ±7.22 mm.	29.28 ± 22.75 mm.	N/A	N/A	Jordano, 1995
Paleotropics	Black, Red, Indigo	Black, Red, Yellow (Primate)	2-69 mm.	2-84 mm.	0.1-20 mm.	0.1-28 mm.	Kitamura et al., 2002
Afrotropics	Red, Black, White, Indigo, Pink, Yellow, Orange	Green, Brown, Yellow, Orange, Red, Indigo (Primate)	N/A	N/A	N/A	N/A	Voigt et al., 2004
Paleotropics	Darker colour	Lighter colour (Bats)	Smaller	Larger (Bats)	N/A	N/A	Lomáscolo et al., 2010
Global	Red, Black, White, Indigo, Pink, Yellow, Orange, Violet	Green, Brown, Yellow, Orange, Red, Indigo, White	Up to 69 cm or < 5g. in small birds	Varied in size, up to 84 mm. or> 5g.	Varied in size, up to 20 mm. or < 0.5 g.	Up to 28 mm. or > 0.5 g.	Overall

1.1.3 Seed handling by frugivores and germination success

Any animals ingesting fruits that contain seeds and then depositing viable seeds are potential seed dispersers (Schupp et al., 2010). Although many fruit-eating animals are seed dispersers, others can be seed destroyers. Chimpanzee (*Pan troglodytes*, Hominidae) pass most fruit safely through their guts, and only destroy around 2% of ingested seeds (Lambert & Garber, 1998). At the other extreme, rodents destroy most seeds by gnawing on them (Gathua, 2000). Small numbers of fig seeds can nonetheless be dispersed by rats (Staddon et al., 2010), so most animals that feed on fruits may disperse some seeds, even if the efficiency is low as in specialist seed predators such as many parrots (Psittacidae). Bulbuls (Pycnonotidae) are particularly important seed dispersers in the tropics, especially in Oriental regions, because they are very abundant, feed on many plants species, and their feeding behavior promotes seed dispersal (Corlett, 1998). In contrast, green pigeons (Columbidae), like parrots, are mainly seed predators because most seeds they eat are destroyed by their gizzards (Crome, 1975).

Although gut treatment may promote, suppress or have no effect on seed germination and survival (Barnea et al., 1991; Murray et al., 1994; Shilton et al., 1999; Traveset et al., 2001), the majority of frugivorous animals appear to enhance seed germination success (Fleming & Sosa, 1994). Seed germination success is strongly affected by the treatment the seeds receive in frugivore guts (Traveset et al., 2001). Seeds of *Ficus enormis* (Miq.) Miq. (Moraceae) ingested by Brown Howler Monkeys (*Alouatta fusca*, Atelidae) have a higher germination success than control seeds (de Figueiredo, 1993). M echanical and chemical digestive processes may soften seed coats and make water and oxygen exchange easier. As a result, the seeds may germinate more quickly. The impact of gut passage can depend on how long the seeds take to pass through the gut and the food type consumed together with the seeds (Barnea et al., 1991; Yagihashi et al., 1998). Moreover, during passage through the frugivore gut, the seeds are separated from the fruit pulp and this may improve germination rates (Traveset et al., 2001). For example, seeds of some species ingested by White-handed gibbon (*Hylobates lar*, Hylobatidae) in Khao Yai National Park, Thailand germinated faster than not-ingested seeds (Whitington, 1990). Faster germination is a common result of ingestion and may benefit plants by increasing early colonization and avoiding pathogen infection (Moore, 2001). Also, seed germination and seedling growth can be enhanced by faecal nutrients acting as natural manure, particularly with seeds germinating on mammalian dung (Traveset et al., 2001).

Most studies of endozoochory focus on birds or mammals, reflecting the most common record of both frugivorous group that feed on fleshly fruit (see Shanahan et al., 2001). However, fish is rarely topics of investigation (Correa et al., 2007), and also reptiles (see Shanahan et al., 2001). Fishes may be the oldest vertebrate seed dispersers, based on the fossil record of riparian coniferous seeds in the Carboniferous period, 300-350 million years ago (Tiffney, 2004). Although at least 275 fish species are recorded as feeding on fruits globally, with most records from the Neotropics, the seed dispersal services by fishes and how they handle seeds after consumption are still poorly known (Horn et al., 2011). Passage through fish digestive tract can damage seeds (Agami & Waisel, 1988; Kubitzki & Ziburski, 1994) or not (Horn, 1997; Mannheimer et al., 2003). The seeds may be crushed when fishes chew or swallow seeds and some herbivorous fishes including the abundant cyprinids (Cyprinidae) have a group of molar-like teeth in the pharyngeal arch. Fish body size can influence their ability to disperse seeds. Adult *Colossoma macropomum* (Serrasalmidae) are more effective seed dispersers in riparian forests of the Neotropics, Peru than smaller-sized juvenile fishes, probably because seeds are ground by juvenile fishes and swallowed whole by adult fishes (Anderson et al., 2009). As with birds and mammals, ingestion by fishes can accelerate seed germination after defaecation (Kubitzki & Ziburski, 1994; Pollux et al., 2006), but can also reduce seed germination in some cases (Kubitzki & Ziburski, 1994; Horn, 1997). It is suggested that seeds covering with a hard coat have higher survival and seed germination rates because of better protection while passing through fish guts (Pollux et al., 2006).

1.1.4 Seed protection: adaptation of plant to get rid of seed predation

The seeds produced by most plants have a rich accumulation of nutrients in their endosperm which is used for embryo development, but which can also be a food resource for animals (Hulme & Benkman, 2002). Therefore, to promote survival rates at the same time as favouring dispersal, plants need to develop strategies to protect their seeds while promoting interactions between diaspores and potential seed dispersers (Hulme & Benkman, 2002). Many plants have seeds containing chemicals that may have a defensive function. These substances include cyanogenic glycosides, alkaloids, saponins, and endopetide inhibitors that can be poisonous to seed predators (Janzen, 1971; Hulme & Benkman, 2002). Adaptations of seed morphology, such as increasing seed coat hardness, can be a direct physical way to protect seeds, and it is suggested that seed predation is reduced by seed weight, seed coat hardness and thickness (Blate et al., 1998). Another example of seed protection is the endocarp development of *Hakea* (Proteaceae). *Hakea* seeds are embedded in a spiny hard shell and grouped together under highly dense spiny leaves to reduce risk of seed predation by granivorous birds (Lamont et al., 2016). A seed coat covered with a sticky mucilage layer is found in some drought-tolerating plants which helps the seeds by adhering with soil and camouflages them from seed predators as well as reducing exposure to extreme conditions (Western, 2012).

1.2 General biology of fig trees

More than 830 fig tree species have been described globally with more than 500 species found in Asia and Australasia (see Berg, 1989; Harrison, 2005; The Plant List, 2018). *Ficus* is known as one of the most diverse plant genera, and displays various life forms, for example hemi-epiphytes, trees, shrubs and lianas (Berg & Corner, 2005). They have been classified into six sub-genera (*Pharmacosycea, Urostigma, Ficus, Sinoecia, Sycidium* and *Sycomorus*) (Berg & Corner, 2005). The morphological characters used to classify them use their sexual systems (monoecious or dioecious), adventitious roots, stipules, waxy glands, fig positions (e.g. in the leaf axil, cauliflorous or ramiflorous) and details of their flowers and inflorescences (figs, sometimes called syconia) such as their stigma form and stamen form and flowers per fig (Berg & Corner, 2005). Members of the *Pharmacosycea* subgenus are monoecious free-standing trees or shrubs (Berg & Corner, 2005). Unlike *Pharmacosycea*, the subgenus *Urostigma* consists mostly of monoecious hemi-epiphytic (strangler) and hemi-epilithic life forms (Berg & Corner, 2005). The subgenera *Ficus, Sinoecia* and *Sycidium* are dioecious, and *Sycomorus* members are both monoecious and dioecious (Berg & Corner, 2005).

In oriental Asia, *Ficus* is distributed in various habitat types, but especially in riparian areas of tropical rain forests (Corner, 1963; Corner, 1969). A great number of riparian species are specific to stream sides (Berg & Corner, 2005) and some figs trees totally rely on running streams or flood plain habitats, where they are able to grow on sandy or rocky material in the stream centre (Pothasin et al., 2016). Many other riparian fig trees have less restricted distributions and are also found in secondary forest and anthropogenic habitats (Maxwell, 2008).

Ficus is well known for their specific pollination association with fig wasps (Agaonidae) (Machado et al., 2001; Weiblen, 2002), and this mutualism has been occurring for at least 34 million years (Compton et al., 2010) and probably for twice that long (Rønsted et al., 2005). A variety of phenological patterns are reported in fig trees (Spencer et al., 1996), but often with asynchronous flowering at both individual and population scales (Janzen, 1979). Populations of the trees' fig wasp pollinators (Agaonidae) gain survival benefits from these unique phenological patterns (Harrison, 2008). In most monoecious *Ficus,* the figs are generally synchronized at the receptive and fig wasp-releasing phases on individual trees, but within-tree asynchrony occurs in some dioecious figs (Harrison et al., 2008). The benefit of within-tree synchronous fruiting, but within-population asynchronous fruiting figs is that it allows pollinator fig wasp populations to persist but also forces outcrossing because the pollinators have to move away from their natal trees in search of figs where they can oviposit (Bronstein, 1989; Jia et al., 2008).

Figs are hollow enclosed inflorescenses, lined by flowers internally. When figs are receptive, the ostiolar bracts are more open, allowing female fig wasps laden with pollen to enter and lay their eggs (Berg & Corner, 2005). One or a small number of fig wasp species pollinate each species of fig tree. Specificity is mainly the result of tree-specific volatile attractants released from receptive figs (Hossaert-McKey et al., 1994). The ostiole structure and fig wasp morphology also specifically fit each other, which favours specificity (van Noort & Compton, 1996). van Noort & Rasplus (2018) summarised the breeding biology of fig wasps as follow: During the pollination stage fig wasps insert their ovipositors along the styles of female flowers in order to lay eggs in the ovules. After laying their eggs, the female fig wasps usually die inside the figs. Galls will be formed in the ovules with wasp eggs, and they will produce the next generation of wasps. In monoecious fig trees, pollinated flowers lacking eggs will develop seeds. In dioecious fig trees, individual plants are separated into functionally male and female sexes. The roles of male figs are to produce pollen and fig wasp offspring to carry the pollen, and seeds are only developed in female figs. Un-pollinated and ungalled figs are discarded from trees. Wasp larva will be fully metamorphosed into adults several weeks or months after oviposition. One fig wasp develops in each galled ovule. Male fig wasps come out from their galls before females and start mating with them. When female wasps start leaving the figs, they bring pollen from the male flowers. In monoecious species, the figs become ripe and attractive to dispersers after the seeds are mature and the young generation of fig wasps has departed from the figs. In figs on female dioecious trees, the figs ripen once the seeds are mature. The female wasps' journeys begin, and they attempt to find receptive figs of their specific host species quickly, because their adult life spans are short (Harrison, 2005; van Noort & Rasplus, 2018).

Water can be an important medium to disperse the seeds of riparian *Ficus* (Horn, 1997; Pothasin et al., 2016). However, animals are the most important seed dispersers of most *Ficus* spp. It has been suggested that mature monoecious figs and female dioecious figs are significant food resources for more than 1,200 species of frugivores globally (Shanahan et al., 2001). Interactions among figs and frugivores involve many vertebrate taxa (fishes, reptiles, mammals, birds) (Shanahan et al., 2001), and even invertebrates, for example, ants (Kaufmann et al., 1991) and crabs (Staddon et al., 2010). *Ficus* species richness is positively correlated with avian frugivore species richness (Kissling et al., 2007), so it can be argued that the diversity of figs is an indicator or even driver of frugivore diversity, supporting the statement that “Everybody eats figs” (Janzen, 1979). Because fig trees often produce several fruit crops each year, and all year round this makes them highly available resources for frugivores, and figs are considered as keystone species in tropical rain forests (Milton et al., 1982; Terborg, 1986; Poonswad et al., 1998). Fig trees are found commonly in tropical and sub-tropical zones and their various life forms, fig colours, fig placements and fig sizes make them attractive to a wide range of different frugivores (Berg & Corner, 2005). Their easily-eaten and calcium-rich figs are other reasons why fig trees are one of the most important genera for frugivores in the Old and New World tropics (Jansen, 1979; O'Brien et al., 1998; Wendeln et al., 2000).

Fig trees are of particular interest to conservation biologists because they provide so many benefits to other organisms (e.g. fig wasps, frugivores, insectivorous birds and leaf-feeding insects) (see Machado et al., 2001; Shanahan et al., 2001; Sreekar et al., 2010; Cheanban et al., 2017). Some *Ficus* are fast-growing pioneer species and have been used as framework species to restore degraded habitats (Elliott et al., 2003). In these degraded habitats, frugivore diversity is usually low, leading to a lack of seed dispersal (Holl, 1999). The major role of *Ficus* in habitat restoration is due to its attraction to various frugivores that disperse plant seeds in general, causing more seed accumulation in areas (Elliott et al., 2003) which usually lack a seed bank (Duncan & Chapman, 1999; Slocum, 2001). *Ficus caulocarpa* (Miq.) Miq. growing in damaged dipterocarp forest in Borneo has been reported to attract 28 bird and 2 mammal species to its ripe figs, and has an excellent ability to attract frugivores to these less pristine areas (Sreekar et al., 2010). Some fig trees also have an excellent ability in suppressing weed density and resisting wild fires, which increases their positive effects in restoration processes (Elliott et al., 2003). Therefore, based on these significant characteristics, *Ficus* have distinctive and important functions in conservation ecology, especially in ecological rehabilitation of tropical landscapes.

1.3 Population genetics structure and gene flow of *Ficus*

Distribution, phylogeography and genetic differentiation of populations are interesting aspects for evolutionary study, and these approaches provide crucial information about populations that can be used for conservation of such species (Hampe & Petit, 2005). Genetic differentiation and genetic structure among isolated populations can define recent population status. They are affected by gene flow, genetic selection and drift, and mutations (Loveless & Hamrick, 1984). Populations and connected groups of populations display gene flow (Slatkin, 1987). Populations with high gene flow rates have routine interchanging of genotypes between reproductive individuals of each population. Lower gene flow rates are caused by the blocking of genetic transfer between populations and this leads to accumulations of unique allele frequencies due to genetic drift (Slatkin, 1987). In addition, geographical barriers, such as mountains, or heterogenous landscapes can limit gene flow between populations (Ernest et al., 2003; Hayden et al., 2003; Zalewski et al., 2009) and may lead to reproductive isolation and eventual speciation (Coyne & Orr, 2004).

Effective population size (N_e) is a widely-used method for estimating genetic drift and inbreeding in populations (Husband & Barrett, 1992). Generally, N_e can be evaluated from several factors affecting population dynamics, e.g. population size (N), sex ratio and variation in traits of each member in such population (Crow & Kimura, 1970). A small N_e is related with high genetic drift in such populations, but a larger N_e may result in high genetic diversity (Frankham, 1996).

Dispersal of pollen and seeds can be inferred indirectly (inferred from gene flow) and directly from population genetic studies (comparing seedling genotypes with their candidate parents) (Ouborg et al., 1999). Several molecular markers, allozymes, RAPDs, AFLPs, RFLPs, minisatellites and microsatellites, have been developed for studying plant dispersal events, with each marker type suitable for different research questions, the degree of polymorphism, and the need for cost effectiveness (Hamrick, 1987; Bruford & Wayne, 1993; Avise, 2004; Jarne & Lagoda, 1996; Ouborg et al., 1999). Microsatellite markers are widely used for studying population genetic questions. Microsatellites are short tandem repeats (STRs) or simple sequence repeats (SSRs), similar to minisatellites, but with shorter repeated sequences (Bruford & Wayne, 1993; Goldstein & Schlotterer, 1999). Microsatellites can be found in both nuclear and cytoplasmic genomes, especially choloroplast sequences (Provan et al., 2001). Microsatellites are very variable, and they spread gradually in the genome. Therefore, they have become popular markers in gene mapping, parentage analysis and population genetics (Goldstein &

Schlotterer, 1999), and also with direct or indirect plant dispersal studies investigating both pollen and seed mediated gene flow (Ouborg et al., 1999).

Although more than 830 *Ficus* species are distributed globally (The Plant List, 2018), the genetic structure of wild *Ficus* populations has been examined in only a small number of species. Only the domestic fig (*Ficus carica*) has been intensively examined, especially in Eurasia and Africa (see Khadari, et al., 2005; Saddoud et al., 2007; Ikegami et al., 2009; Aradhya et al., 2010). Apart from *F. carica,* population genetic studies of other *Ficus* have been carried out in Asia and South America (e.g. Chen et al., 2008; Nazareno & Cavalho, 2009; Wang et al., 2009; Zhou & Chen, 2010; Chen et al., 2011; Dev et al., 2011; Yu et al., 2010; Yu & Nason, 2013; Nazareno et al., 2013; Duarte et al., 2015; Heer et al., 2015; Liu et al., 2015; Wang et al., 2018, Table 1.2). However, the genetic structures of *Ficus* species in tropical South-East Asia, where the genus *Ficus* is most diverse, remain unclear. It has been nonetheless reported that some dioecious riparian figs in South-East Asian tropical forests often fail to be dispersed by animals (Compton S. G., pers. com.), and this might be predicted to restrict gene flow of those *Ficus* species. Genetic structure reflects gene flow patterns shaped by pollination and seed dispersal (Vekemans & Hardy, 2004). Wright's isolation by distance (IBD) stated that the correlation of genetic distance affects due to limited dispersal between different populations (Slatkin, 1993). Isolation by distance has been detected across populations in several *Ficus* species and may be a result of gene flow inhibited by geographical barriers (Chen et al., 2011; Liu et al., 2015). Some fig trees also have asynchronous flowering phenology, and growth forms that also possibly result in spatial genetic structure (SGS) (Vekemans & Hardy, 2004; Wang et al., 2009). The main factor leading to spatial genetic structure formation is restricted gene flow which relates directly to limited pollen and seed dispersal (Ennos, 2001; Vekemans & Hardy, 2004) although other factors, such as, habitat characteristics, population size, reproductive system, genetic drift, selection and dispersal patterns may also influence SGS in plants (Vekemans & Hardy, 2004; Zhou & Chen, 2010). However, the SGS generation processes and its related factors are not well understood (Zhou & Chen, 2010). Monoecious and dioecious fig tree species tend to display different spatial genetic structures. Spatial genetic structure among dioecious fig trees is approximately six times higher than in monoecious species (Nazareno et al., 2013). It has been suggested that long distance pollen flow occurs less in dioecious species and that this increases SGS (Zhou & Chen, 2010; Nazareno et al., 2013). In contrast, pollen of *Ficus sycomorus* L. can be transported for long distances, up to 160 kilometres (Ahmed et al., 2009). However, some dioecious figs also display long distance pollen dispersal, for example, *Ficus hirta* Vahl (Yu et al., 2010) and it is possible that local seed dispersal of dioecious *Ficus hispida* L. f. is responsible for the SGS of this species (Dev et al., 2011). Another recent updated study of *F. hirta* in Thailand and China also shows low nuclear and high chloroplast differentiation, reflecting low gene flow assisted by seed dispersal (Yu & Nason, 2013).

Table 1.2. Summary of population genetic studies of *Ficus* in natural habitats.

Figs species	Sexual system	Pollinators	Animal seed dispersers	Sampling location	Molecular markers	Major findings	References
Ficus pumila L.	Dioecy	*Weibesia pumilae*	Possibly bats, rodents, ants	Eastern Zhejiang, China	Microsatellites	Low level of genetic diversity detected from both mainland and island populations, and genetic differentiation was not significantly correlated with geographical distance	Chen et al., 2008
Ficus arpazusa Casar. Synonym of : *Ficus pertusa* L.f.	Monoecy	*Pegoscapus* sp.	-	Brazil	Allozyme	High genetic diversity was reported for this species, and inbreeding was not detected.	Nazareno & Cavalho, 2009
Ficus pumila L.	Dioecy	*Weibesia pumilae*	Possibly bats, rodents, ants	Eastern Zhejiang, China	Microsatellites	Strong SGS, restricted gene flow	Wang et al., 2009
Ficus cyrtophylla (Miq.) Miq.	Dioecy	*Kradibia* sp.	Small birds (*Pycnonotus* spp.)	South-east Xishuangbanna, Yunnan, China	Microsatellites	Long distance seeds and pollens dispersal were reported. Local SGS was found only in seedling stages which may reflect selection	Zhou & Chen, 2010
Ficus tikoua Bureau	Dioecy	*Ceratosolen* sp.	Small and large mammals	Sichuan and Yunnan, China	Microsatellites	Moderate level of genetic diversity – the highest diversity in dioecious figs. Isolation by distance was detected.	Chen et al., 2011
Ficus exasperata Vahl	Dioecy	*Kradibia gestroi*	Small birds	western Ghat, India	Microsatellites	SGS was detected, and parent-offspring distance was short, approximately, 200m. Also, genetic diversity remained high which may reflect immigration of genes	Dev et al., 2011
Ficus hispida L.f.	Dioecy	*Ceratosolen solmsi*	Bats and rodents	western Ghat, India	Microsatellites		
Ficus hirta Vahl	Dioecy	*Valisia javana*	Birds	Thailand and southern China	Microsatellites and cpDNA sequencing	Low nuclear genetic differentiation among populations, limited seed dispersal inferred from high cpDNA differentiation	Yu et al., 2010
Ficus citrifolia Mill.	Monoecy	*Pegoscapus* sp.	Bats and birds	Sao Paulo, Brazil	Microsatellites	Low level of SGS in comparison with dioecious figs	Nazareno et al., 2013
Ficus eximia Schott	Monoecy	*Pegoscapus* sp.	Bats and birds	Sao Paulo, Brazil	Microsatellites		
Ficus bonijesulapensis R.M.Castro	-	-	-	Bahia, Brazil	ISSR primers	High genetic diversity, and there was no pattern of SGS detected	Duarte et al., 2015
Ficus insipida Willd.	Monoecy	*Tetrapus costaricanus*	Phyllostomid bats	Panama, Costa Rica and Peru	Microsatellites	SGS was detected in these four *Ficus* species. Based on simulation, pollination possibly occurred over more than 1 km., and local seed dispersal may be the major cause of SGS	Heer et al., 2015
Ficus citrifolia Mill.	Monoecy	*Pegoscapus tonduzi*	Phyllostomid bats	Panama, Costa Rica and Peru	Microsatellites		
Ficus obtusifolia Kunth	Monoecy	*Pegoscapus hoffmeyeri*	Phyllostomid bats	Panama, Costa Rica and Peru	Microsatellites		
Ficus yoponensis Desv.	Monoecy	*Tetrapus ecuadoranus*	Phyllostomid bats	Panama, Costa Rica and Peru	Microsatellites		
Ficus pumila L.	Dioecy	*Weibesia pumilae*	Possibly bats, rodents, ants	South China	Microsatellites and cpDNA sequencing	Isolation by distance was detected, and genetic differentiation was lower than in its pollinator	Lui et al., 2015
Ficus sarmentosa Buch.-Ham. ex Sm.	Dioecy	*Weibesia callida*	Birds, rats, ants	South East China	Microsatellites	High genetic diversity, but low genetics structure, indicating extensive gene flow	Wang et al., 2018

1.4 Research themes

Based mainly on studies of fig trees in western Thailand, the major research themes of this thesis examine the interactions between South-East Asian riparian *Ficus* and frugivorous animals. The fig trees studied were mainly small and dioecious– the growth form and breeding system that largely represents the extreme species richness of Asian *Ficus*, but which has been little studied from a seed dispersal perspective. Riparian habitats support the most diverse *Ficus* faunas in the area but are often under threat from human activities. Dispersal by water, and the fishes that inhabit the water, is possibly important for gene flow in riparian species, and may have generated associated adaptations in some of the species.

The effectiveness of frugivores in seed dispersal of *Ficus* was investigated by examining fig removal patterns and seed handling by the frugivores. The annual phenology of four riparian *Ficus* species was studied. The function of a gelatinous substance that covers some *Ficus* seeds in terms of seed germination and invertebrate attraction was also investigated. The implication of pollination and seed dispersal for gene flow in a South-East Asian dioecious *Ficus* species were revealed by investigating its population genetic structure. An updated global record of figs eaters based on results of this study and from the scientific records published between 2000 and 2017 was generated to examine the world-wide significance of fig trees and to determine whether data weaknesses identified in an earlier study (Shanahan et al., 2001) have been rectified.

The research outline of this thesis is as follows:

Chapter 1 outlines general principle of mutualism, seed dispersal approaches, the biology of *Ficus* and population genetic studies of the genus.

Chapter 2 investigates the annual vegetative and reproductive phenology of four riparian fig species with these research questions:

1. What are the leaf and fig phenology patterns of the riparian *Ficus* species?
2. Do leaf and fig production correlate with climatic factors?
3. Do fig crop numbers and sizes differ between sexes within dioecious species and between species?
4. Are figs on male and female trees presented differently?

Chapter 3 describes the terrestrial frugivore assemblages of the four riparian fig species. This chapter examines interactions between small fig trees (*Ficus ischnopoda* Miq. and *F. montana* Burm.f.) and frugivores in comparison with medium and larger fig trees (*Ficus oligodon* Miq. and *F. racemosa* L.) with these research questions:

1. Is water possible for dispersal agent of four non-*Urostigma* fig species (*F. montana*, *F. ischnopoda*, *F. oligodon* and *F. racemosa*) in riparian forest of western Thailand?
2. How many figs likely to fall down from those four riparian fig trees?
3. How do frugivores interact with these four fig species, including the frugivore feeding behaviours on fig trees?
4. How frequently and fast do frugivores remove figs from those fig trees?

Chapter 4 examines the role of cyprinid fishes (*Neolissochilus stracheyi* and *Barbonymus altus*) in dispersal of seeds of a riparian fig tree (*Ficus montana* Burm.f.) by studying the effect of seed consumption on seed survival and germination. Research questions of this chapter are:

1. What proportion figs fall into the water, and does it vary with season?
2. Do the frugivorous fish species and abundance sizes differ between the two major riparian systems in western Thailand?
3. Does the speed of fish consuming at which fallen figs vary between the riparian systems?
4. Do fish body sizes affect feeding rates and survival of fig seeds eaten by the fishes?
5. How does feeding and gut passage inside fishes influence seed germination?

Chapter 5 examines the function of a gelatinous substance (jelly) that covers *Ficus oligodon* Miq. seeds. Specific research questions are:

1. How does the presence of the jelly influence seed germination?
2. Does the jelly attract ants?

Chapter 6 describes the genetic structure and assesses gene flow in a small dioecious riparian fig tree (*Ficus montana* Burm.f.) in western Thailand. Several research questions are raised in this chapter:

1. What is the population genetic structure of *Ficus montana* Burm.f. in western Thailand?
2. How does genetic structure relate to pollination and seed dispersal patterns?
3. Do the genetic structures obtained from nuclear and chloroplast DNA differ in *F. montana*?
4. Does isolation by distance pattern occur among different population of *F. montana*?
5. Is gene flow of *F. montana* in western Thailand related to river systems and geographic barriers such as mountain ridges?

Chapter 7 updates a previously-published global database of *Ficus* and fig eaters gathered from scientific publish sources from 2000 to 2017. The research questions below are discussed based on a meta-analysis of the database contents.

1. How many fig species have been examined in terms of what eats their figs?
2. What are the frugivore groups feeding on figs?
3. What is the variation among fig eaters in different regions?
4. Are both monoecious and dioecious figs important resources for frugivores?

Chapter 8 summarises and synthesises knowledge gained in the earlier chapters.

Chapter 2 The phenology of four fig tree species (*Ficus racemosa*, *F. oligodon*, *F. ischnopoda* and *F. montana*) in riparian forest of western Thailand

2.1 Abstract

Vegetative and reproductive phenologies of plants are influenced by climatic factors and interactions with other organisms. *Ficus* spp. are known as keystone resources in tropical forest ecosystems globally. Although *Ficus* is one of the most diverse plant genera, consisting of more than 830 species, relatively few studies have described the phenology of fig trees. Here, the leaf and fig phenological patterns of four riparian fig tree species in Kanchanaburi, western Thailand are described across one year (January – December 2016). New leaf production occurred all year round but varied in detail among species. Crops of the dioecious species *F. oligodon, F. ischnopoda* and *F. montana* peaked seasonally, and fruiting appears to be influenced by temperature. The monoecious *F. racemosa* produced figs all year round with less seasonal effects, making it a potential keystone resource for frugivorous wildlife. Within-tree asynchrony in fig production made it easier for fig wasps to cycle on male trees. The lowest proportion of within-tree asynchronous fig crops was detected in *F. racemosa,* but self-pollination may still occur in this monoecious species. *F. racemosa* produced figs almost up to canopy level (> 5 m), but the three smaller dioecious fig species mainly bore figs close to the ground (0-1 m) suggesting that these fig trees may interact with different frugivore groups foraging at different height levels.

2.2 Introduction

The dynamics of plant vegetative and reproductive development through time are influenced by many abiotic, such as climate, and biological factors such as interactions with pollinators, seed dispersers and herbivores (Fenner, 1998; Harrison et al., 2000). Phenological studies improve understanding about how changing environments affect flowering or fruiting patterns and are particularly important now, at a time of climate change (Zhang et al., 2006).

There are at least 830 *Ficus* species distributed in a wide range of habitats across the tropics and sub-tropics, so genus *Ficus* is one of the most widely-distributed plant genera (The Plant List, 2018). Fig trees also vary greatly in growth form and display different breeding systems. Fig trees are known for their specific pollination by fig wasps (Agaonidae) (Bronstein, 1992; Machodo et al., 2001). Fig trees produce unusual inflorescences (figs, also called syconia) that vary in characteristics such as size, colour and where they are produced on the trees. This influences the animals that feed on the figs and they provide resources for many species of frugivorous birds, mammals, reptiles or even fishes (Shanahan et al., 2001). Moreover, figs are soft and easy to eat, and fig trees can be abundant. Some species also bear figs all year round, allowing them to be the important food item for wildlife during low fruit production periods of other plants (Janzen, 1979). Hence, the statement of Janzen (1979) that ‘Everybody eats figs’ is not greatly exaggerated.

In *Ficus*, seasonal changes in leaf and fig production have been described by several studies (Corlett, 1984; Bronstein, 1989; Patel, 1997; Harrison et al., 2000; Kuaraksa et al., 2012; Zhang et al., 2014; Chen et al., 2015; Pothasin et al., 2016).

Significantly lower fig production has been reported in subtropical fig trees during the winter season (Patel, 1997; Zhang et al., 2014), but some subtropical fig trees bear higher fig crops during winter which will ripen in the dry season (Chen et al., 2015). Elevated rainfall (Spencer et al., 1996) and higher temperatures (Harrison et al., 2000; Pothasin et al., 2016) nonetheless usually strongly correlate with fig production. However, climatic factors do not influence on fig production in some cases (David et al., 2012). To complete their reproductive cycles, both fig trees and their fig wasp pollinators need to interact to ensure survivorship for each other (Visser et al., 2005; Cook et al., 2003; Moe et al., 2011). In monoecious fig trees, asynchronous fig production often occurs across different individuals at the population level, but most crops within trees display synchrony (Janzen, 1979; Jia et al., 2008). This allows fig trees to support populations of fig wasps throughout the year (Smith & Bronstein, 1996). However, in dioecious fig trees, synchronous crops within trees are less common (Bronstein & Patel, 1992; Harrison et al., 2008; Kuaraksa et al., 2012) and only male trees support fig wasp populations. Small or isolated fig tree populations (Bronstein, 1989) may benefit from having pollinators cycle on single male trees and the pollinators of dioecious species typically disperse less widely than pollinators of monoecious fig trees (Harrison & Rasplus, 2006). Dioecy also allows female fig trees to concentrate their fruiting during optimal times of the year and such climatic factors clearly influence fig availability, so the complexity of phenology is addressed in genus *Ficus* (Spencer et al., 1996).

As phenological information indicates how fig trees express their vegetative and reproductive behavior, and this relates directly to pollination and seed dispersal events, this study aims to investigate the following specific questions: (i) What are the leaf and fig phenological patterns of four riparian fig species? (ii) Do leaf and fig production of the four species correlate with climatic factors, such as temperature or rainfall? (iii) Do fig numbers and differ between sexes within dioecious species and between the species? (iv) Where do the trees present their figs to potential dispersers, and does this vary between male and female plants of the same species?

2.3 Methods

2.3.1 Study sites

The research was carried out at several riparian sites in different national parks located in Kanchanaburi province, western Thailand for a one-year period running from January to December 2016 (Table 2.1; Fig. 2.1). The elevation range is from 100 – 1200 m. a.s.l. The geological structure mainly consists of igneous granite rock and several sedimentary rocks, for example limestone, shale and sandstone. The soil is mostly from the decay of those rocks, giving a red-brown colour (Suksawang, 1995).

The climate of the area is classified as typical of the tropical monsoon zone, and average annual rainfall is about 1750 mm. Based on data from the Kanchanaburi Meteorological Centre, which is located about 50 km from the nearest study site, the rainy season ranges from May to October, and the dry season from November to April (Fig 2.2). The temperatures peaked in April 2016 and were lowest in December to January. The relative humidity started rising from April to July, decreasing down a little in August, and rising to a peak in October (Fig 2.2). The relative humidity was negatively correlated with maximum temperatures, but positively correlated with rainfall (Table 2.2).

The five study areas were located in streamside forests. The streams of Phatad and Kratengjeng waterfalls are connected to the Kwai Noi river basin, and the rest join the Kwai Yai River. Water flowed all year round at most sites, but shortages of water occurred for a short period in March at the Phatad waterfall, although the water level then rose after rainfall in April. All the sites are surrounded by tourist attractions, and several nature trails are present. The forest structure is mostly mixed deciduous forest. The major trees include *Xylia xylocarpa* (Fabaceae), *Pterocarpus macrocarpus* (Fabaceae), *Afzelia xylocarpa* (Fabaceae), *Vitex peduncularis* (Lamiaceae) and *Lagerstroemia calyculata* (Lythraceae) (Chantarasuwan et al., 2007).

Table 2.1. Sample sizes (number of trees), study locations and geographical coordinates of four riparian figs species in Kanchanaburi, western Thailand.

Ficus Species	N (trees)	Study sites (codes)	Latitude/Longitude
F. racemosa	6	Phatad (PT)	14°39'N/98°46'E
	4	Erawan (E)	14°22'N/99°08'E
	8	Phatart Cave (PTC)	14°39'N/99°08'E
	5	Hueymaekamin (H)	14°40'N/99°03'E
F. oligodon	18	Kratenjeng (KTJ)	15°02'N/98°58'E
	16	Phatad (PT)	14°39'N/98°46'E
F. ischnopoda	34	Phatad (PT)	14°39'N/98°46'E
F. montana	58	Kratenjeng (KTJ)	15°02'N/98°58'E

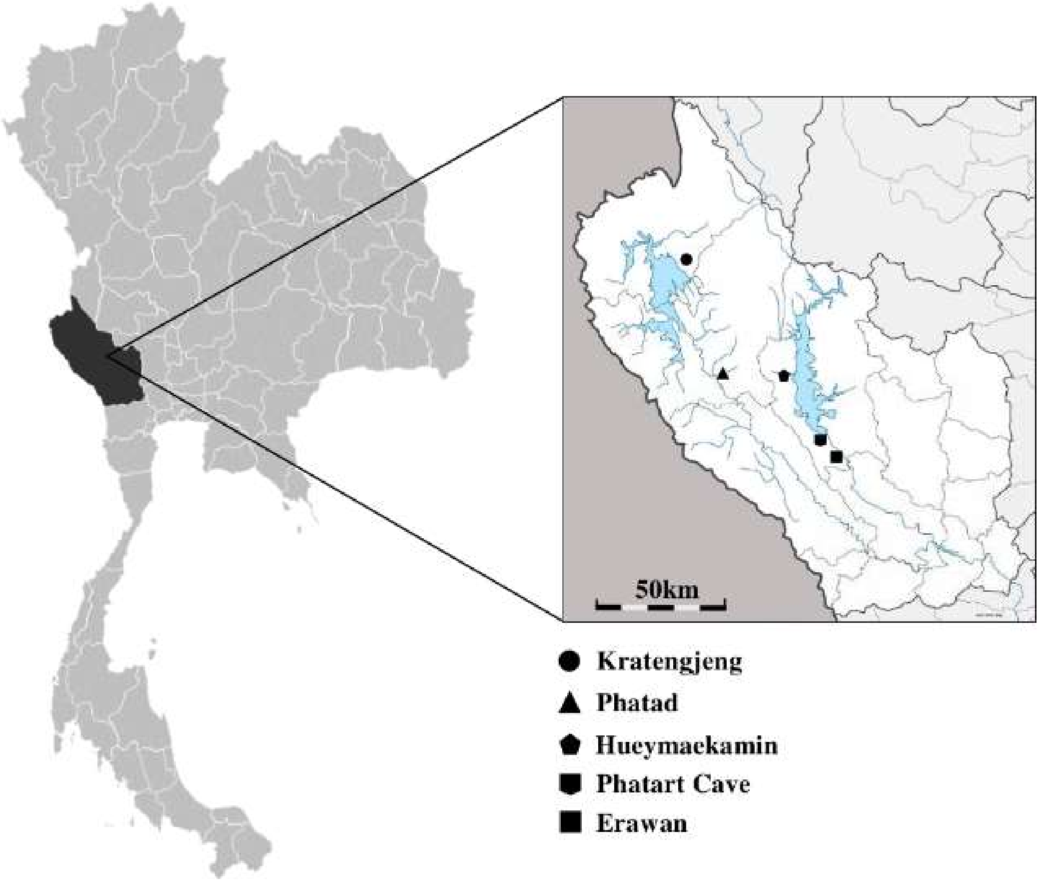

Fig. 2.1. Map of study sites of four riparian figs species in Kanchanaburi, western Thailand.

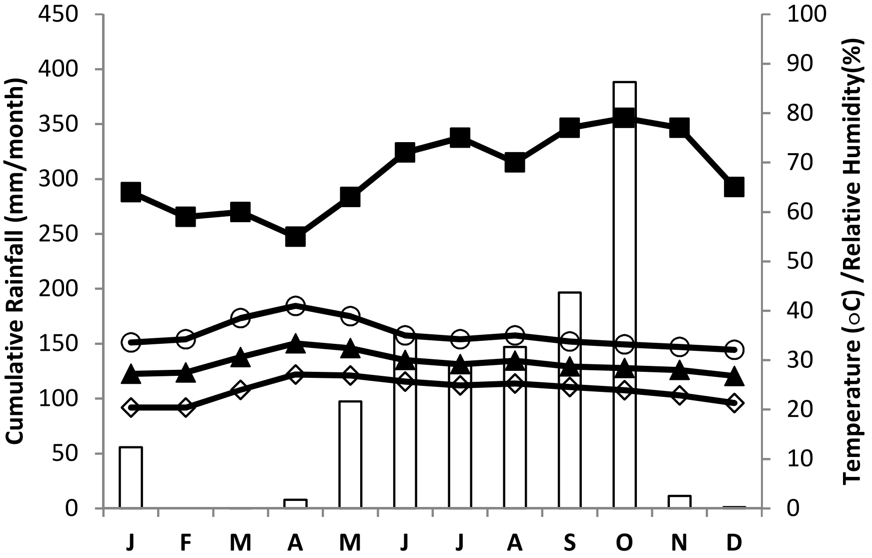

Fig. 2.2. Monthly rainfall (mm); open bars, Relative humidity (%); squares, Average, Minimum and Maximum temperature (°C); Triangles, open spades and open circles, respectively, at the Kanchanaburi Meteorological Centre from January to December 2016.

Table 2.2. Spearman's rank correlation tests among monthly metrological factors over the twelve month study period. AT = Average temperature, MiT = Minimum temperature, MaT = Maximum temperature, RH = Relative humidity and RF = Monthly accumulative rainfall.*P < 0.05, **P < 0.01. Tests were performed in R. 3.4.3.

	MiT	**MaT**	**RH**	**RF**
AT	0.907**	0.909**	-0.301	0.140
MiT		0.761**	-0.098	0.361
MaT			-0.608*	-0.098
RH				0.757**

2.3.2 Study species

2.3.2.1 *Ficus racemosa*

F. racemosa (Subgenus *Sycomorus*; Section *Sycomorus*) is a monoecious fig tree and distributed widely from India and China to Australia (Corner, 1965). It can be found along riparian areas, in mixed deciduous to evergreen forest, up to 1,000 m *a.s.l.* It is a 20 – 30 m tall tree when mature, becoming buttressed. Its leaves vary from lanceolate to subobovate. Young leaves are reddish to purple reddish in colour and turn to green when mature. Figs are produced in clusters on the trunk. The mature figs exhibit a pinkish to ruby red or orange colour, and the mature figs range from 3 – 5 cm in diameter (Berg et al., 2011). *F. racemosa* is pollinated by *Ceratosolen fusciceps* (Agaonidae) (Kobmoo et al., 2010). To date the five species of non-pollinating wasps, *Platyneura testacea*, *Platyneura mayri*, *Platyneura agraensis*, *Apocrypta westwoodi* and *Apocrypta* sp., were recognized (Zhang et al., 2004). *F. racemosa* interacts with numerous species of frugivores, including mammals, birds and fishes (Shanahan et al., 2001; CHAPTER 3; 4).

2.3.2.2 *Ficus oligodon*

F. oligodon is a dioecious fig tree, growing to 15-20 m tall that also belongs to subgenus *Sycomorus* section *Sycomorus*. This species exhibits a wide geographical range, from Pakistan to Peninsular Malaysia. It is mostly found near streams in evergreen, mixed deciduous and montane forests at elevations up to 1,600 m a.s.l. *F. oligodon* produces elongate and narrow toothed ovate, elliptic, oblong, subobovate or suborbicular leaves. Young leaves are often red colour changing to green when fully mature. Figs are produced in clusters on leafless branches, branchlets or rooted branchlets. The subglobose figs can be up to 10 cm in diameter, and often purple to reddish colour when mature (Berg et al., 2011). *F. oligodon* shares a pollinator with *F. auriculata* which is *Ceratosolen emarginatus*. Recorded non-pollinator fig wasps include *Philotrypesis longicaudata*, *Philotrypesis* sp., and *Sycophaga* sp. (Kuaraksa et al., 2012). Only three mammal species: Asiatic Black Bear, *Selenarctos thibetanus* (Ursidae), Grey-bellied squirrel, *Callosciurus caniceps* (Sciuridae), and rat, *Maxomys* sp. or *Rattus* sp. (Muridae), one bulbul species: Black-crested bulbul, *Pycnonotus flaviventris* (Pycnonotidae), and cyprinid fishes consume figs of *F. oligodon* that fall into the water (Shanahan et al., 2001; CHAPTER 3; 4).

2.3.2.3 *Ficus ischnopoda*

F. ischnopoda (Subgenus *Ficus*; Section *Ficus*) is a small dioecious shrub or treelet, growing 3-6 m. tall. It is distributed across tropical East Asia, from Northeastern India to peninsular Malaysia. This species is a rheophyte which mostly grows on rocks in fast running streams. It can be found in many forest habitats, such as mixed deciduous, evergreen and montane forests. Leaves shapes are oblanceolate to obovate. Immature leaves are entirely purple and become greenish when mature. Figs are produced singly in leaf axils, are 2-3 cm. in diameter when mature, subovoid in shape, and coloured black or purple when fully mature (Berg et al., 2011). *F. ischnopoda* is pollinated by *Blastophaga* sp. (Wiebes, 1993). In Kanchanaburi, seeds of *F. ischnopoda* are potentially dispersed by various birds including Stripe-throated bulbul, *Pycnonotus finlaysoni* (Pycnonotidae), Black-crested bulbul, *Pycnonotus flaviventris* (Pycnonotidae), Blue whistling thrush, *Myophonus caeruleus* (Muscicapidae) and White-breasted waterhen, *Amaurornis phoenicurus* (Rallidae). Some fallen figs are also eaten by Cyprinidae fishes (CHAPTER 3; 4).

2.3.2.4 *Ficus montana*

Ficus montana is a member of subgenus *Sycidium*, section *Sycidium*. It is a small dioecious shrub up to 2 m tall, or sometimes can be found as a creeper. Its distribution ranges cover India, Myanmar, peninsular Malaysia, Indonesia, the Philippines and Papua New Guinea (Berg et al., 2011). It is sometimes a rheophytic plant, mostly found in understorey on stream banks in evergreen to dry evergreen forest, at elevations up to 1300 m. a.s.l. (Berg et al., 2011). Young leaves often have a purple colour, usually changing to green when mature, but some individuals retain purple underside leaves throughout. Leaf shapes vary from toothed entire to lobed (Tarachai et al., 2012). Single or paired figs, up to about 1 cm. in diameter, are borne in leaf axils or on spurs from older wood. At maturity, female figs show a bright orange to reddish colour. The fig wasp *Kradibia tentacularis*, is a pollinator of this fig species, and the undescribed parasitoid *Sycoscapter* sp. has the pollinator as host (Suleman et al., 2011). In Kanchanaburi, figs are eaten by birds and mammals, for example Black-crested bulbul, *Pycnonotus flaviventris* (Pycnonotidae), Black-headed bulbul, *Pycnonotus atriceps* (Pycnonotidae), Blue whistling thrush, *Myophonus caeruleus* (Muscicapidae), Green broadbill, *Calyptomena viridis* (Eurylaimidae) and Grey-bellied squirrel, *Callosciurus caniceps* (Sciuridae) (CHAPTER 3). Some fallen figs that enter the water are eaten by Cyprinidae fishes, such as, Blue mahseer, *Neolissochilus stracheyi* (CHAPTER 4).

2.3.3 Phenology observations

Fruiting phenology of the four riparian *Ficus* species (*F. racemosa*, *F. oligodon*, *F. ischnopoda* and *F. montana*) were monitored every 14-17 days, resulting in 24 observations in one year (two observations a month) for each tree. At the time of the second observation, the height of each tree was estimated using trigonometry methods for *F. racemosa* and *F. oligodon*, and the angle of elevation was estimated using the application iHandy Level Free with ASUS Zenfone^{TM} smart phone. However, the smaller trees, *F. ischnopoda* and *F. montana*, were measured directly using measuring tape. The heights of the trees were grouped into four categories for some analyses (0-2 m, 2-5 m, 5-10 m and > 10 m).

F. racemosa and *F. oligodon* were usually found in small numbers at each study site, so phenology data for these fig trees were collected from several sites (Table 2.1). Pheno-phases of figs were categorized into different developmental stages (see Galil & Eisikowitch, 1968; Kuaraksa et al., 2012) initially by opening figs to investigate the developmental stage and later inferring from fig size and colour. There are immature figs (early small-sized figs with no fig wasps present; A phase), receptive (early inflorescence development, when the trees are attractive to pollinators; B phase), developing (fig wasp offspring or seeds are present inside; C phase), fig wasp offspring releasing phase in male trees only (D phase) or ripening/withering phases in female and male trees respectively (E phase). In the monoecious *F. racemosa*, the D and E phases were combined together as mature figs (D+E phase). Immature and receptive phases were also pooled together (A+B phase) as it is difficult to distinguish between these two phases. Fig production at each developmental stage was recorded by direct counting every branch to estimate overall fruit production. In the large species *F. racemosa*, figs were counted on each branch and estimated to the nearest 100 figs, or directly counted if possible. Fig numbers on each tree were separated into four height categories from the ground (0-0.5 m, 0.5-1 m, 1-5 m and > 5 m).

The crop numbers of each fig tree species and sex at several different sites were calculated by counting the maximum numbers of immature figs (A phase) for each crop for a one-year period. The extent of asynchrony of each individual fig tree was calculated by counting the numbers of A and B phase figs (potentially attractive or soon to be attractive to pollinators) together with D or E phase figs that were potentially releasing pollinators. The data were then combined to generate proportional values for each species and sex at each site. Crops where all the figs aborted were also recorded and the proportion of aborted fig crops was calculated.

Leaf production was noted by recording those fig trees with new leaves and displaying leaf bud initiation, and trees with senescing leaves were also recorded. Meteorological data of Kanchanaburi province, including mean monthly minimum, maximum and average temperature (°C), relative humidity (%), and monthly rainfall (mm.) were obtained from the Kanchanaburi meteorological station, in Kanchanaburi town, Thai Meteorological Department.

2.3.4 Data analysis

All statistical analysis was done in R 3.4.3. As collected field data were not normally distributed and did not meet requirements of applying parametric statistics, non-parametric statistics were applied. The relationships between fig and leaf production and climatic variables were examined using Spearman rank correlations. Crop numbers and crop size differences among the four fig tree species and among sites were compared using Kruskal-Wallis or Mann-Whitney U tests. To compare crop numbers and crop sizes within species for different sexes or sites, Kruskal-Wallis or Mann-Whitney U tests were applied. The maximum asynchrony within the same tree and crop abortion are reported as proportions for different sexes in dioecious fig species. The proportion of figs present at different height was reported between sexes and sites.

The phenology of each species is reported as the proportion of different stages, A+B, C and D/E across all observed trees. The deviation from a uniform distribution of frequency of trees producing new leaves and figs throughout the year was tested using circular statistics, one-sampled Kuiper's test (Zar, 2010), in program ORIANA V.4.0 (Kovach, 2010).

2.4 Results

2.4.1 *Ficus racemosa* phenology

F. racemosa trees were consistently evergreen, but with small amounts of leaf fall (less than 5% of canopy density) detected from every tree throughout the year. Young leaves developed to mature leaves within three to six weeks. New leaf initiation was not uniformly distributed through the year and peaked in June and November (Figs. 2.3-2.7, Table 2.11). Across all sites, based on 19 trees, new leaf initiation showed positive correlations with average and minimum temperatures and monthly rainfall, but not with maximum temperature and relative humidity. New leaf production at Erawan and Pratart Cave was also positively correlated with relative humidity. The proportion of fig trees producing new leaves was not correlated with the proportion of trees that were producing figs (Table 2.14).

Across all sites, the fruiting phenology of 23 *F. racemosa* individuals was observed, but only 19 trees produced figs (Table 2.3). The four *F. racemosa* trees from Phatad waterfall that did not bear any figs were excluded from analysis. Figs were produced throughout the year with at least 60% of trees bearing figs at any one time (Figs. 2.3-2.7; Tables 2.3, 2.12). *F. racemosa* bore four to seven crops a year (Mean ± SE: = 5.37± 0.19 crops) and produced an estimated 300 to 8650 figs per crop (Mean ± SE = 2330.6 ± 191.29 figs/crop) (Table 2.10). The mean crop number and mean crop size were not significantly different among the four sites (Crop number: Kruskal Wallis Test: H = 3.923, df = 3, P = 0.270; Crop size: Kruskal Wallis Test: H = 4.171, df = 3, P = 0.244). Moreover, Crop numbers per year and crop sizes of *F. racemosa* was significantly bigger than those of the other three species (male and female figs trees were pooled in dioecious species), (Crop numbers: Kruskal Wallis Test: H = 33.612, df = 3, P < 0.001, Crop sizes: Kruskal Wallis Test: H = 260.171, df = 3, P < 0.001) (Table 2.10).

In total, 0.21 (range = 0.17 in Erawan to 0.23 in Phatad and Pratart Cave) of a total of 410 observations over 12 months detected flowering asynchrony sufficient for self-pollination within trees, as releasing phase figs overlapped with the immature figs within a tree. No whole-crop abortions were detected in *F. racemosa* (Table 2.10).

Based on 24 observations in one year, from 0.46 ± 0.04 (Erawan) to 0.86 ± 0.04 (Phatad), Mean ± SE, of overall fig production was on branches that were located more than five meters from the ground, and from 0.14 ± 0.04 (Phatad) to 0.54 ± 0.04 (Erawan), Mean ± SE, of overall fig proportion was located from 1 to 5 meters above the ground. Only 0.01 ± 0.002 (Mean ± SE) of its figs were produced less than 1 meter from the ground which found only in some individuals at Pratart Cave site (Table 2.13; Fig 2.8). A higher proportion of shorter fig trees (5 – 10 m. in height) was found in Erawan (0.50) and Pratart Cave (0.375) of all conspecific trees, suggesting that figs were likely to be produced closer to the ground at these sites (Table 2.6).

The proportion of trees bearing figs was aseasonal across all sites (Kuiper's test: $V = 1.299$, $P > 0.05$; Table 2.12). Immature and receptive phase figs were produced constantly from January to June, but the fig production declined slightly in July. Young fig production slowly increased from late July, peaked again in September, and suddenly dropped in November. In December, some new figs were initiated by trees not producing fig crops in November. The pattern of fig production of *F. racemosa* was stable all year round, though there were short periods of July and November showing overall fig production decline (Fig. 2.7). Their numbers peaked in January and September, with stable produced from February to May. The ripening and releasing phrases figs were also found all year round but peaked in June and October (Fig. 2.3 – 2.7). Across all sites, young fig production was negatively correlated with relative humidity. It also showed a significantly positive correlation with temperature at some sites (Erawan, Pratart Cave and Hueymaekhamin). Mature figs production did not significantly correlate with any climate factors, except in Pratart Cave and Hueymaekhamin where fig numbers were positively correlated with some temperature measures (Table 2.14).

Table 2.3. Annual variation in individuals of *F. racemosa* producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey. PT: Phatad waterfall, E: Erawan waterfall, PTC: Pratart Cave, H: Hueymaekamin waterfall.

Tree Code	Site	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
816	PT	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■
824	PT	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
870	E		■	■	■	■	■	■	■	■	■	■	■			■	■	■	■	■	■	■		■	■
871	E	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	
872	E	■	■	■				■	■	■	■	■			■	■	■	■	■	■			■	■	■
873	E	■	■		■	■			■	■	■	■	■			■	■	■	■	■	■	■			■
874	PTC	■	■	■	■	■	■	■	■	■	■	■			■	■	■	■	■	■	■			■	■
875	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■
876	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■
877	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■			■	■
878	PTC	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■
879	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■
880	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■
881	PTC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
882	H	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■			■	■
883	H	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■			■	■
886	H	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■
887	H	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■			■	■	■
888	H	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■			

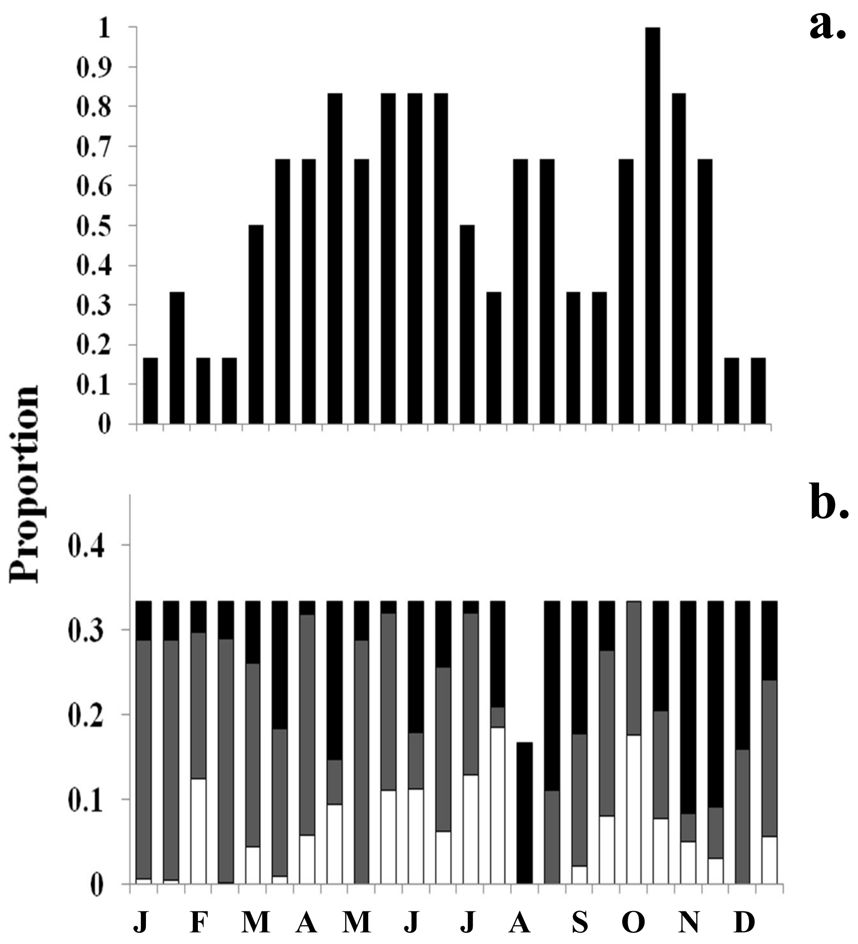

Fig. 2.3. Annual variation in the proportion of *F. racemosa* at Phatad with young leaves, N = 6 trees (a), and trees with figs present, N = 2 trees (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars).

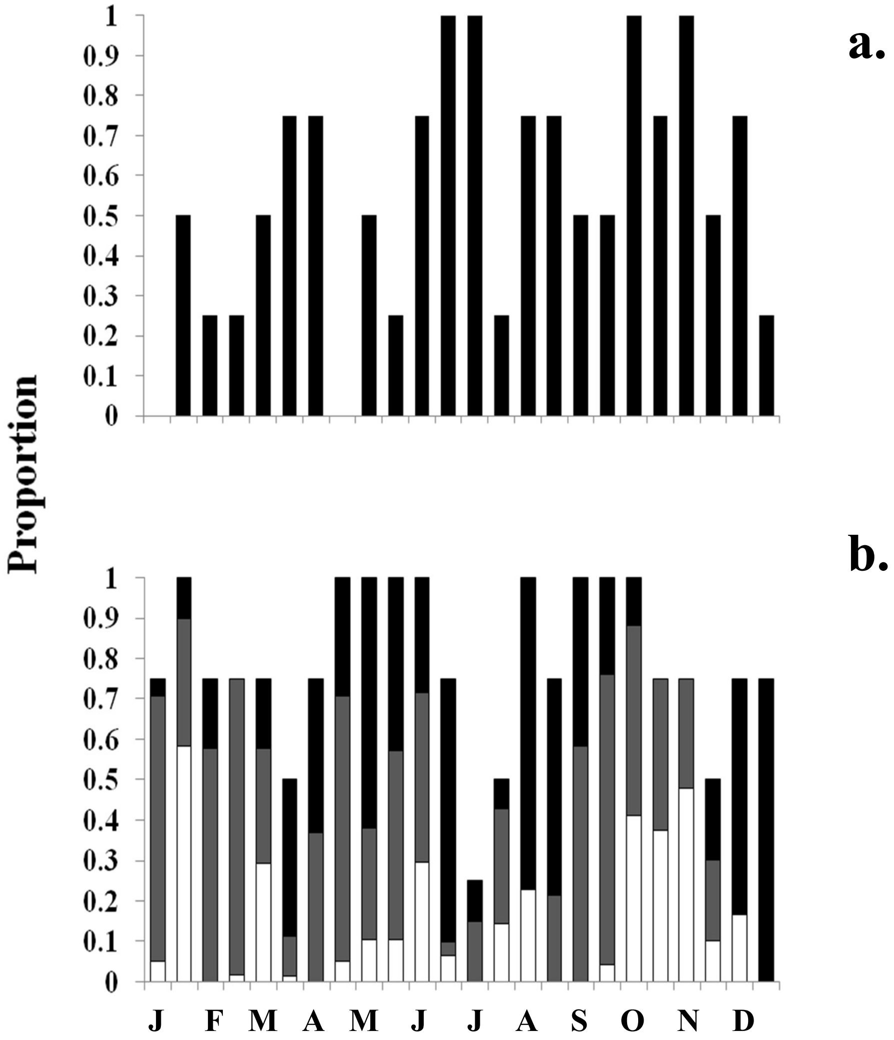

Fig. 2.4. Annual variation in the proportion of *F. racemosa* at Erawan with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 4 trees, all of which produced figs.

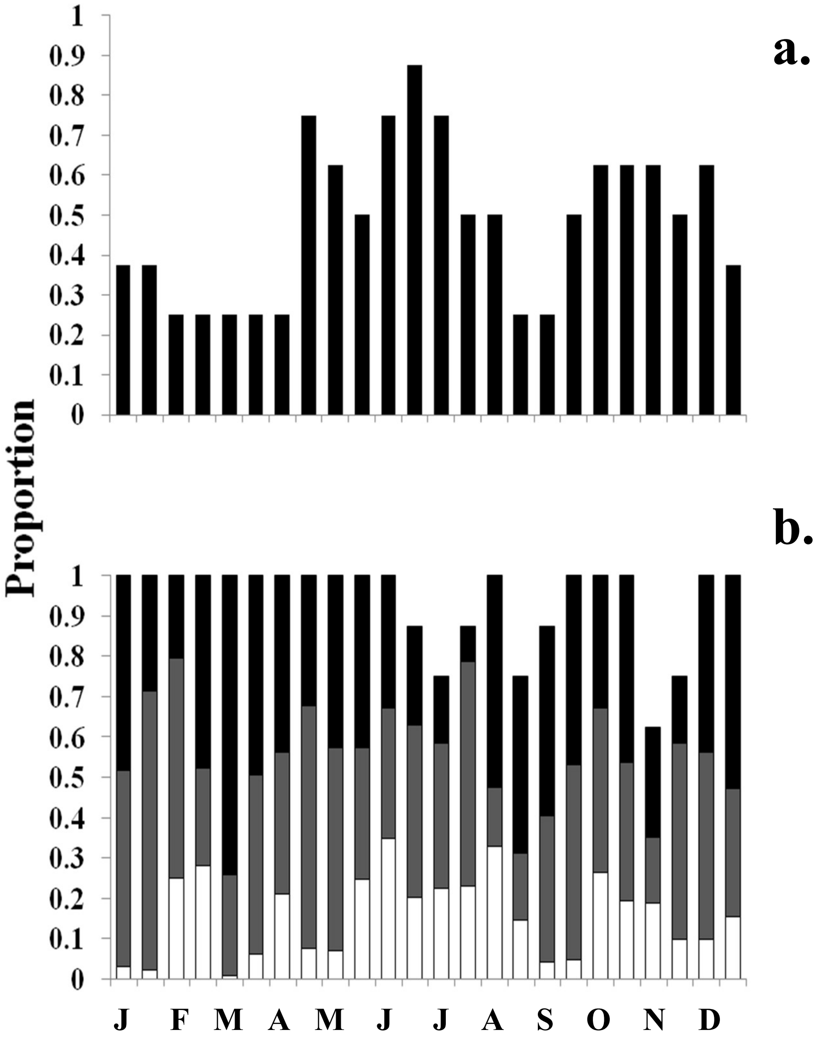

Fig. 2.5. Annual variation in the proportion of *F. racemosa* at Pratart Cave with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 8 trees, all of which produced figs.

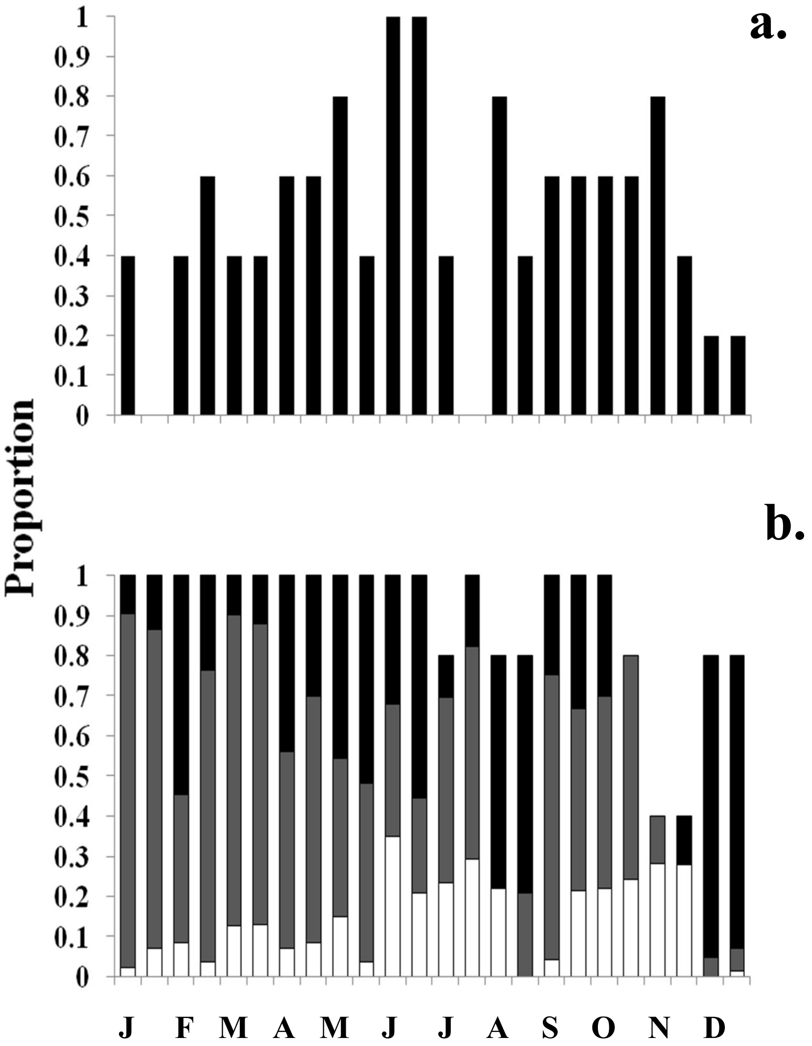

Fig. 2.6. Annual variation in the proportion of *F. racemosa* at Hueymaekhamin with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 5 trees, all of which produced figs.

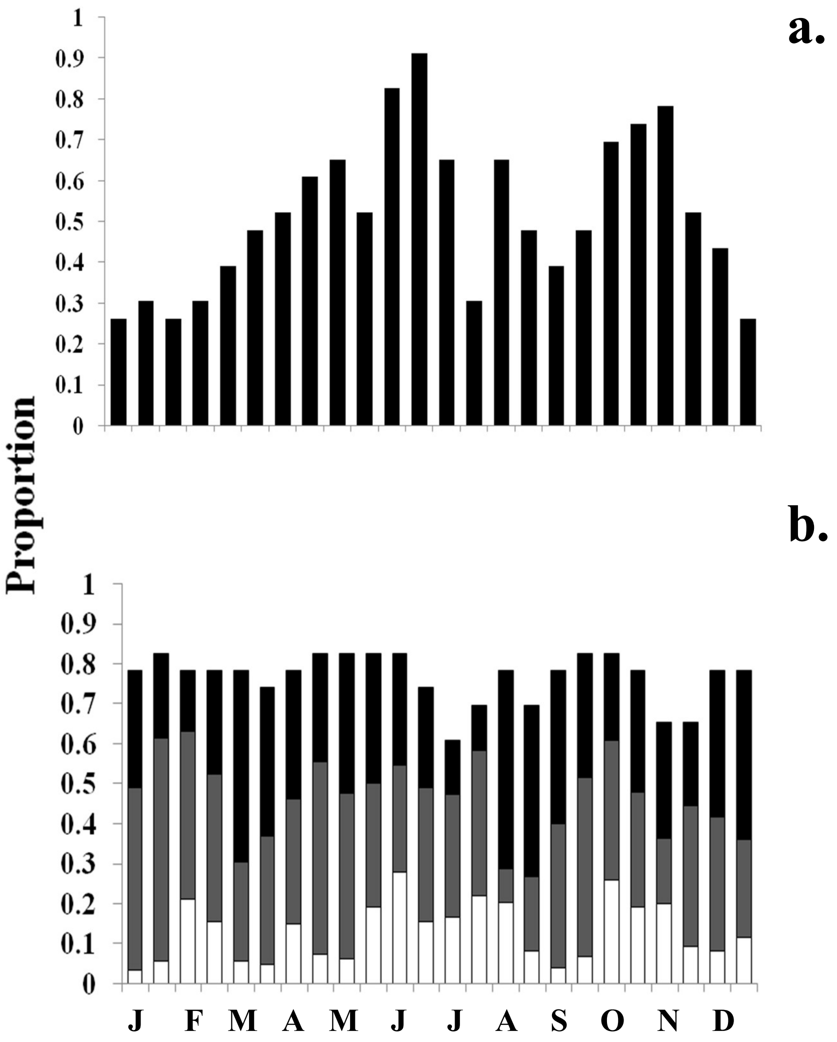

Fig. 2.7. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of *F. racemosa.* Pooled data from all sites (N = 23 trees of which 19 produced figs).

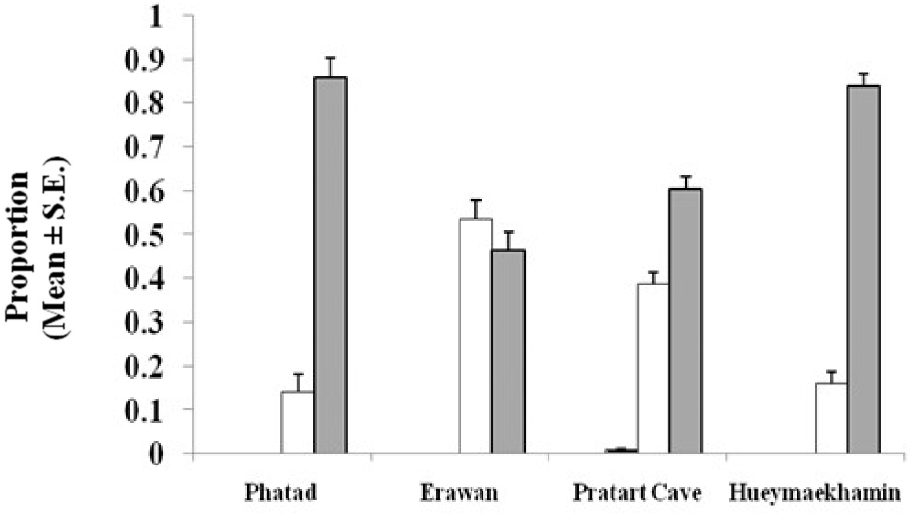

Fig. 2.8. The vertical distribution of figs on *F. racemosa* trees at four sites over 12 months: 0.5-1m (Black), 1-5m (White), > 5m. (Grey).

2.4.2 *Ficus oligodon* phenology

Both sexes of *F. oligodon* (Female: N = 15, Male: N = 15) produced new leaves all year round, but there were two peaks of new leaf production, from March to May and September to November (Figs. 2.9-2.13; Table 2.11). Small amounts of leaves fell all year round, ranging from less than 1% to 4% of the leaves present being senescing. Young leaves took three to seven weeks for development to mature leaves. New leaf production in both sexes did not correlate with any meteorological factor, except that female trees in Kratengjeng were positively correlated with average temperature. New fig production was positively correlated with new leaves in female but not in male trees (Table 2.14).

A total of 34 *F. oligodon* individuals were observed in 2016. Only 30 individuals produced figs (Female: N = 15, Male: N = 15, Table 2.4-2.5). Across all sites combined, figs were not uniformly produced throughout the year (Female trees: Kuiper's test: $V = 2.275$, P < 0.01, Male trees: Kuiper's test: $V = 2.605$, P < 0.01, Table 2.12). Although non-uniformity of fig production was not detected in female *F. oligodon* at Phatad, it nearly reached significance there (Table 2.12). New fig production was found from 0.20 to 0.87 of the female trees during different observation visits, but male trees often produced new figs all year round (ranging from 0.30 to 1.00, Fig 2.9-2.13). Female trees bore one to four crops a year (Mean ± SE: 2.60 ± 0.32 crops/year); with males ranging from two to four crops (Mean ± SE: 3.13 ± 0.17 crops/year: Table 2.10). There was no significant difference between crop numbers on female and male *F. oligodon* across all sites (Mann-Whitney U-test: U = 97.5, P = 0.516). However, within sites, the mean crop number of male and female trees (Kratengjeng, female: Mean ± SE = 3.11 ± 0.82 crops/year, male: Mean

± SE = 2.60 ± 0.39 crops/year; Phatad, female: Mean ± SE = 1.83 ± 0.70 crops/year, male: Mean ± SE = 3.10 ± 0.52 crops/year; Table 2.10) was slightly different at two sites, where male trees produced more crops in one year (Kratengjeng: Mann-Whitney U-test: U = 29.5, P = 0.264; Phatad: Mann-Whitney U-test: U = 10.0, P = 0.022). Female trees in Kratengjeng produced a significantly higher annual crop number than at Phatad, but there was no difference between male trees at the two sites (Female trees: Mann-Whitney U-test: U = 31.5, P = 0.044; Male trees: Mann-Whitney U-test: U = 15.5, P = 0.200) (Table 2.10).

Pooling the two sites, the crop sizes of male trees (Mean ± SE = 117.0 ± 16.36 figs/crop, ranging from 7 to 425 figs) seemed slightly larger than female trees (Mean ± SE = 89.1 ± 19.34 figs/crop, ranging from 1 to 540 figs), but there was no significant difference (Mann-Whitney U-test: U = 70.0, P = 0.078). Within sites, mean crop size between two sexes (Kratengjeng, female: Mean ± SE = 68.4± 15.89 figs/crop, male: Mean ± SE = 112.9 ± 31.51 figs/crop; Phatad, female: Mean ± SE = 143.6 ± 53.95 figs/crop, male: Mean ± SE = 118.9 ± 19.24 figs/crop; Table 2.10) was not significantly difference (Kratengjeng: Mann-Whitney U-test: U = 11.0, P = 0.125; Phatad: Mann-Whitney U-test: U = 21.0, P = 0.329). Also, when testing within sex between sites, mean crop size between the two sites was not significantly different (Female trees: Mann-Whitney U-test: U = 25.0, P = 0.813; Male trees: Mann-Whitney U-test: U = 23.0, P = 0.806) (Table 2.10). Pooled across all sites, 0.25 of all male crop proportion (Kratangjeng = 0.29, Phatad = 0.23) was asynchronous within trees, and 0.23 in female trees (Kratangjeng = 0.20, Phatad = 0.23). No whole crop abortion was found in either sex of this fig species (Table 2.10).

The majority of fig production (proportion) in both sexes was between 0 – 0.5 meters above ground level (Kratengjeng, Mean ± SE, female: 0.86 ± 0.03; male: 0.95 ± 0.01, Phatad, Mean ± SE, female: 0.63 ± 0.05; male: 0.75 ± 0.03), although some figs could be found on higher branches up to 5 meters above the ground, and very rarely there were figs produced on the branches higher than five meters above ground (Table 2.13, Figs. 2.15-2.16).

Both sexes produced fig all year round and showed a fruiting peak from April to June. The immature and receptive figs of female trees were present mostly from January to February, April to June, and August to late September. However, these phases on male trees were from February to April, and smaller peaks were shown from August to September. Developing C phase figs were present throughout the year, but peaked in January, from April to May and November to December in male trees and from March to April and in October in female trees, respectively. Mature figs releasing fig wasps were found on all the trees from March to June, providing the pollinators of the mature female figs that peaked in July (Fig 2.9-2.14). At the Kratengjeng site, young fig production of both sexes was positively correlated with average and maximum temperatures, but there was a negative correlation with relative humidity in both sexes and rainfall only in male trees. However, at the Phatad site, only young fig production of male trees was positively correlated with average and maximum, but there was a negative correlation with relative humidity. Moreover, young fig production of female trees was not significantly correlated with any climatic factors. Mature fig numbers on male trees showed a positive correlation with only temperature in both sites. Mature fig numbers on female trees were only correlated with temperature at the Kratengjeng site in female trees. Therefore, the relationship between fig production and climatic factors varied both among sexes and sites (Table 2.14).

Table 2.4. Annual variation in individuals of female *F. oligodon* individuals in riparian forest of Kanchanaburi. producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey. KTJ: Kratengjeng waterfall, PT: Phatad waterfall.

Tree Code	Site	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
749	KTJ	■	■	■	■	■	■	■	■	■	■	■	■			■	■	■	■	■	■	■	■	■	
754	KTJ						■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		
755	KTJ	■	■	■	■	■		■	■		■	■				■	■	■	■	■	■				
757	KTJ							■	■	■	■	■	■	■	■										
773	KTJ	■	■	■	■	■	■	■	■	■	■	■	■	■	■							■	■		
786	KTJ															■	■	■	■	■	■				
802	KTJ					■	■	■	■	■	■	■	■	■	■										
813	KTJ	■	■	■	■	■	■	■	■	■	■	■	■	■	■				■	■	■	■	■	■	■
814	KTJ	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■			■	■	■	■	■		
827	PT								■	■	■														
830	PT					■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
834	PT	■	■	■	■	■	■	■	■	■	■	■	■	■	■				■	■	■	■	■	■	■
836	PT							■	■	■	■	■	■	■	■										
841	PT								■	■	■	■				■	■	■	■	■					
838	PT																		■	■	■	■	■	■	■

Table 2.5. Annual variation in individuals of male *F. oligodon* individuals in riparian forest of Kanchanaburi. producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey. KTJ: Kratengjeng waterfall, PT: Phatad waterfall.

Tree Code	Site	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
743	KTJ	■	■	■	■	■	■	■	■	■	■	■	■	■											
747	KTJ	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
765	KTJ							■	■	■	■	■	■	■	■	■						■	■	■	■
766	KTJ					■	■	■	■	■	■	■													
791	KTJ							■	■	■	■	■	■	■	■	■	■	■	■	■	■				
819	PT								■	■	■	■	■			■	■	■	■	■	■	■	■	■	■
821	PT	■				■	■	■	■	■	■	■	■	■											
821	PT	■	■	■	■	■	■	■	■	■	■	■								■	■	■	■	■	
828	PT					■	■	■	■	■	■									■	■	■	■	■	■
833	PT	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						
835	PT	■	■	■	■	■	■	■	■	■	■	■	■	■						■	■	■	■	■	■
840	PT	■	■	■	■	■	■	■	■	■	■	■	■							■	■	■	■	■	■
861	PT	■	■	■	■	■	■	■	■	■	■	■	■	■						■	■	■	■	■	■
868	PT	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
869	PT	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■

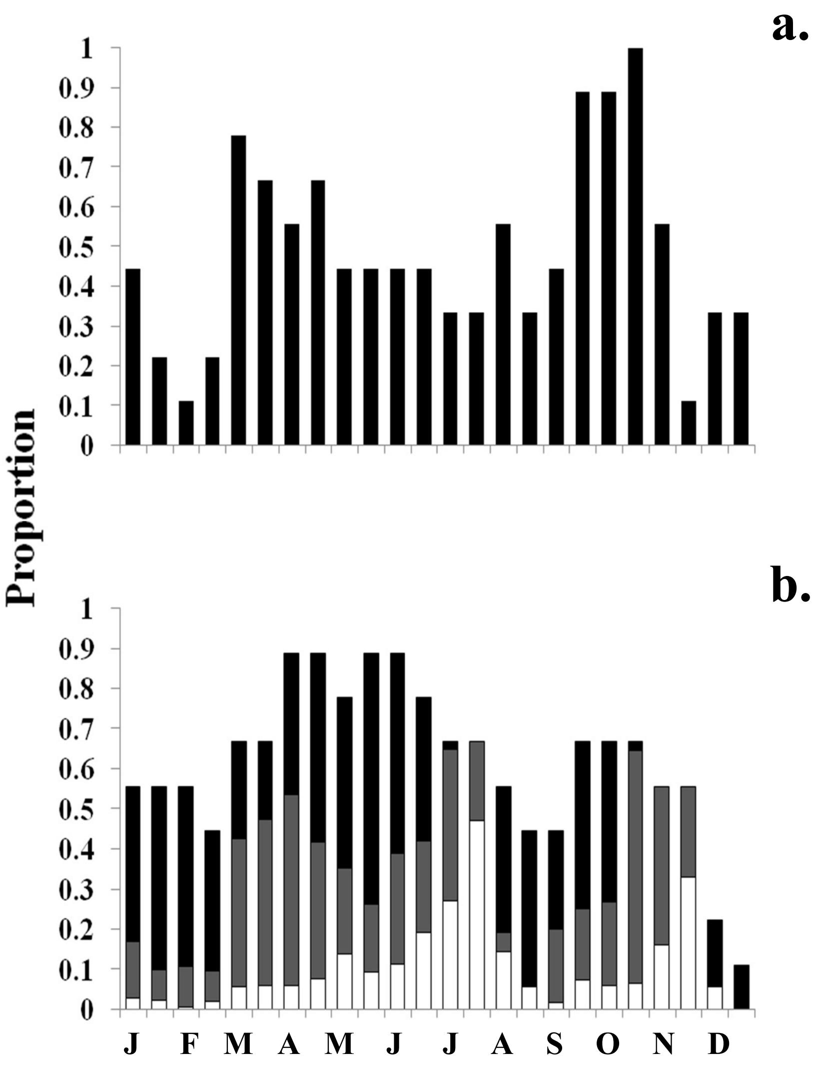

Fig. 2.9. Annual variation in the proportion of female *F. oligodon* at Kratengjeng with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 9 trees, all of which produced figs.

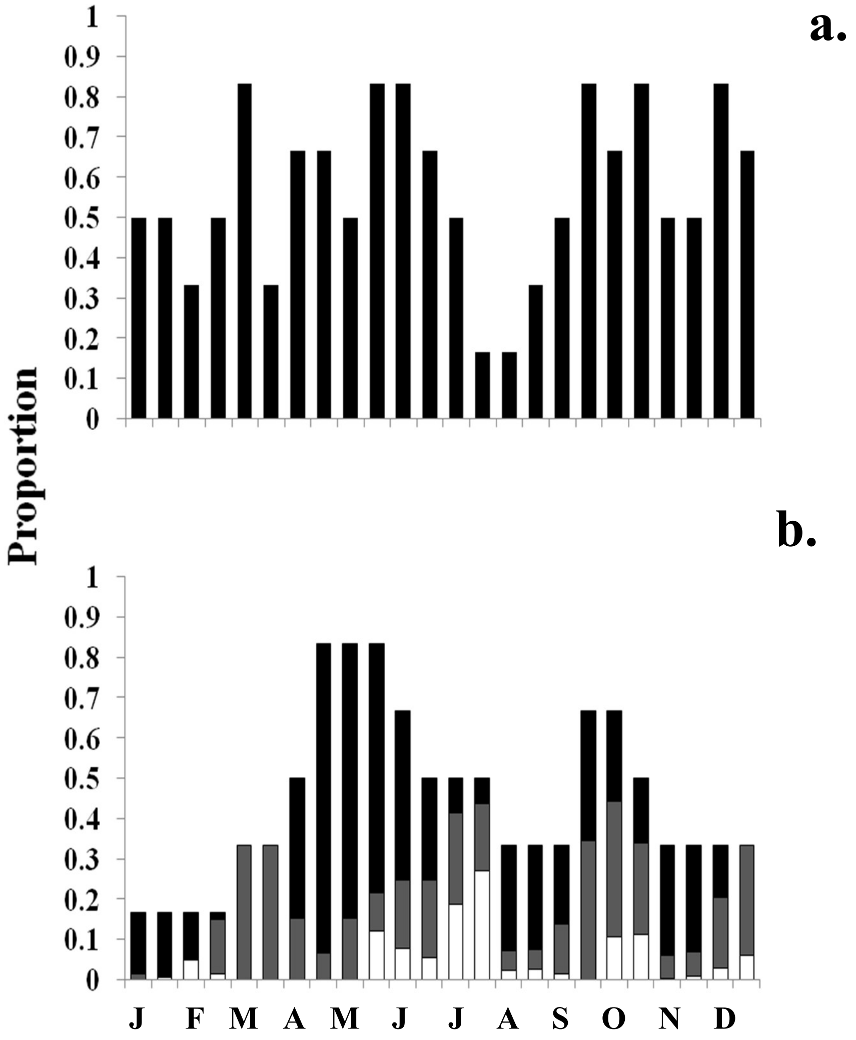

Fig. 2.10. Annual variation in the proportion of female *F. oligodon* at Phatad with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 6 trees, all of which produced figs.

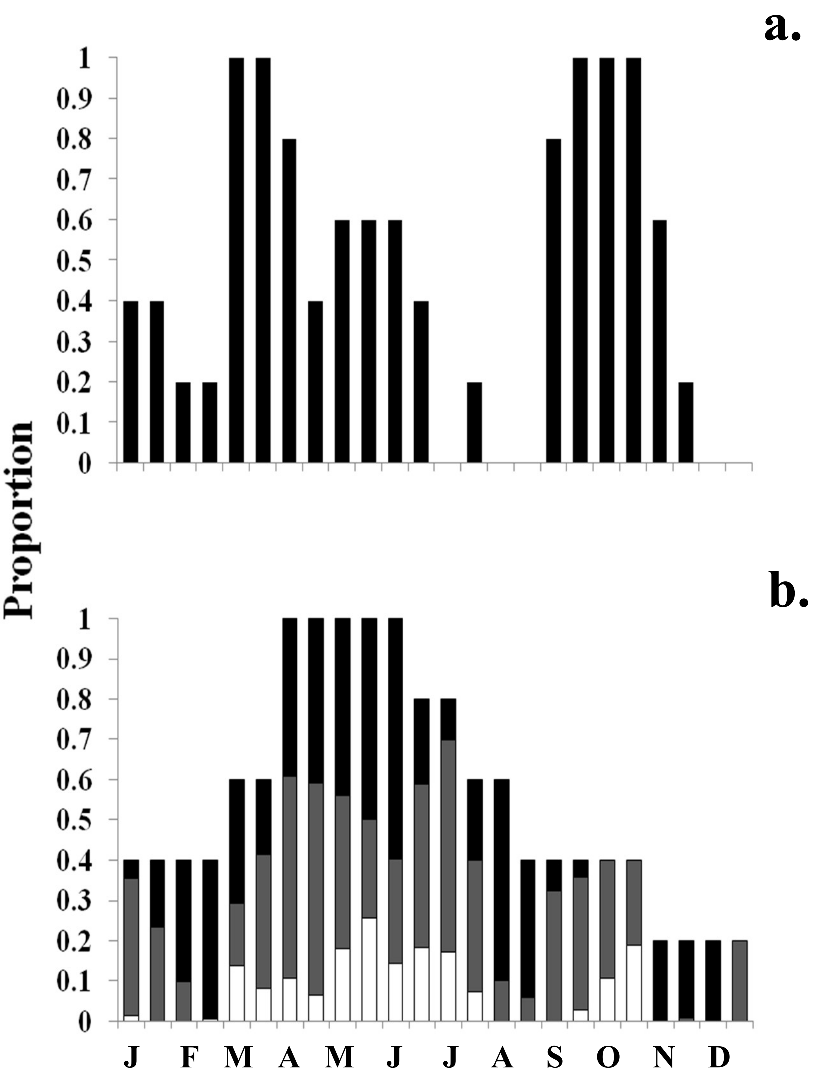

Fig. 2.11. Annual variation in the proportion of male *F. oligodon* at Kratengjeng with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 5 trees, all of which produced figs.

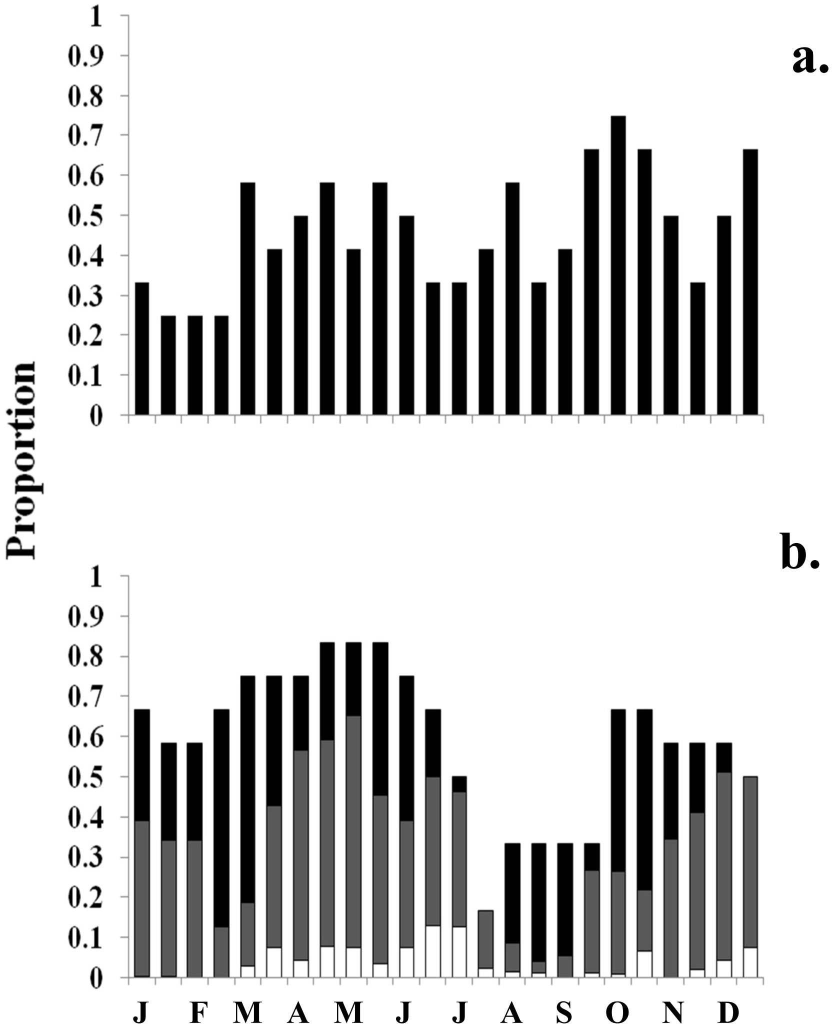

Fig. 2.12. Annual variation in the proportion of male *F. oligodon* at Phatad with young leaves (a) and trees with figs present (b). A+B figs (black bars), C figs (grey bars), D/E figs (white bars). N = 10 trees, all of which produced figs.

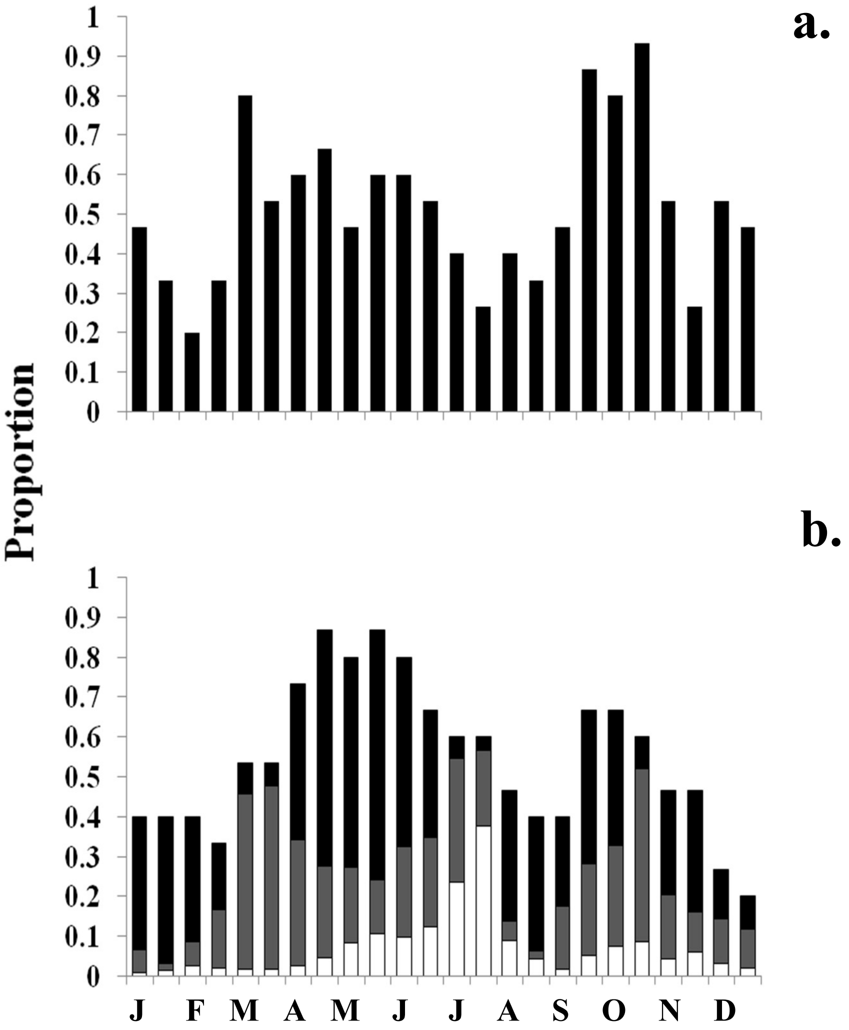

Fig. 2.13. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of female *F. oligodon.* Pooled data from all sites, N = 15 trees, all of which produced figs.

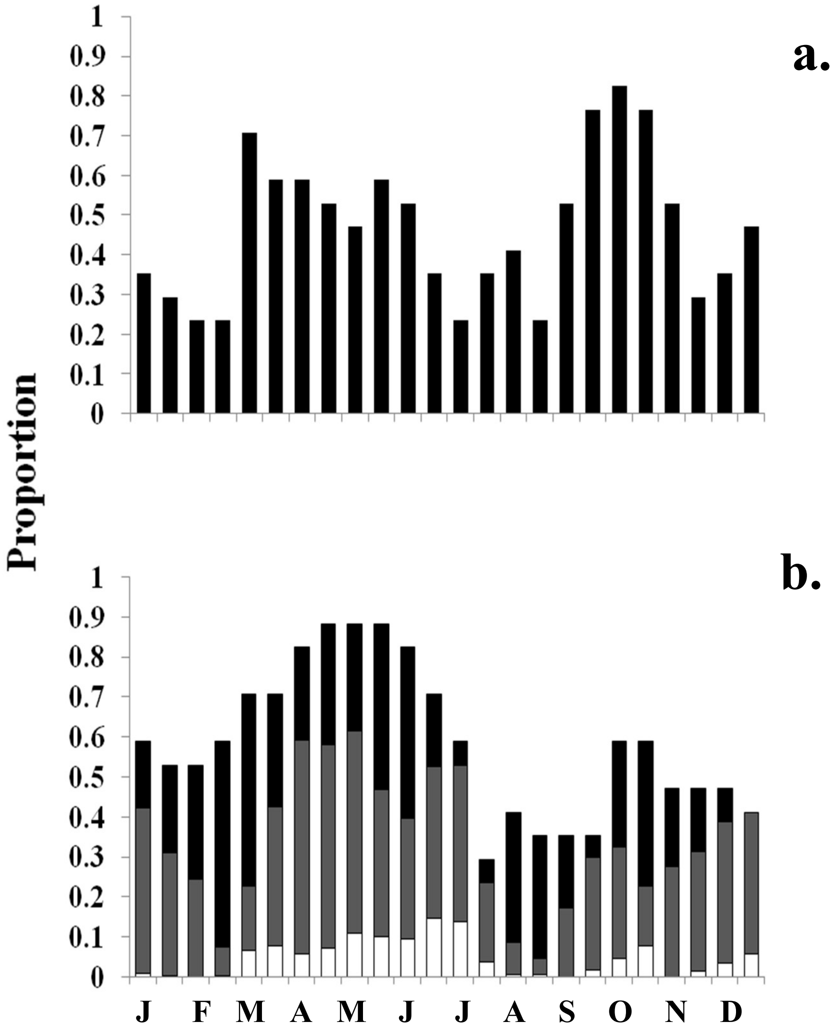

Fig. 2.14. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of male *F. oligodon.* Pooled data from all sites, N = 15 trees, all of which produced figs.

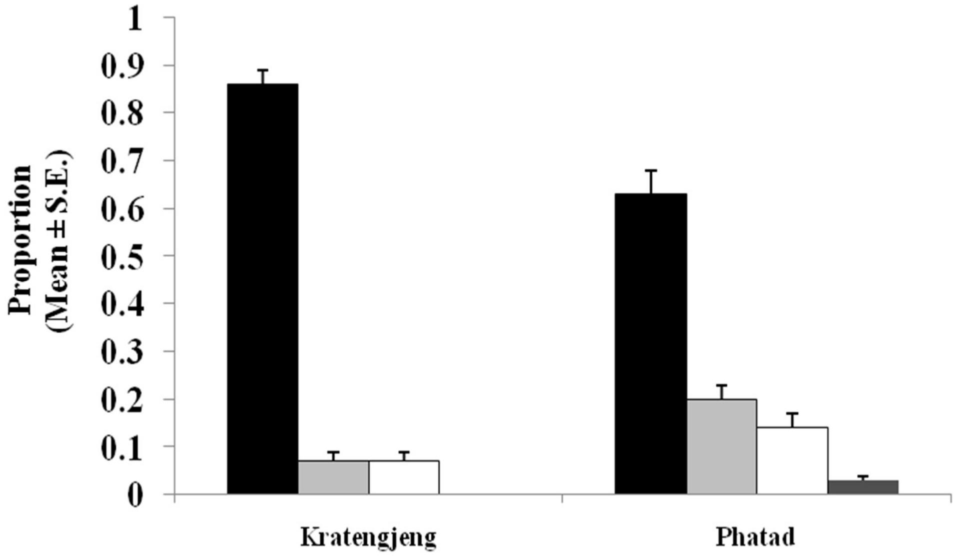

Fig. 2.15. Heights of figs above the ground on female *F. oligodon* trees in two different sites: 0-0.5 m (Black), 0.5-1 m (Light grey), 1-5 m (White), > 5 m (Dark grey).

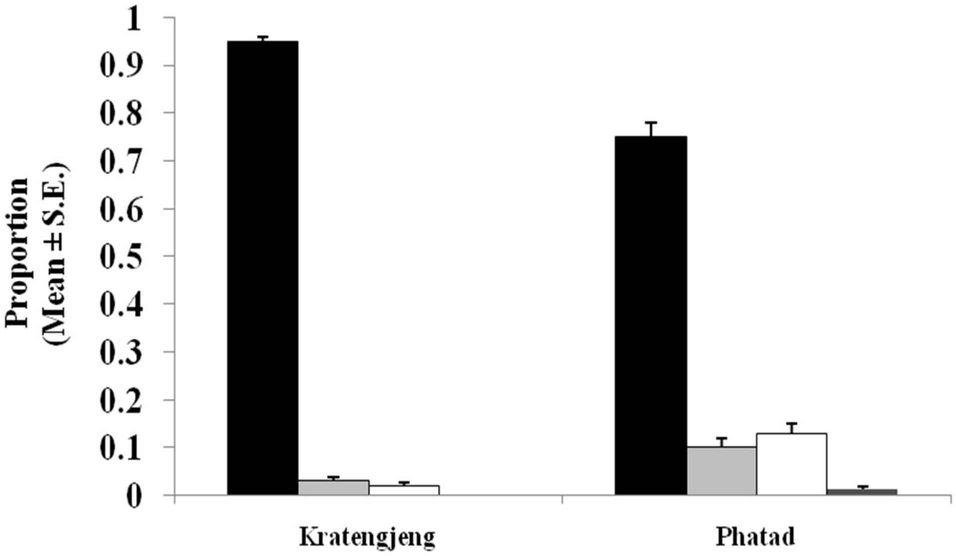

Fig. 2.16. Heights of figs above the ground on male *F. oligodon* trees in two different sites: 0-0.5 m (Black), 0.5-1 m (Light grey), 1-5 m (White), > 5 m (Dark grey).

2.4.3 *Ficus ischnopoda* phenology

Both sexes of this riparian fig tree species were evergreen (Female trees: N = 14, Male trees: N = 13). New leaves production was not uniform throughout the year and peaked from March to June and from September to October in male trees, but only in May and from September to October in female trees (Figs. 2.17-2.18; Table 2.11). In both sexes, leaf senescence occurred in small amounts all year round, and ranged from 0.5% to 4.5% of overall leaf cover. New leaves developed to mature leaves after three to five weeks in both sexes. New leaf initiation had a positive correlation with minimum temperature in female trees, and a positive correlation with average, minimum and maximum temperatures in male trees (Table 2.14).

Fruiting phenology was recorded from 34 individuals of *F. ischnopoda* at only Phatad site. However, most (27) of these trees produced at least one fig crop in 2016 (Tables 2.6 - 2.7). New figs production was not uniform throughout the year in both sexes (Table 2.12). Both sexes of *F. ischnopoda* produced different numbers of figs none at different times of the year round the proportion of individuals bearing figs at any one time ranged from 0.13 to 0.80 and 0.23 to 0.92 in female and male trees respectively (Figs. 2.17 - 2.18; Table 2.12). Female trees bore 3.43 ± 0.45 crops/year (Mean ± SE), ranging from one to seven crops/year, and male trees produced 3.00 ± 0.52 crops/year (Mean ± SE), ranging from one to six crops/year (Table 2.10). There was no significant difference between crop numbers of female and male *F. ischnopoda* (Mann-Whitney U-test: U = 83.5, P = 0.711). Male *F. ischnopoda* produced slightly bigger crops of figs (Mean ± SE = 30.2 ± 3.48 figs/crop that ranged from 1 to 82), than female trees (Mean ± SE = 21.4 ± 2.48 figs/crop ranging from 1 to 75 figs), but there was no significant difference (Mann-

Whitney U-test: U = 721.5, P = 0.063) (Table 2.10). Male crops displayed slightly more asynchrony within trees than female crops, with a value of 0.34 compared with 0.27 of all observations (Table 2.10). Only 0.05 and 0.04 of the observation periods recorded male and female crops that were totally aborted (Table 2.10).

In terms of the heights of figs on the trees, the majority of the female *F. ischnopoda* figs were produced at less than one meter above the ground (Mean ± SE, 0-0.5 m: 0.19 ± 0.04; 0.5-1 m: 0.76 ± 0.03). Only 0.05 ± 0.01 (Mean ± SE) of the figs were located between one to five meters above the ground and none higher (Table 2.13). Male *F. ischnopoda* produced 0.15 ± 0.02 (Mean ± SE) of their figs less than 0.5 m above the ground (Table 2.13; Fig 2.19), 0.47 ± 0.06 (Mean ± SE) of their figs from 0.5 to 1 m, and 0.38 ± 0.04 (Mean ± SE) from one to five meters. 0.154 of all the male trees (2 out of 13 trees) were taller than two meters (from 2-5 m in height), suggesting that some figs that produced 1-5 m above ground can be found more frequently in male trees (Table 2.13).

The immature and receptive figs were produced all year round but peaked in February, June and from October to November (smaller peak) in female trees, and in January, late May to June and September to October (smaller peak) in male trees. The figs developed to the C phrase within two to five weeks. The ripening figs of female peaked in April and August. Most male trees released fig wasps throughout the year, but releases peaked in May and late July (Figs. 2.17-2.18). Young fig production in both sexes was negatively correlated with relative humidity and also showed a slight positive correlation with maximum temperature in female trees. The mature fig production of female trees was positively correlated with temperature measures, but there was a negative correlation between mature fig production and rainfall in male trees (Table 2.14).

Table 2.6. Annual variation in individuals of female *F. ischnopoda* individuals at Phatad waterfall in riparian forest of Kanchanaburi. producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey. The red bar indicate when fig trees were noted as dead individuals.

Tree Code	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
839	■	■	■	■	■	■						■	■	■	■	■	■							
842-1	■	■	■	■	■	■	■	■	■	■	■													
842-2	■				■	■	■	■				■	■	■	■	■		🟥	🟥	🟥	🟥	🟥	🟥	🟥
843	■	■	■	■	■	■	■	■	■															
845	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■							■
847	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						
850	■	■	■	■	■			■	■	■	■	■	■	■	■	■								
854	■	■	■	■	■	■	■	■	■	■	■													■
860	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						
863	■	■	■																	■	■			
865	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
866	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
858										■	■	■								■	■	■	■	
867																				■	■	■		

Table 2.7. Annual variation in individuals of male *F. ischnopoda* individuals at Phatad waterfall in riparian forest of Kanchanaburi.

producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey.

Tree Code	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
820	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■			■	■	■	■	■	■
823	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
826	■			■					■	■	■	■	■	■	■	■			■	■	■	■	■	■
831	■	■																						
837	■	■	■				■	■	■	■	■	■	■	■		■	■	■	■	■				
849	■	■	■	■	■	■																		■
851	■																							
852	■			■	■	■	■	■	■	■	■	■	■	■	■	■	■							
853	■	■	■	■																				
856	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■									
857	■	■	■	■	■	■	■	■	■	■	■	■	■								■	■	■	■
859	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■
863																					■	■	■	■

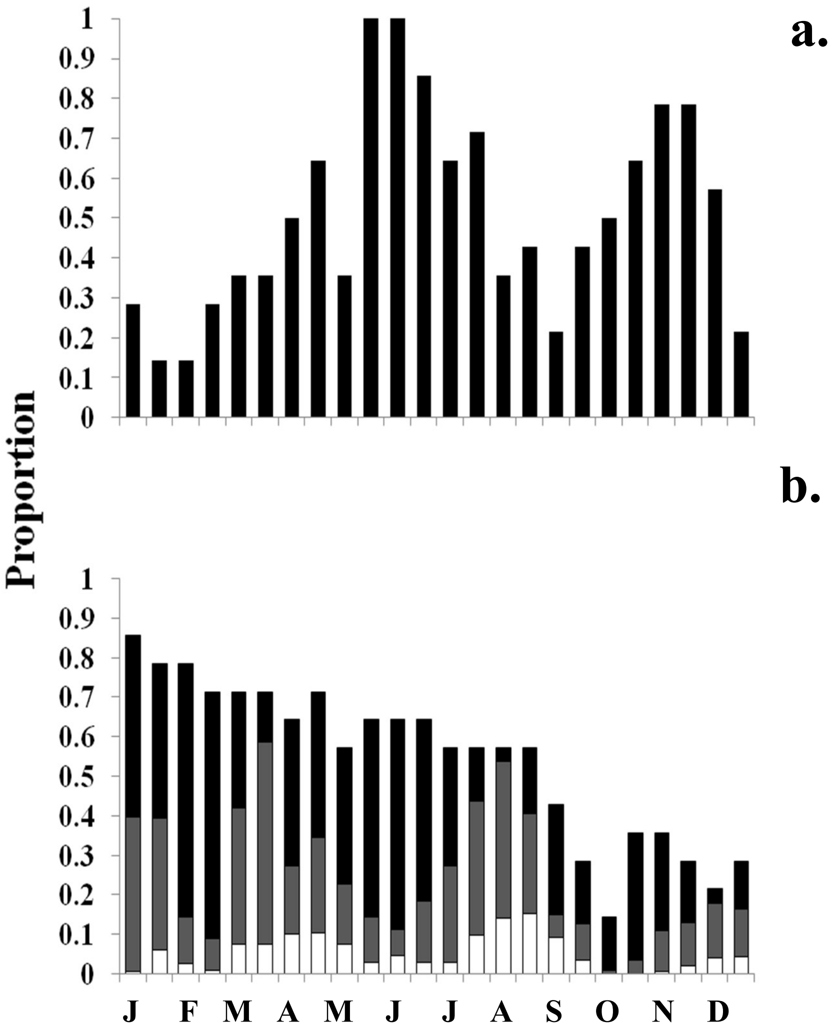

Fig. 2.17. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of female *F. ischnopoda* at Phatad. N = 14 trees, all of which produced figs.

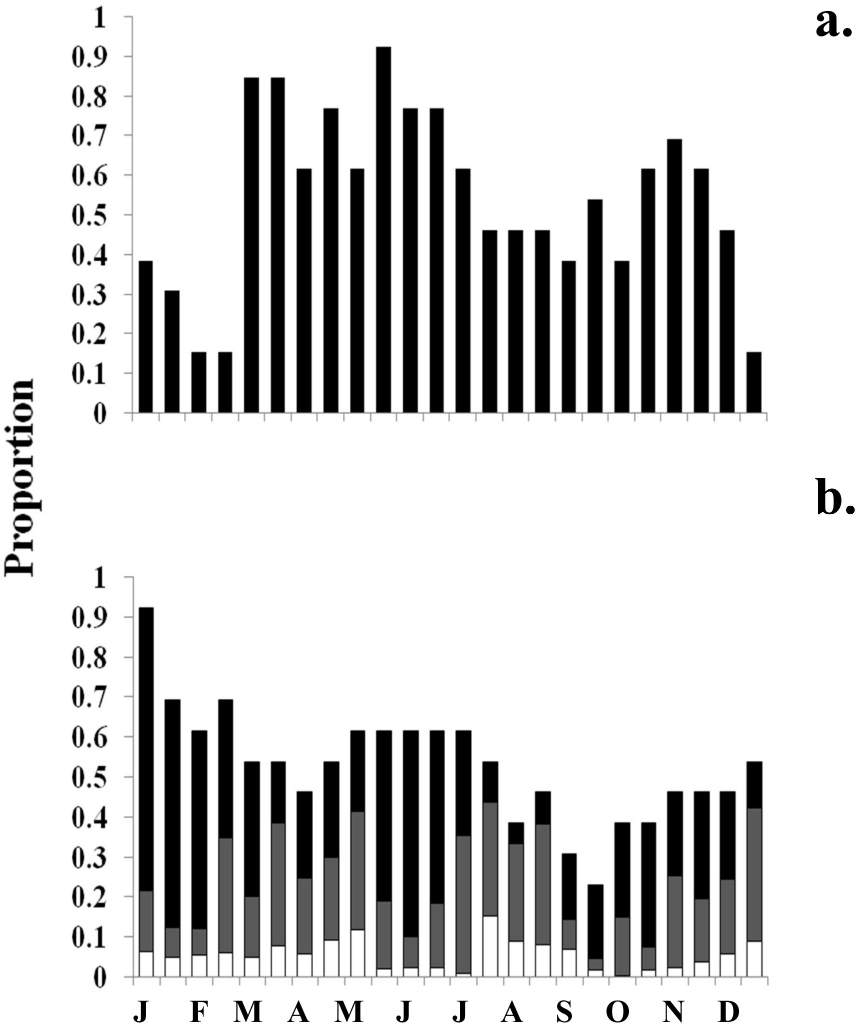

Fig. 2.18. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of male *F. ischnopoda* at Phatad. N = 13 trees, all of which produced figs.

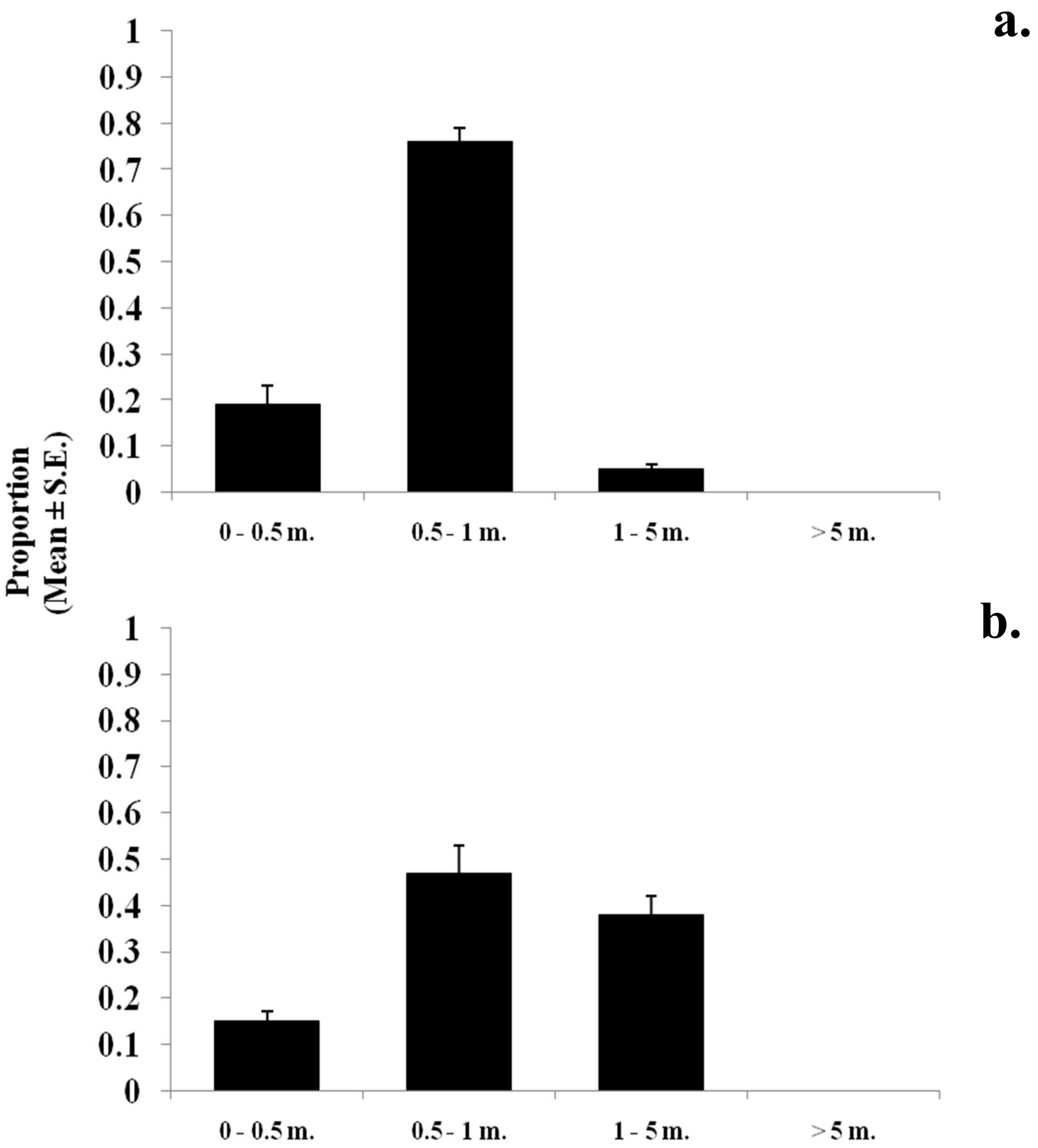

Fig. 2.19. Heights of figs above the ground on female (a.) and male (b.) *F. ischnopoda* trees at Phatad.

2.4.4 *Ficus montana* phenology

F montana was evergreen, producing new leaves in small and varying amounts throughout the year (Female trees: N = 20, Male trees: N = 19). New leaf production by the female trees peaked in March and in March and October in the male trees (Figs. 2.20-2.21; Table 2.11). Senescing leaves were also found all year round in small amounts, contributing up to 2.5% of overall leaf cover. New leaves developed to mature leaves from 3 to 6 weeks later in both sexes. New leaf production in female trees had a positive correlation with average, minimum and maximum temperature, but was negatively correlated with relative humidity. New leaf production of male trees was positively correlated only with average temperature. Fig production was positively correlated with new leaf production in female trees, but not male trees (Table 2.14).

The fruiting phenology of 58 *F. montana* individuals was observed, but only 20 female trees and 19 male trees produced any figs during the one year observation period (Tables 2.8-2.9). New figs production was not uniform throughout the year in both sexes (Table 2.12). *F. montana* bore figs all year round, and at different times 0.15 to 0.90 of the 20 female trees and 0.16 to 1.00 of the 19 male trees that produced figs (Figs 2.20-2.21; Table 2.12). The mean annual crop numbers of female trees were 3.50 ± 0.30 crops/year (Mean ± SE), ranging from one to five crops/year, and in male trees 3.58 ± 0.33 crops/year (Mean ± SE), ranging from one to five crops/year (Table 2.10). There was no significant difference between crop numbers of female and male *F. montana* (Mann-Whitney U-test: U = 179.5, P = 0.762). Male *F. montana* tended to produce larger fig crops (Mean ± SE = 17.3 ± 2.64, range = 1-89 figs/crop) than female trees (Mean ± SE = 13.5 ± 1.23, range = 1-

41 figs/crop), but there was no significant difference (Mann-Whitney U-test: U = 1468.0, P = 0.918) (Table 2.10). The proportion of asynchronous crops within trees was 0.37 of overall observations in both sexes (Table 2.10).

Only small proportions of the male (0.04) and female (0.02) overall observations recorded crops that aborted entirely (Table 2.10). Almost all *F. montana* figs were produced less than 0.5 m above the ground (Proportions (Mean ± SE): Female: 0.98 ± 0.004, Male: 0.83 ± 0.03). Very few figs were produced from 0.5 to one meter (Proportions (Mean ± SE): Female: 0.01 ± 0.003, Male: 0.17 ± 0.03) and only 0.01 ± 0.003 female and no male *F. montana* figs were found on branches higher than 1 m. (Table 2.13; Fig 2.22). No male and female fig trees were taller than two metres (Table 2.13).

Both sexes of *F. montana* had all stages of figs present all year round, but most trees had figs present from April to June. Young immature and receptive phrase figs were produced at similar times in both sexes. Developing figs were mostly found from March to May in female and from March to June in male trees. Mature ripening female figs peaked in February, May and July, and the releasing phase figs of male trees peaked from June to July (Figs. 2.20 - 2.21). Young fig production of both female and male trees was positively correlated with temperature factors, but negatively correlated with relative humidity. Mature fig production by both sexes was also positively correlated with temperature factors (Table 2.14).

Table 2.8. Annual variation in individuals of female *F. montana* individuals at Kratengjeng waterfall in riparian forest of Kanchanaburi. producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey.

Tree Code	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
738								■	■	■	■	■	■	■	■									
739	■	■		■	■	■	■									■	■	■	■	■				
740							■																	■
758	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■								
769	■	■					■	■	■	■	■	■	■	■										
771					■	■	■	■	■	■	■	■	■	■	■	■								
776							■	■	■	■														
785	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						
787	■	■	■	■	■	■	■	■	■	■	■	■									■	■	■	■
789	■	■	■	■	■	■	■	■	■	■	■	■									■	■	■	
003	■	■	■	■	■	■	■	■	■	■	■	■	■	■										
793								■	■	■								■	■	■	■			■
800	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						■	■		
801	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
803	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
804							■	■	■	■	■	■												
806					■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
809					■	■	■	■	■	■	■	■	■											
810					■	■	■	■	■	■	■	■	■	■	■	■	■							
767							■	■	■	■	■	■												

Table 2.9. Annual variation in individuals of male *F. montana* individuals at Kratengjeng waterfall in riparian forest of Kanchanaburi. producing figs in riparian forests of Kanchanaburi. The black bars indicate when figs were present in each survey.

Tree Code	Jan-16		Feb-16		Mar-16		Apr-16		May-16		Jun-16		Jul-16		Aug-16		Sep-16		Oct-16		Nov-16		Dec-16	
748					■	■	■	■	■	■	■	■	■	■	■	■			■	■	■	■	■	
751	■	■	■	■			■	■	■	■	■	■	■											
756					■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
762	■	■	■		■	■	■	■	■	■	■													
763	■	■			■	■	■	■	■	■	■	■	■	■					■	■	■	■		
768				■	■	■	■	■	■	■	■									■			■	■
001	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■						■	■		
002	■	■	■	■	■	■	■	■	■	■	■	■												
779							■	■	■	■														
780	■	■					■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		
782	■	■	■	■	■	■	■	■	■	■	■	■	■								■	■	■	■
783	■	■	■	■	■	■	■	■	■	■	■	■	■	■							■	■		
788					■	■	■	■	■	■	■	■	■											
790	■	■	■		■	■	■	■			■	■												
798	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
805					■	■	■	■	■	■	■	■	■	■										
760							■			■	■													
796							■	■	■	■	■	■	■											
799								■	■	■	■	■	■											

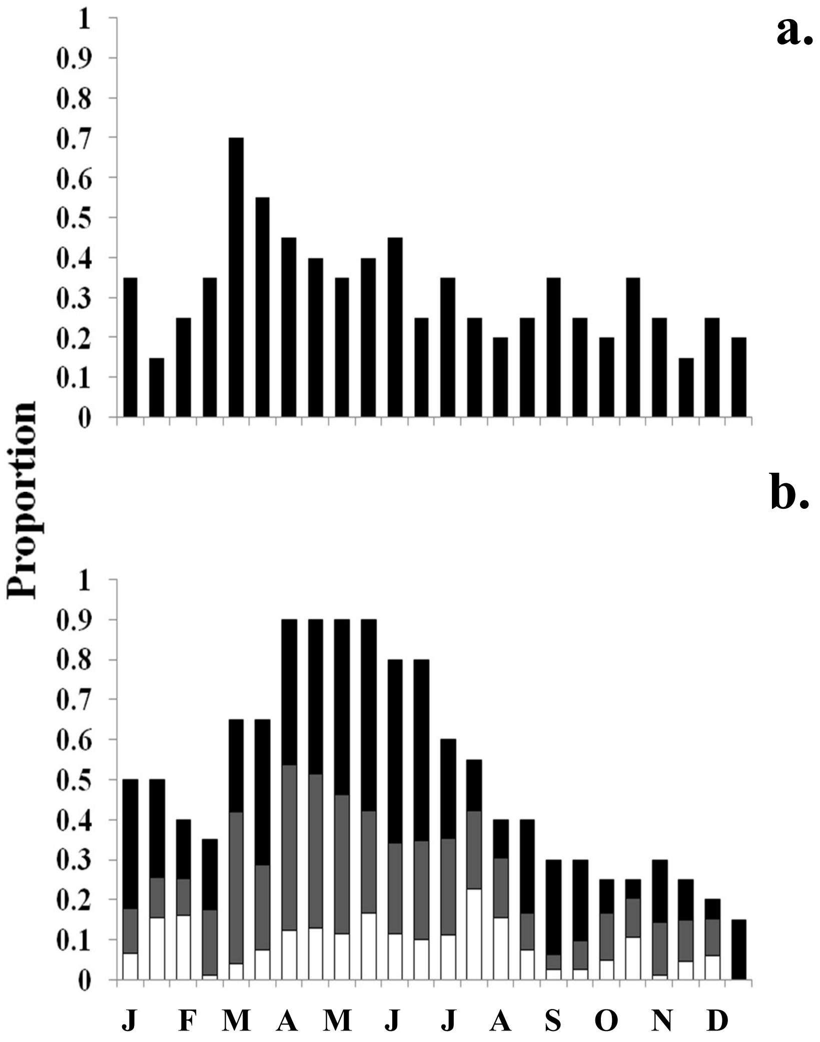

Fig. 2.20. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of female *F. montana* at Kratengjeng. N = 20 trees, all of which produced figs.

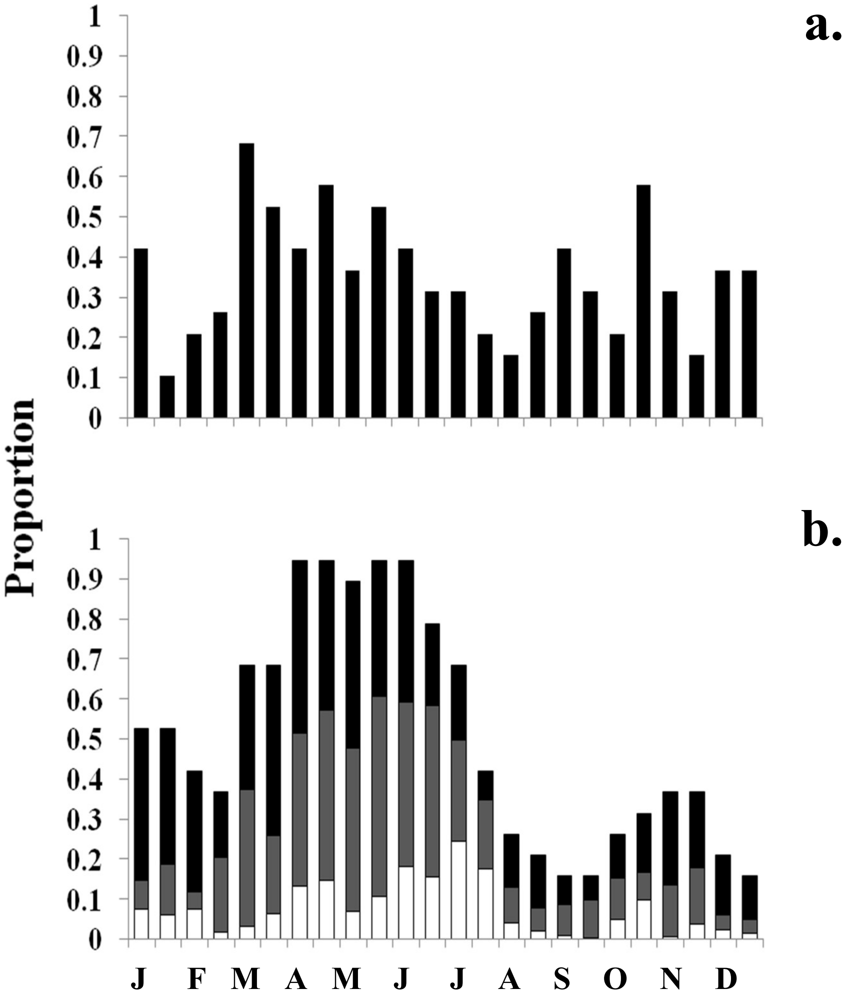

Fig. 2.21. Annual young leaves (a.) and trees with figs production: A+B figs (black bars), C figs (grey bars), D/E figs (white bars) (b.) of female *F. montana* at Kratengjeng. N = 19 trees, all of which produced figs.

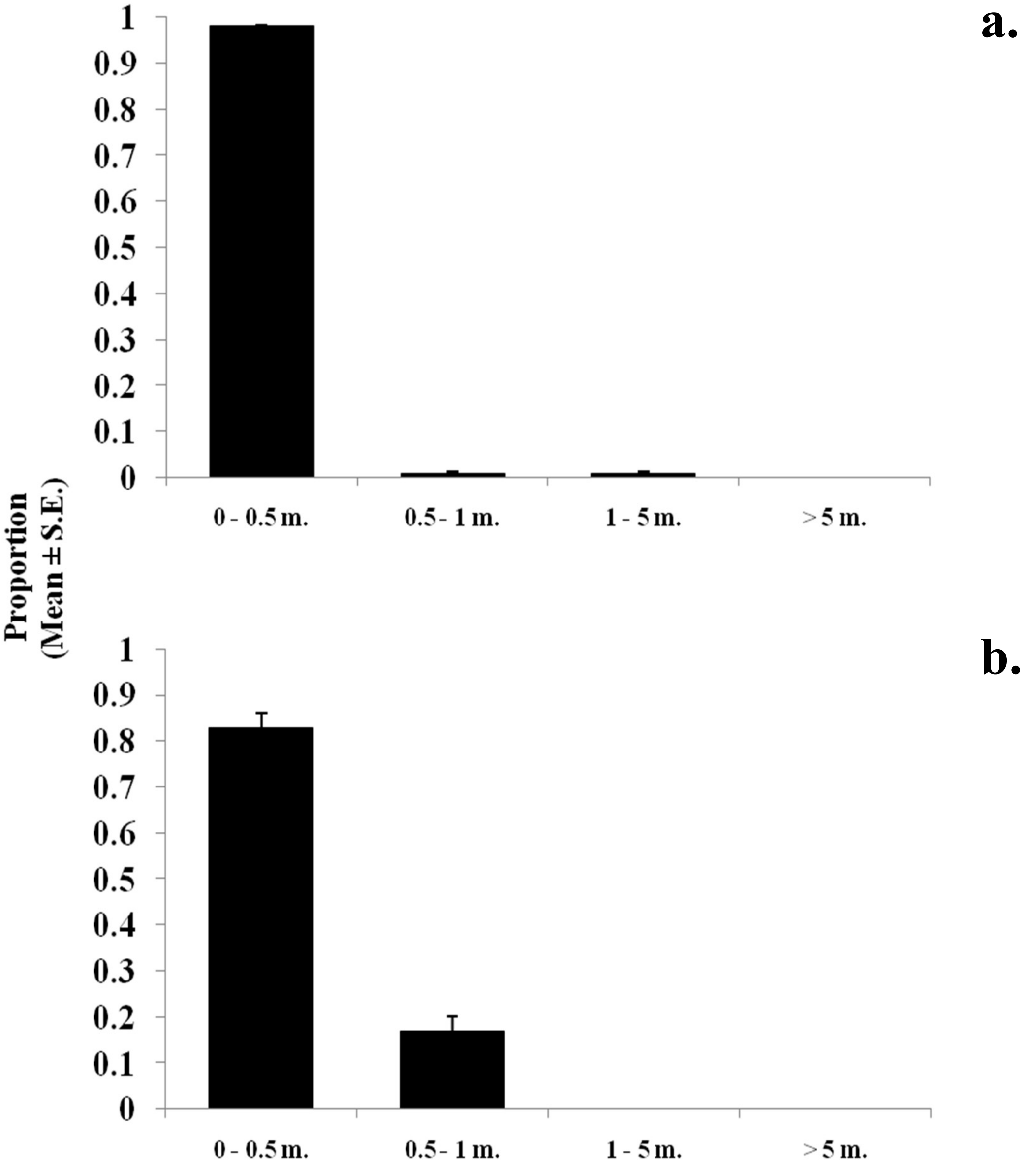

Fig. 2.22. Heights of figs above the ground on female (a.) and male (b.) *F. montana* trees at Kratengjeng.

Table 2.10. Fig crop numbers, crop sizes, proportion of maximum asynchrony (fig trees producing A+B and D/E figs at the same time during each observation), and the proportion of entirely aborted crops from four riparian fig trees over twelve months.

Species	Sex	Sites	Crop numbers			Crop size			Maximum Asynchrony		Crop abortion	
			n	Mean ± S.E.	Range	n	Mean ± S.E.	Range	n	Proportion	n	Proportion
F. racemosa	Monoecious	Phatad (PT)	2	5.00 ± 0.00	5	10	1710.3 ± 289.15	500-3500	47	0.23	10	0
		Erawan (E)	4	4.50 ± 0.29	4-5	18	1321.9 ± 181.32	300-3000	76	0.17	18	0
		Pratart Cave (PTC)	8	5.25 ± 0.37	4-7	42	2815.1 ± 341.12	500-8650	180	0.23	42	0
		Hueymaekhamin (H)	5	5.60 ± 0.40	4-6	28	2566.5 ± 358.26	300-6537	107	0.18	28	0
		Pooled all sites	**19**	**5.37 ± 0.19**	**4-7**	**98**	**2330.6 ± 191.29**	**300-8650**	**410**	**0.21**	**98**	**0**
F. oligodon	Female	Kratengjeng (KTJ)	9	3.11 ± 0.82	1-4	28	68.4 ± 15.89	1-243	138	0.20	28	0
	Male		5	2.60 ± 0.39	1-3	13	112.9 ± 31.51	24-355	69	0.29	13	0
	Female	Phatad (PT)	6	1.83 ± 0.70	1-3	11	143.6 ± 53.95	8-540	63	0.30	11	0
	Male		10	3.10 ± 0.52	1-3	31	118.9 ± 19.24	7-425	172	0.23	31	0
	Female	**Pooled all sites**	**15**	**2.60 ± 0.32**	**1-4**	**39**	**89.1 ± 19.34**	**1-540**	**201**	**0.23**	**39**	**0**
	Male	**Pooled all sites**	**15**	**3.13 ± 0.17**	**2-4**	**44**	**117.0 ± 16.36**	**7-425**	**241**	**0.25**	**44**	**0**
	Pooled both sexes	**Pooled all sites**	**30**	**2.77 ± 0.18**	**1-4**	**83**	**104.2 ± 12.54**	**1-540**	**442**	**0.24**	**83**	**0**
F. ischnopoda	Female	Phatad (PT)	14	3.43 ± 0.45	1-7	47	21.4 ± 2.48	1-75	177	0.27	47	0.04
	Male		13	3.00 ± 0.52	1-6	40	30.2 ± 3.48	1-82	165	0.34	40	0.05
	Pooled both sexes		**27**	**2.96 ± 0.31**	**1-7**	**87**	**25.8 ± 2.14**	**1-82**	**342**	**0.30**	**87**	**0.05**
F. montana	Female	Kratengjeng (KTJ)	20	3.50 ± 0.30	1-5	55	13.5 ± 1.23	1-41	253	0.37	55	0.02
	Male		19	3.58 ± 0.33	1-5	55	17.3 ± 2.64	1-89	234	0.37	55	0.04
	Pooled both sexes		**39**	**2.82 ± 0.20**	**1-5**	**110**	**15.5 ± 1.48**	**1-89**	**487**	**0.37**	**110**	**0.03**

Table 2.11. Circular statistics (Kuiper's test) assessing the uniformity of frequency of trees initiating new leaves throughout the year. The significant values mean non-uniformity. *: P < 0.05, **: P < 0.01, ***: P < 0.001

Species	**Sex**	**Site**	**n**	***V* statistics**	***P* value**
F. racemosa	Monoecious	Phatad (PT)	2	**1.849***	< 0.05
		Erawan (E)	4	1.535	> 0.15
		Pratart Cave (PTC)	8	1.677	0.05 <*P*< 0.10
		Hueymaekhamin (H)	5	1.365	> 0.15
		Pooled all sites	**19**	**2.702****	< 0.01
F. oligodon	Female	Kratengjeng (KTJ)	9	**1.862***	< 0.05
	Male		5	1.697	0.05 <*P*< 0.10
	Female	Phatad (PT)	6	1.183	> 0.15
	Male		10	1.359	> 0.15
	Female	**Pooled all sites**	**15**	**1.763***	< 0.05
	Male	**Pooled all sites**	**15**	**1.917***	< 0.05
F. ischnopoda	Female	Phatad (PT)	14	**2.509****	< 0.01
	Male		13	**2.468****	< 0.01
F. montana	Female	Kratengjeng (KTJ)	20	**2.295****	< 0.01
	Male		19	**2.110****	< 0.01

Table 2.12. Circular statistics (Kuiper's test) assessing the uniformity of frequency of trees producing figs throughout the year. The significant values mean non-uniformity. *: P < 0.05, **: P < 0.01, ***: P < 0.001

Species	Sex	Site	n	*V* statistics	*P* value
F. racemosa	Monoecious	Phatad (PT)	2	0.437	> 0.15
		Erawan (E)	4	0.781	> 0.15
		Pratart Cave (PTC)	8	1.057	> 0.15
		Hueymaekhamin (H)	5	1.077	> 0.15
		Pooled all sites	**19**	1.299	> 0.15
F. oligodon	Female	Kratengjeng (KTJ)	9	**1.772***	< 0.05
	Male		5	**2.134****	< 0.01
	Female	Phatad (PT)	6	1.705	0.05 <*P*< 0.10
	Male		10	**2.005****	< 0.01
	Female	**Pooled all sites**	**15**	**2.275****	< 0.01
	Male	**Pooled all sites**	**15**	**2.605****	< 0.01
F. ischnopoda	Female	Phatad (PT)	14	**2.667****	< 0.01
	Male		13	**1.795***	< 0.05
F. montana	Female	Kratengjeng (KTJ)	20	**3.980****	< 0.01
	Male		19	**4.328****	< 0.01

Table 2.13. Proportions of tree height and figs produced at different heights above the ground (Means ± S.E.) of four riparian fig trees over twelve months.

Species	Sex	Site	Tree heights					Fig heights (Mean ± S.E.)					
			N (Trees)	0 - 2 m.	2 - 5 m.	5 - 10 m.	> 10 m.	N (Observations)	Total figs	0 - 0.5 m.	0.5 - 1 m.	1 - 5 m.	> 5 m.
F. racemosa	Monoecious	Phatad (PT)	2	0	0	0	1.000	24	58003	0	0	0.14 ± 0.04	0.86 ± 0.04
		Erawan (E)	4	0	0	0.500	0.500	24	64114	0	0	0.54 ± 0.04	0.46 ± 0.04
		Pratart Cave (PTC)	8	0	0	0.375	0.625	24	319588	0	0.01 ± 0.002	0.39 ± 0.03	0.60 ± 0.03
		Hueymaekhamin (H)	5	0	0	0.200	0.800	24	188387	0	0	0.16 ± 0.03	0.84 ± 0.03
		Pooled all sites	**19**	0	0	0.316	0.684	**96**	**630092**	**0**	**0.002 ± 0.0006**	**0.305 ± 0.025**	**0.693 ± 0.0025**
F. oligodon	Female	Kratengjeng (KTJ)	9	0	0.333	0.667	0	24	6571	0.86 ± 0.03	0.07 ± 0.02	0.07 ± 0.02	0.002 ± 0.001
	Male		5	0	0.400	0.600	0	24	6688	0.95 ± 0.01	0.03 ± 0.007	0.02 ± 0.007	0
	Female	Phatad (PT)	6	0	0.333	0.667	0	24	6259	0.63 ± 0.05	0.20 ± 0.03	0.14 ± 0.03	0.03 ± 0.009
	Male		10	0	0.200	0.800	0	24	13518	0.75 ± 0.03	0.10 ± 0.02	0.13 ± 0.02	0.014 ± 0.005
	Female	**Pooled all sites**	**15**	0	0.333	0.667	0	**48**	**13100**	**0.75 ± 0.04**	**0.13 ± 0.02**	**0.10 ± 0.02**	**0.02 ± 0.005**
	Male	**Pooled all sites**	**15**	0	0.267	0.733	0	**48**	**20206**	**0.85 ± 0.02**	**0.06 ± 0.01**	**0.08 ± 0.01**	**0.007 ± 0.003**
F. ischnopoda	Female	Phatad (PT)	14	1.000	0	0	0	24	3117	0.19 ± 0.04	0.76 ± 0.03	0.05 ± 0.01	0
	Male		13	0.846	0.154	0	0	24	3781	0.15 ± 0.02	0.47 ± 0.06	0.38 ± 0.04	0
F. montana	Female	Kratengjeng (KTJ)	20	1.000	0	0	0	24	2335	0.98 ± 0.004	0.01 ± 0.003	0.01 ± 0.003	0
	Male		19	1.000	0	0	0	24	2852	0.83 ± 0.03	0.17 ± 0.03	0	0

Table 2.14. Spearman's correlations between metrological factors and *Ficus* phenology. AT, MiT and MaT = Average, minimum and Maximum temperature respectively, RH = Relative humidity, RF = Monthly accumulative rainfall. NL = proportion of fig trees with new leaves, FB = Proportion of trees with figs present, A+B = Immature and Receptive fig development phases, D/E = pollinator releasing and ripening phases.* P < 0.05, ** P < 0.01

	F. racemosa					***F. oligodon***						***F. ischnopoda***		***F. montana***	
	Phatad	**Erawan**	**Pratart Cave**	**Huey-maekamin**	**Pooled all sites**	**Kratengjeng**		**Phatad**		**Pooled all sites**		**Phatad**		**Kratengjeng**	
	Monoecious					**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
	(n=2)	**(n=4)**	**(n=8)**	**(n=5)**	**(n=19)**	**(n=9)**	**(n=5)**	**(n=6)**	**(n=10)**	**(n=15)**	**(n=15)**	**(n=14)**	**(n=13)**	**(n=20)**	**(n=19)**
New Leaves															
AT vs NL	**0.627****	0.124	0.127	**0.411***	**0.502***	**0.461***	0.368	0.097	0.216	0.382	0.355	0.337	**0.712****	**0.638****	**0.410***
MT vs NL	**0.629****	0.187	0.334	**0.453***	**0.580****	0.370	0.166	0.148	0.289	0.318	0.270	**0.461***	**0.619****	**0.446***	0.276
MaTvs NL	0.382	-0.098	-0.086	0.298	0.235	0.244	0.206	-0.047	-0.034	0.170	0.112	0.075	**0.497***	**0.657****	0.344
RH vs NL	0.212	**0.480***	**0.411***	0.170	0.366	0.170	0.114	0.076	0.257	0.094	0.193	0.373	0.036	**-0.451***	-0.292
RF vs NL	**0.413***	**0.406***	**0.448***	0.402	**0.508***	0.369	0.252	0.152	0.307	0.262	0.305	0.343	0.158	-0.178	-0.126
Young Figs															
AT vs A+B	0.019	**0.594****	**0.435***	0.272	0.235	**0.461***	**0.428***	0.286	0.382	**0.514***	**0.477***	0.133	0.002	**0.724****	**0.538****
MT vs A+B	-0.105	**0.798****	0.290	0.356	0.161	0.368	0.239	0.399	0.071	**0.488***	0.178	0.043	-0.185	**0.582****	0.350
MaTvs A+B	-0.121	**0.530****	**0.405***	**0.465***	0.378	**0.691****	**0.715****	0.318	**0.535****	**0.603****	**0.619****	**0.421***	0.184	**0.805****	**0.662****
RH vs A+B	-0.030	-0.113	-0.349	**-0.543****	**-0.548****	**-0.741****	**-0.787****	-0.243	**-0.595****	-0.346	**-0.675****	**-0.635****	**-0.468***	**-0.559****	**-0.622****
RF vs A+B	-0.151	0.295	-0.069	-0.165	-0.269	-0.227	**-0.049***	0.082	-0.385	0.194	**-0.417***	-0.364	-0.391	-0.111	-0.235
Mature Figs															
AT vs D/E	0.215	0.112	0.296	**0.465***	0.334	**0.795****	**0.742****	-0.292	**0.653****	0.270	**0.621****	**0.475***	-0.272	**0.753****	**0.569***
MT vs D/E	0.233	0.087	**0.416***	0.396	0.230	**0.810****	**0.598****	-0.110	**0.650****	0.347	**0.612****	**0.432***	-0.366	**0.743****	**0.474***
MaTvs D/E	0.129	-0.035	0.230	0.342	0.367	**0.662****	**0.681****	-0.267	**0.534****	0.108	**0.507***	**0.547****	-0.108	**0.746****	**0.517****
RH vs D/E	0.159	0.304	0.096	0.186	-0.248	-0.055	-0.275	0.282	-0.227	0.221	-0.239	-0.355	-0.353	-0.269	-0.299
RF vs D/E	0.193	0.368	0.223	0.275	0.083	0.235	0.093	0.225	0.014	0.187	0.002	-0.097	**-0.575****	0.163	0.038
Figs vs Leaves															
FB vs NL	-0.077	-0.126	-0.152	0.094	-0.014	**0.485***	0.227	**0.463***	0.139	**0.546****	0.304	-0.234	-0.025	**0.648****	0.342

2.5 Discussion

This study examined the phenological patterns of four *Ficus* species that are commonly found in riparian habitats of Kanchanaburi, western Thailand. Although leaf production among individuals of all four species varied somewhat, the species exhibited evergreen leaf production patterns, with small amounts of new leaves initiated throughout the year. An evergreen leaf pattern has been reported previously in many fig tree species from tropical and subtropical East Asia (Kuaraksa et al., 2012; Zhang et al., 2014; Chen et al., 2015; Pothasin et al., 2016). Across all four Thailand species, new leaves were more commonly produced between the midsummer and the beginning of the rainy season (March - June), and also in the peak period for rain from September to October. Leaf initiation in *F. squamosa*, a riparian specialist species, occurred all year round in Northern Thailand and also peaked in the beginning of the rainy season (Pothasin et al., 2016) which is comparable to this study. Similarly, seven native fig tree species that inhabit mixed deciduous dipterocarp-oak and evergreen forest of Northern Thailand (*F. auriculata*, *F. fulva*, *F. hispida*, *F. oligodon*, *F. semicordata*, *F. triloba* and *F. variegata*) are also evergreen with new leaves produced all year round but showing comparable peaks to this study (Kuaraksa et al., 2012). New leaves production of *F. fulva* in Sarawak was also found to be all year round (Harrison et al., 2000). In the African *F. burtt-davyi,* new leaf initiation seems to be partly related to rainfall although some trees were producing new leaves throughout the year (Compton, 1993). Leaf senescence of all four of the riparian fig trees in this study occurred in small amounts all year round, representing at any one time mostly less than 5% of canopy cover. Similarly, other fig trees in South-East Asia exchange new and old leaves all year round (Kuaraksa et al., 2012; Pothasin et al., 2016).

It is suggested that trees in tropical rainforests typically produce new leaves when the temperature is high, rainfall amounts are minimal and day lengths are longer (Sundarapandian et al., 2005). For most of the four fig tree species, the number of fig trees producing new leaves was positively correlated with temperature. A similar pattern is present in *F. squamosa* (Pothasin et al., 2016) and also in *F. semicordata* and male *F. triloba* (Kuaraksa et al., 2012). The exceptions were both sexes of *F. oligodon* and female *F. ischnopoda*, which nonetheless showed slightly positive responses to temperature. The proportion of new trees producing new leaves did not correlate with monthly mean temperatures in other species reported by Kuaraksa et al. (2012) (*F. auriculata*, *F. fulva*, *F. hispida*, *F. oligodon*, and *F. variegata* in Northern Thailand) and also *F. tinctoria* in China (Chen et al., 2015). It is known that drought can increase leaf fall in fig trees, with new leaves produced after the first rains come (Harrison et al., 2000). Other factors affecting leaves producing in plants could be day length, temperature (Kirby, 1995; Sundarapandian et al., 2005), photoperiod (Rivera et al., 2002; Singh et al., 2005) or rainfall (Compton, 1993; Sundarapandian et al., 2005). For riparian species, water availability is less likely to be a physiological constraint than in drier habitats. However, having more leaves will nonetheless increase water losses through transpiration (Taiz & Zeiger, 2002).

As all the fig tree species in this study were growing along riparian sites where water supply is available all year round, water shortage also seems unlikely to be a limiting factor for fig production. The monoecious *F. racemosa* bore significantly larger crops and fruited more continuously than the three dioecious fig tree species. As well as breeding system, the major difference between *F. racemosa* and the other three riparian fig species is tree size. The crown size of *F. racemosa* can be larger than 10 m in diameter (CHAPTER 3) and the tree can grow up to 25 m tall (Jia et al., 2008). The larger canopy of *F. racemosa* trees provides more surface area to absorb sunlight and this may result in better fruit production.

At the population level, asynchronous fig production was found in all four of the riparian fig trees, but fewer asynchronous crops were recorded on *F. racemosa* trees than the other three species. Thus, self-pollination is likely to be less common in *F. racemosa*. It has been revealed that monoecious fig trees tended to bear more synchronous crops on each tree (Zhang et al., 2006; Wang & Zheng, 2008). However, in this study, the percentage of asynchronous crops was estimated using the maximum asynchrony value, because it is difficult to identify the differences between immature figs (A phase figs) and receptive figs (B phase figs). Another report of *F. racemosa* elsewhere suggested a lower percentage of within-tree asynchrony but was based on the presence of both receptive and releasing phrases figs at the same time (Jia et al., 2008).

The asynchronous crops within trees of the three dioecious species in this study are consistent with other studies (Patel, 1996; Kuaraksa et al., 2012; Pothasin et al., 2016). The asynchronous fig production in male trees allows them to maintain their pollinator populations by providing immature figs in the same tree for the short lived female fig wasps to colonise quickly after they emerge from their natal male figs (Compton et al., 1994; Kuaraksa et al., 2012). Those that fly further contribute to the reproductive success of the male tree, but most are likely to die when travelling between trees. Fig abortion was not found in any individuals of *F. racemosa* and neither sex of *F. oligodon*, but up to five percent of the figs on both sexes of *F. ischnopoda* and *F. montana* were aborted in 2016. This suggests a shortage of pollinators can be occurred in some fig tree species (Harrison et al., 2000; Kuaraksa et al., 2012), though other factors including damage by other insects can also cause abortions (Compton S. G., pers. comm.).

All four of the riparian fig tree species produced figs all year round. However, their patterns of fig production were different. Fig production by the monoecious *F. racemosa* seems stable with not clear seasonal pattern, although fig production decreased in July and November. It is suggested that there are limited seasonal effects on the phenological patterns of monoecious *F. racemosa* and *F. rubiginosa* in Australia (Jia et al., 2008), *F. citrifolia* in Neotropics of Brazil (Pereira et al., 2007) because climate factors such as temperature fluctuate less fluctuation than at higher latitudes. However, in sub-tropical zones, the effects of season on fig phenology are likely to be stronger than that in the tropics. For example, most individuals of the monoecious *F. virens* do not bear fig during the winter season in South China, where temperatures can drop to near or below zero (Zhang et al., 2014).

Among the dioecious fig trees, the immature and receptive figs of male *F. oligodon* trees clearly developed before the equivalent stages on female trees. This allows them to release pollinators at times when there is a better chance that their pollen and generate seeds. Phenological studies of *F. oligodon* and some other dioecious fig trees (*F. auriculata*, *F. variegata*, *F. fulva* and *F. variegata*, Kuaraksa et al., 2012), and *F. squamosa* (Pothasin et al., 2016) detected this pattern. However, fig development of *F. montana* and *F. ischnopoda* similar in both sexes and is comparable with the *F. hispida* (Kuaraksa et al., 2012). Under controlled conditions

F. montana also displayed similar fruiting in male and female trees (Suleman et al., 2011).

Due to the different reproductive modes of male (producing pollen-carrying fig wasps) and female fig trees (producing seeds), dioecious fig species may be affected differently by environmental and climatic factors than monoecious fig tree species (Kjellberg & Maurice, 1989). Fig production by male trees, most noticeably in *F. oligodon,* was higher than female trees in the dry season. The dry season is the most suitable time for releasing fig wasps as the immature female figs are become available during the late dry season (Pothasin et al., 2016). Conversely, seed survival seems more likely in the wet season and the reproductive success of male trees depends on the export of fig wasps to immature female figs some weeks earlier. Conversely, it has been suggested that immature male figs of some fig tree species are less abundant in the rainy season because flight is more difficult due to the more turbulent air (Peng et al., 2003).

Figs availability was negatively correlated with total fruit productivity (especially, *F. montana*: $r_s = -0.662$, $P < 0.05$ and *F. ischnopoda:* $r_s = -0.625$, $P < 0.05$) in mixed deciduous forest in Kanchanaburi, western Thailand, suggesting that several figs tree species in this area provide food resource for frugivores when fruits are scarce from March to June (Hata et al., 2015). This study included some *Ficus* species and differences may reflect contrasts between riparian and forest habitats as well as between different *Ficus* species. Although it has been suggested that fig tree fruiting peaks can in places be the same as with non-fig trees (Borges, 1993; Patel, 1997) and figs may offer poor nutrition in comparison with coexisting non-fig species (Borges, 1993), figs are still heavily consumed by frugivores, especially, the large strangler fig trees (Korine et al., 2000; Shanahan et al., 2001; CHAPTER 7). Fig trees vary in size, colour, positions and odour, allowing them to interact with several different guilds of frugivores and suggesting they can be a food resource for many different species (Shanahan et al., 2001; CHAPTER 3). Also, many fig tree species, especially the tall trees with a large canopy size and large crops interact with large numbers of individuals belong to numerous frugivore species. Examples include *F. caulocarpa, F. racemosa* and several *Urostigma* (strangler) fig trees (Korine et al., 2000, Sreekar et al., 2010; CHAPTER 7). High fig productivity during seasons of general fruit shortage and production of figs all year round both underline that figs can be a keystone resource for frugivores (Borges, 1993). However, the seasonal significance of their fruiting phenology was shown in a study of Malabar Giant Squirrels (*Ratufa indica*, Sciuridae) which were found to mainly eat figs during periods of general fruit shortage in tropical forest habitats of India. There was only a minor food resource when fig trees did not occur in the home ranges of the squirrels or were at low population densities (Borges, 1993). Similarly, fig trees are only a seasonally important food resource of Red-eyed bulbuls (*Pycnonotus brunneus*, Pycnonotidae) during the dry season in tropical lowland forest of Southern Thailand, (Kerdkaew et al., 2014).

In the riparian forests of Kanchanaburi Province the major fig tree species were mostly shrubs or medium-sized trees producing small crops close to the ground (0-1 m.) (*F. oligodon*, *F. montana* and *F. ischnopoda*), and these fig trees interact with only small numbers of frugivore species that provide low fig removal rates. These small fig trees may be of less importance for frugivores than larger species (CHAPTER 3). However, the large canopy fig tree species in this area, *F. racemosa*, produced the majority of its figs well above the ground (at more than 5 m), showed high fig removal rate, interacted with many frugivore species, all year round and had large fig crops, so *F. racemosa* can be considered as a keystone resource tree in this area (CHAPTER 3).

The height at which fleshy fruits are presented is likely to have a major influence on the species of vertebrates that feed on them and disperse the seeds inside (Shanahan & Compton, 2001; CHAPTER 3). The vertical stratification of figs, together with other fig characteristics (crop size and colour) affects the composition of different seed dispersal guilds in tall trees and understorey figs in Borneo (Shanahan & Compton, 2001). Similarly, canopy feeding birds, such as hornbills, were recorded eating *F. racemosa* figs but not figs belonging to the other species (CHAPTER 3) whereas ground feeding thrushes and waterhens, fed only on the smaller shrub-like fig tree species (CHAPTER 3). Large frugivorous animals (such as chimpanzees, monkeys and hornbills) prefer to eat larger figs in Uganda, probably because it is less efficient for them to forage on small figs (Wrangham et al., 1993). The large figs of *F. racemosa* in Asia may also make them more attractive to larger species. Therefore, the importance of fig trees as a food resource for frugivores will be different among *Ficus* species and this importance will vary between different frugivore taxonomic groups (CHAPTER 7).

This study provides information about the overall patterns of fig production in a riparian area of western Thailand. Further studies should emphasize interactions between these fig trees with local pollinators and seed dispersers. Also, the gene flow of these fig trees is determined by these interactions and underpins their population dynamics and resilience in the face of the threats generated by human development and tourism in these riparian areas.

Chapter 3 The frugivore assemblages of four *Ficus* species in riparian habitats of western Thailand

3.1 Abstract

The genus *Ficus* is recognised as a major provider of food resources for wildlife, especially in tropical rain forests. Most of the fig tree species in Thailand are found in riparian habitats. There is little information about fig-frugivore interactions in these riparian areas, especially for those trees that produce small fig crops. In 2016, several crops of four major riparian *Ficus* species: *Ficus oligodon* (N = 25 trees), *F. ischnopoda* (N = 15 trees), *F. montana* (N = 30 trees), and *F. racemosa* (N = 6 trees) were monitored by direct observation or using camera traps along streams and waterfall in evergreen rainforest at Erawan, Srinagarind Dam and Khaolaem National Parks, Karnchanaburi, western Thailand. Their crop sizes were counted and fallen fig destinations (whether above water or land) were also noted. Only a few fig crops of the smaller species *F. oligodon* (4 crops), *F. ischnopoda* (4 crops) and *F. montana* (8 crops) were visited by frugivores. Their figs were and eaten by three, four and seven species respectively, and fruit removal rates of these species were low. Eight frugivore species fed on the larger crops of the big free-standing tree *F. racemosa*. The major frugivores of *F. montana* and *F. ischnopoda* were bulbuls (Pycnonotidae), especially the Black-crested bulbul (*Pycnonotus flaviventris*) and a riparian specialist bird, the Blue whistling thrush (*Myophonus caeruleus*, Muscicapidae). The major frugivore of *F. oligodon* and *F. racemosa* figs was the Grey-bellied squirrel (*Callosciurus caniceps*, Sciuridae). However, most of the figs of all four riparian fig species were not fed on by any frugivores and fell down to the water and ground. Due to the apparent shortage of frugivores feeding on

these riparian figs, water dispersal and fish may play an important role in dispersing the seeds of these riparian figs. Further studies should emphasize the role of aquatic animals in seed dispersal services in SE Asian riparian ecosystems.

3.2 Introduction

The genus *Ficus* comprises at least 830 species distributed in warmer regions of the planet (The Plant List, 2018). The largest numbers of *Ficus* species are found in the Indo-Australasian region, including, Asia, Malesia, and Oceania, where at least 511 species are present (van Noort & Rasplus, 2018). Because fig trees produce fruits throughout the year with their figs varying in detail (in fig size, crop size, fig colour and places where figs are present), figs are considered as important food resources for a wide variety of frugivores (Lambert & Marshall, 1991; Shanahan, 2001; Peh & Chong, 2003). For example, at least 1432 bird and 435 mammal species are known to be fig eaters worldwide (CHAPTER 7). Moreover, other vertebrates, such as fishes and reptiles, also feed on figs (Shanahan et al., 2001; CHAPTER 7). However, the composition and quality of figs in the diet is different among frugivore groups, with figs produced by different species attracting different frugivore assemblages and figs as a major or minor part of their diets. For example, in the hornbills (Bucerotidae), a disproportionate 38-98 percent of all dietary records are of figs, suggesting that figs are particularly important in the diet of hornbills (Balasubramanian et al., 2004; Hadiprakarsa & Kinnaird, 2004; Kanwatanakid-Savini et al., 2009).

It is suggested that the majority of plants rely on animals to disperse their seeds (Jordano, 1987). The interaction between *Ficus* and frugivores is one example of this mutualistic relationship, where fig trees provide a sugar-rich food supply for frugivores and fig trees gain benefit by having more chance to colonizing new areas after the seed dispersal services by animals (Lambert, 1991). Each frugivore group has distinct patterns and behavior when handling fruits because of their different morphological characters (Wheelwright, 1985; Levey, 1987; Ally, 2010). For instance, some birds have larger gape widths than the fruits they eat and always swallow whole fruits when feeding on them (Wheelwright, 1985). In contrast, some mammals, such as rodents or ungulates, always masticate fruit before swallowing them (Janzen, 1971; Bodmer, 1991). These different feeding behaviours affect seed treatments and seed swallowers are more likely to disperse viable seeds than the biters, which are likely to destroy some ingested seeds when chewing on them (Compton et al., 1996). Consequently, not all animals that feed on fleshy fruits contribute dispersal services. The duration of feeding on trees is another factor affecting seed dispersal. For example, bulbuls typically spend approximately three minutes feeding on fruiting trees, which is shorter than their gut passage time and means that they defecate seeds in other areas and not under parent trees (Graham et al., 1995). In contrast, some pigeons stay on fruiting trees to feed for hours and seeds may be deposited under the parent trees (Pratt & Stiles, 1983; Shanahan, 2001).

Some fig trees are restricted to or more abundant in riparian areas close to water bodies (Chantarasuwan et al., 2007; Pothasin et al., 2014). Seeds of some of those riparian fig trees can potentially be dispersed by water as the ripe figs can fall down directly into the water if the branches grow vertically by the water or roll into the water if they fall nearby. Once in the water, seeds can be dispersed by the water itself or by aquatic animals such as fishes (Banack et al., 2002; Pothasin et al., 2016). Ripe figs have a cavity inside them and most float on the water. This allows them to be moved by flowing water currents, and this can promote long distance seed dispersal of riparian fig trees (Compton S. G., pers. comm.). Some riparian fig tree species rely mainly or entirely on water for dispersal (Pothasin et al., 2016) but most will also interact with terrestrial frugivores, and they can gain advantage by having two modes of dispersal. However, it is still not known whether the majority of riparian fig trees depend more on dispersal by water or animals.

Some fig species may interact with more than a hundred species of frugivores, especially the large synchronized crops of strangler figs (Subgenus *Urostigma*) and studies of fig-frugivore interactions have mostly focused on this subgenus. Examples are provided by *Ficus microcarpa* and *F. benjamina*, which interact with at least 240 and 158 frugivore species respectively (CHAPTER 7). By producing huge crops all year round including periods when fruits of other species are scarce, strangler figs can be described by the term “Keystone species” in that they maintain frugivore populations in the communities where the fig trees are present (Lambert & Marshall, 1991; Shanahan et al., 2001). However, in Afrotropical Madagascar, where fig trees are less abundant, figs are not considered as a keystone group, unlike in other tropical habitats worldwide (Goodman & Ganzhorn, 1997). Fig trees that do not grow as stranglers, for example those in subgenera *Ficus*, *Sycidium* and *Sycomorus,* and especially the many small shrubby species, are less likely to be keystone resources, but far fewer species have been studied. Peh & Chong (2003) reported seven and 15 frugivore species feeding on *F. fistulosa* (Subgenus *Sycomorus*) and *F. grossularioides* (Subgenus *Ficus)* respectively in disturbed tropical forest of Singapore during 36 hours of observation. This contrasts with the *Urostigma* fig tree *F. caulocarpa*, which interacted with at least 28 frugivore species in a dipterocarp forest of Malaysia within 32 hours of observation (Sreekar et al., 2010).

In this study of four riparian fig trees species in western Thailand, we examined (i) How many of their figs are likely to fall down into the water if they are not dispersed by animals (ii) which frugivores interact with these four fig tree species, (iii) what is their feeding behaviors and (iv) what proportion of the figs do they remove?

3.3 Methods

3.3.1 Study sites and species

The details of study sites and plant species are provided in CHAPTER 2.

3.3.2 Sampling details

Characteristics of trees belonging to the four selected fig trees (female trees of *F. montana*, *F. ischnopoda*, *F. oligodon* and monoecious *F. racemosa*), including crop sizes, fig fall destination (above water or the ground) and crown width were recorded. These fig trees species are distributed specifically along riparian areas, especially, *F. ischnopoda* and *F. racemosa* (Pothasin et al., 2014). All the crops were located on trees growing close to streams (within 1 m), and their figs were in late mature (C phase) to ripening stages (E phase) only. The small crops of *F. montana*, *F. ischnopoda* and *F. oligodon* allowed fig numbers to be counted directly, but the large crops of *F. racemosa* were estimated by counting the overall branches and trunks with figs, selecting four branches with typical fig numbers for counting directly, and multiplying fig numbers by branch numbers. Fig fall destinations were categorized as either above water or ground. Figs were counted directly on the branches locating above the ground or water in *F. montana*, *F. ischnopoda* and *F. oligodon*. For *F. racemosa*, the criteria for estimating fig number were similar to crop size, but all branches with figs were noted as either “above ground” or “above water”. The longest radius of crown width of *F. montana* and *F. ischnopoda* were measured directly by measuring tape, but in *F. oligodon* and *F. racemosa,* the longest radius of crown width was calculated by marking two opposite points with an observer standing under the edge of the canopy and measuring the straight line distance between.

Between February and October 2016, frugivore assemblages were monitored by camera traps located near to female *Ficus montana* (27 crops, for a total 6482 hours, Mean ± SE = 240.07 ± 23.47 hours/crop, range = 48 – 576 hours), *F. ischnopoda* (13 crops, for a total 2376 hours, Mean ± SE = 182.77 ± 30.45 hours/crop, range = 24 – 336 hours) and *F. oligodon* (20 crops, for a total 5112 hours, Mean ± SE = 255.60 ± 16.90 hours/crop, range = 96 – 336 hours) (Tables 3.1 - 3.3). The camera traps (Bushnell Trophy Cam HD^{TM}) were set to record frugivore visits at figs plants for 24 hours applying the 60 second video recording mode with fastest speed shutter set up available, 0.3 ms. All camera traps were set within 2-4 meters from the crops as these distances allowed the automatic trigger to work consistently, even with small objects 5 cm long. Only one camera trap was set against each observed fig trees for all three species. These fig trees produced small fig crops which allowed all the figs to be visible in the recording frame of the camera trap. Although some *F. oligodon* crops had larger crops a single camera trap could record visits to all the figs. The benefits of using camera traps for observing frugivores are that they generate fewer disturbance events to animals provide continuous frugivore recording, and all captured photos or videos can be rechecked for validity. Video clips of frugivores passing camera traps were captured every 60 seconds from the first visits. The camera traps also recorded video clips and provided time stamps of visits by each frugivore. If frugivores visited crops for longer 60 seconds, the next video clip was recorded immediately. Video clips of the same frugivore species that occurred within five minutes after the first recorded clip were considered as part of the same feeding bout. These video clips provided records of the time spent feeding on fig crops of frugivores to the nearest 1-5 seconds and their feeding behaviours (swallowers, mashers or biters). Also, the number of figs removed per visit and the number of individual of frugivores that visited a crop at one time were recorded. All camera traps were checked every two or three days for downloading of video clips. Camera traps were removed from a tree after all the ripe female figs had disappeared from trees.

F. racemosa trees were too large to make use of the camera trap technique, and most figs were produced on the branches located higher than 5 meters from the ground. For *F. racemosa* and some crops of the other species, frugivore visits to the trees were recorded by direct observations: *F. montana* (3 crops, 18 hours), *F. ischnopoda* (2 crops, 12 hours), *F. oligodon* (5 crops, 30 hours) and *F. racemosa* (6 crops, 36 hours) (Tables 3.1 - 3.3). These trees were observed using 8x40 binoculars (Olympus^{TM} 8X40 DPS-I). To avoid interference with the frugivores, the observer was in a shelter (bird hide) situated approximately 10-15 m from each tree. The observations were separated into morning and afternoon censuses. The morning censuses started at 07:00 and ran to 10:00 in the morning as frugivorous animals are active in this period. The afternoon censuses began at 14:00 and continued to 17:00. Frugivore feeding behaviour, numbers of figs removed, time spent on the trees, numbers of individuals visiting at one time were recorded with the time spent on the trees recorded to the nearest 1-5 seconds. Frugivore species, numbers of fruit removed and numbers of frugivore visits were noted. Frugivorous mammals were identified following “A Field Guide to the Mammals of South-East Asia” (Francis, 2008), and bird identification was based on “Birds of Thailand” (Nabhitabhata et al., 2008). The species richness of frugivores found on each *Ficus* species were plotted against time. If the species richness reached a plateau, it was assumed that sampling effort was good enough with most of the local frugivore community that visited the trees observed.

Table 3.1. Sampled crops and geographical locations of *Ficus montana* at Kratengjeng waterfall.

Crop	Crown width (m.)	Crop size	Method	Sampling date	Sampling Duration (Hrs)	Geographical Locations	
						East	North
1	0.3	4	Direct observation	9th Feb 16	6	98° 36’ 30.10”	15° 01’ 59.83”
2	0.6	2	Direct observation	10th Feb 16	6	98° 36’ 22.18”	15° 01’ 48.26”
3	1.0	1	Direct observation	10th Feb 16	6	98° 36’ 32.13”	15° 02’ 00.81”
4	0.8	1	Camera traps	10th -13rd Feb 16	72	98° 36’ 27.55”	15° 01’ 55.92”
5	1.0	1	Camera traps	10th -13rd Feb 16	72	98° 36’ 32.20”	15° 02’ 00.87”
6	1.2	1	Camera traps	10th -17th Feb 16	170	98° 36’ 32.03”	15° 02’ 00.65”
7	1.3	5	Camera traps	13rd - 29th Mar 16	384	98° 36’ 25.68”	15° 01’ 55.13”
8	0.8	8	Camera traps	14th - 29th Mar 16	360	98° 36’ 31.77”	15° 02’ 00.81”
9	1.5	3	Camera traps	15th - 29th Mar 16	336	98° 36’ 33.00”	15° 02’ 01.49”
10	2.1	4	Camera traps	4th - 13th Apr 16	240	98° 36’ 08.66”	15° 01’ 40.62”
11	1.5	4	Camera traps	4th - 13th Apr 16	240	98° 36’ 32.36”	15° 02’ 01.95”
12	1.2	7	Camera traps	22th Apr - 2th May 16	240	98° 36’ 32.20”	15° 02’ 00.84”
13	3.6	21	Camera traps	30th Apr - 24th May 16	576	98° 36’ 29.99”	15° 02’ 00.31”
14	1.5	4	Camera traps	10th -13nd May 16	72	98° 36’ 22.54”	15° 01’ 52.03”
15	3.2	2	Camera traps	10th -13rd May 16	72	98° 36’ 22.20”	15° 01’ 52.23”
16	1.3	9	Camera traps	11st -20th May 16	240	98° 36’ 32.80”	15° 02’ 02.86”
17	1.7	3	Camera traps	12nd -21th May 16	240	98° 36’ 42.07”	15° 02’ 06.49”
18	2.2	17	Camera traps	30th May - 4th Jun 16	144	98° 36’ 33.00”	15° 02’ 01.49”
19	1.0	2	Camera traps	3rd - 4th Jun 16	48	98° 36’ 32.20”	15° 02’ 00.87”
20	0.3	4	Camera traps	3rd - 5th Jun 16	72	98° 36’ 30.10”	15° 01’ 59.83”
21	3.6	11	Camera traps	11st -25th Aug 16	312	98° 36’ 29.99”	15° 02’ 00.31”
22	1.5	7	Camera traps	11st -25th Aug 16	312	98° 36’ 34.21”	15° 02’ 01.72”
23	1.1	9	Camera traps	11st -25th Aug 16	312	98° 36’ 48.13”	15° 02’ 09.07”
24	1.5	5	Camera traps	13rd -25th Aug 16	288	98° 36’ 33.00”	15° 02’ 01.49”
25	2.1	5	Camera traps	9th -22nd Sep 16	336	98° 36’ 08.66”	15° 01’ 40.62”
26	1.5	4	Camera traps	9th -22nd Sep 16	336	98° 36’ 32.36”	15° 02’ 01.95”
27	1.8	3	Camera traps	10th - 20nd Sep 16	264	98° 36’ 41.73”	15° 02’ 06.10”
28	0.9	5	Camera traps	10th - 20nd Sep 16	264	98° 36’ 42.07”	15° 02’ 06.49”
29	1.2	6	Camera traps	11st - 20nd Oct 16	240	98° 36’ 32.03”	15° 02’ 00.65”
30	1.6	3	Camera traps	11st - 20nd Oct 16	240	98° 36’ 42.34”	15° 02’ 06.91”
				Total	**6500**		

Table 3.2. Sampled crops and geographical locations of *Ficus ischnopoda* at Phatad and Erawan waterfalls.

Crop	Crown width (m.)	Crop size	Method	Sampling date	Sampling Duration (Hrs)	Geographical Locations	
						East	North
1	0.8	3	Camera traps	13rd – 17th Feb 16	120	98° 46’ 32.37”	14° 39’ 06.73”
2	1.6	1	Camera traps	28th – 29th Feb 16	24	99° 08’ 32.68”	14° 21’ 34.80”
3	2.0	1	Camera traps	28th Feb – 1st Mar 16	72	99° 08’ 37.30”	14° 22’ 03.31”
4	2.6	7	Camera traps	28th Feb – 12nd Mar 16	336	98° 46’ 24.75”	14° 38’ 56.31”
5	1.8	2	Camera traps	28th Feb – 10th Mar 16	288	99° 08’ 37.11”	14° 22’ 03.92”
6	1.4	1	Direct observation	9th Mar 16	6	99° 08’ 49.10”	14° 22’ 14.17”
7	1.1	7	Camera traps	10th – 19th Mar 16	240	99° 08’ 48.64”	14° 22’ 20.94”
8	2.6	3	Direct observation	6th Apr 16	6	99° 08’ 47.83”	14° 22’ 14.86”
9	1.5	9	Camera traps	6th - 9th Apr 16	96	99° 08’ 47.70”	14° 22’ 13.95”
10	0.9	17	Camera traps	2th - 15th Apr 16	336	99° 08’ 49.37”	14° 22’ 15.67”
11	1.5	14	Camera traps	6th - 15th Apr 16	240	99° 08’ 41.95”	14° 22’ 05.71”
12	1.5	7	Camera traps	26th - 28th May 16	72	98° 46’ 31.70”	14° 39’ 07.41”
13	2.2	13	Camera traps	26th - 28th May 16	72	98° 46’ 31.93”	14° 39’ 07.35”
14	1.7	8	Camera traps	13rd -23rd Jun 16	240	98° 46’ 31.86”	14° 39’ 07.68”
15	1.2	8	Camera traps	13rd -23rd Jun 16	240	98° 46’ 31.57”	14° 39’ 07.51”
				Total	**2388**		

Table 3.3. Sampled crops and geographical locations of *Ficus oligodon* at Kratengjeng and Phatad waterfalls.

Crop	Crown width (m.)	Crop size	Method	Sampling date	Sampling Duration (Hrs)	Geographical Locations	
						East	North
1	8.0	5	Direct observation	26th Mar 16	6	98° 35’ 56.73”	15° 01’ 28.10”
2	7.5	29	Direct observation	26th Mar 16	6	98° 35’ 56.86”	15° 01’ 28.23”
3	6.0	11	Camera traps	11st – 16th Apr 16	144	98° 36’ 30.46”	15° 01’ 59.05”
4	7.0	6	Camera traps	11st – 16th Apr 16	144	98° 36’ 43.27”	15° 02’ 07.99”
5	6.0	21	Camera traps	12nd – 23rd May 16	288	98° 36’ 29.86”	15° 02’ 00.12”
6	5.0	13	Camera traps	12nd – 23rd May 16	288	98° 36’ 30.52”	15° 02’ 02.01”
7	7.5	9	Camera traps	24th – 27th May 16	96	98° 35’ 58.23”	15° 01’ 28.82”
8	6.0	10	Camera traps	24th – 27th May 16	96	98° 36’ 29.92”	15° 02’ 00.87”
9	5.5	5	Camera traps	3th – 14th Jun 16	288	98° 36’ 31.13”	15° 02’ 00.64”
10	7.0	59	Camera traps	28th May – 10th Jun 16	312	98° 46’ 29.93”	14° 37’ 25.31”
11	6.0	79	Camera traps	14th Jun – 10th Jul 16	336	98° 36’ 12.23”	15° 01’ 45.96”
12	6.0	25	Camera traps	14th Jun – 10th Jul 16	336	98° 36’ 41.46”	15° 02’ 07.27”
13	5.3	12	Direct observation	13th Jul 16	6	98° 36’ 31.39”	15° 02’ 00.38”
14	4.5	21	Direct observation	14th Jul 16	6	98° 36’ 08.96”	15° 01’ 39.64”
15	6.5	4	Direct observation	15th Jul 16	6	98° 46’ 30.36”	14° 39’ 03.12”
16	5.5	41	Camera traps	12nd – 23rd Aug 16	288	98° 35’ 56.73”	15° 01’ 28.10”
17	7.5	49	Camera traps	12nd – 23rd Aug 16	288	98° 35’ 56.86”	15° 01’ 28.23”
18	6.0	24	Camera traps	12nd – 23rd Aug 16	288	98° 36’ 12.23”	15° 01’ 45.96”
19	6.0	32	Camera traps	9th – 18th Sep 16	240	98° 36’ 29.86”	15° 02’ 00.12”
20	5.0	19	Camera traps	9th – 18th Sep 16	240	98° 36’ 30.52”	15° 02’ 02.01”
21	7.0	46	Camera traps	9th – 18th Sep 16	240	98° 36’ 43.27”	15° 02’ 07.99”
22	5.5	11	Camera traps	12nd – 24th Oct 16	312	98° 36’ 31.13”	15° 02’ 00.64”
23	6.0	24	Camera traps	12nd – 24th Oct 16	312	98° 36’ 29.92”	15° 02’ 00.87”
24	6.0	19	Camera traps	12nd – 24th Oct 16	312	98° 36’ 30.46”	15° 01’ 59.05”
25	6.5	31	Camera traps	14nd – 24th Oct 16	264	98° 46’ 30.36”	14° 39’ 03.12”
				Total	**5142**		

Table 3.4. Sampled crops and geographical locations of *Ficus racemosa* at Erawan waterfall and Pratart cave.

Crop	Crown width (m.)	Crop size	Method	Sampling date	Sampling Duration (Hrs)	Geographical Locations	
						East	North
1	11	2000	Direct observation	17th Jun 16	6	99° 04’ 58.31”	14° 23’ 58.93”
2	14	2000	Direct observation	18th Jun 16	6	99° 04’ 56.30”	14° 23’ 52.19”
3	10	5000	Direct observation	19th Jun 16	6	99° 04’ 58.21”	14° 23’ 50.79”
4	9	3000	Direct observation	20th Jun 16	6	99° 04’ 56.87”	14° 23’ 52.52”
5	12	3000	Direct observation	8th Jul 16	6	98° 46’ 21.88”	14° 38’ 53.41”
6	10	1000	Direct observation	9th Jul 16	6	98° 46’ 28.26”	14° 38’ 59.21”
				Total	**36**		

3.3.3 Data analysis

In *F. montana* and *F. ischnopoda* the data obtaining from direct observations were pooled with the camera trap data before analysis, as almost all the figs present were removed or fallen. However, in *F. oligodon*, only two visits were recorded by direct observation (2 feeding records on 2 figs by 2 frugivore species).

Differences between crop sizes and crown widths of each species was compared by generalized linear models (GLM) applying a Poisson and Gaussian distribution with square root transformation, respectively. The proportion of fig fall destinations of the four fig trees was examined using generalized linear models (GLM) applying a Quasi-binomial distribution. The relationship of crown width and how many figs were likely to fall to the ground, and crown width and crop sizes, were tested by non-parametric Spearman rank correlation as the data did not meet the requirements of parametric test.

The frequency of crops visited by frugivores, were compared among fig trees species using Chi-square. Fig removal rates (number of figs removed per hour) were calculated by the number of removed figs divided by total hours of observation and compared using generalized linear models (GLM) with Gamma distributions as the variances increased with the mean. The total number of bird and mammal visitors, were compared using Chi-square tests. Fig removal numbers and time spent in the trees was analysed using generalized linear models (GLM) with a Quasi-Poisson and Gaussian distribution, respectively. Time spent by each frugivore species was examined by generalized linear models (GLM) with Gamma distributions when data showed variance increase with the mean. The pairwise comparisons were done in the package lsmeans using the lsmeans() function. All statistical tests were performed in R 3.4.3. Means ± S.E.s are reported.

3.4 Results

3.4.1 Crop characteristics

F. racemosa was the largest of the four fig tree species, and had the widest crowns (mean ± S.E. = 11.00 ± 0.73 m, range = 9-14 m, N = 6 trees). *F. oligodon* (6.17 ± 0.18 m, range = 4.5-8 m, N = 25 trees), *F. ischnopoda* (1.62 ± 0.14 m, range = 0.8-2.6 m, N = 15 trees) and *F. montana* (1.50 ± 0.15 m, range = 0.3-3.6 m, N = 30 trees) were much smaller species. Crown widths varied significantly among the four *Ficus* species but not between *F. montana* and *F. ischnopoda* (GLM: *F. montana* v. *F. ischnopoda*, Z = 0.900, P = 0.8050; *F. montana* v. *F. oligodon*, Z = -18.484, P < 0.0001; *F montana* v. *F. racemosa*, Z = -18.358, P < 0.0001; *F. ischnopoda*v. *F. oligodon*, Z = -14.455, P < 0.0001; *F. ischnopoda* v. *F. racemosa,* Z = -16.407, P < 0.0001; *F. oligodon* v. *F. racemosa*, Z = -7.099, P < 0.0001).

The three smaller fig tree species had very few figs present at any one time. Overall, at the beginning of observation periods, the average crop size of *Ficus montana* was 5.17 ± 0.74 (mean ± S.E.), range = 1-21, N = 30 trees and was similar to that of *F. ischnopoda* (6.12 ± 1.07, range = 1-14, N = 15 trees). *F. oligodon* produced slightly larger fig crops (24.20 ± 3.73, range = 4-79, N = 25 trees), whereas *F. racemosa* had far larger crops (2666.67 ± 557.79, range = 1000-5000, N = 6). The crop sizes were significantly different among the four fig trees (GLM: *F.*

montana v. *F. ischnopoda*, Z = 0.489, P = 0.9617; *F. montana* v. *F. oligodon*, Z = -4.900, P < 0.0001; *F montana* v. *F. racemosa*, Z = -22.982, P < 0.0001; *F. ischnopoda*v. *F. oligodon*, Z = -3.477, P < 0.001; *F. ischnopoda* v. *F. racemosa,* Z = -17.241, P < 0.0001; *F. oligodon* v. *F. racemosa*, Z = -21.800, P < 0.0001).

The fig trees were growing in or very near to the rivers. The comparisons of the locations of *F. montana* and *F. ischnopoda* figs, relative to the water, showed that more than half of any ripe figs, if they fell vertically, would be likely to fall into the water rather than on the ground. The percentage of figs that were likely to fall to the ground was higher in the larger fig trees, *F. oligodon* and *F. racemosa* (Fig. 3.1). Reflecting this, the proportion of figs likely to fall into the water varied significantly with the crown width when all four fig tree species were combined (GLM: $F_{(3,72)}$ = 9.04, df = 1, P < 0.001; Fig 3.2).

A positive relationship between crop size and crown width was detected (all four species combined), Spearman rank correlation: crop size and crown width r_s = 0.684, P < 0.0001, N = 76. (Fig. 3.3). Within species, a positive relationship between crop size and crown width was only significant in *F. montana* (r_s = 0.531, P = 0.003, N = 30), but not in the other three fig tree species (*F. ischnopoda*: r_s = -0.198, P = 0.479, N = 15, *F. oligodon*: r_s = 0.059, P = 0.780, N = 25, *F. racemosa*: r_s = -0.239, P = 0.649, N = 6, Figs. 3.3 – 3.4). This may have reflected less variation in crown width of these three species.

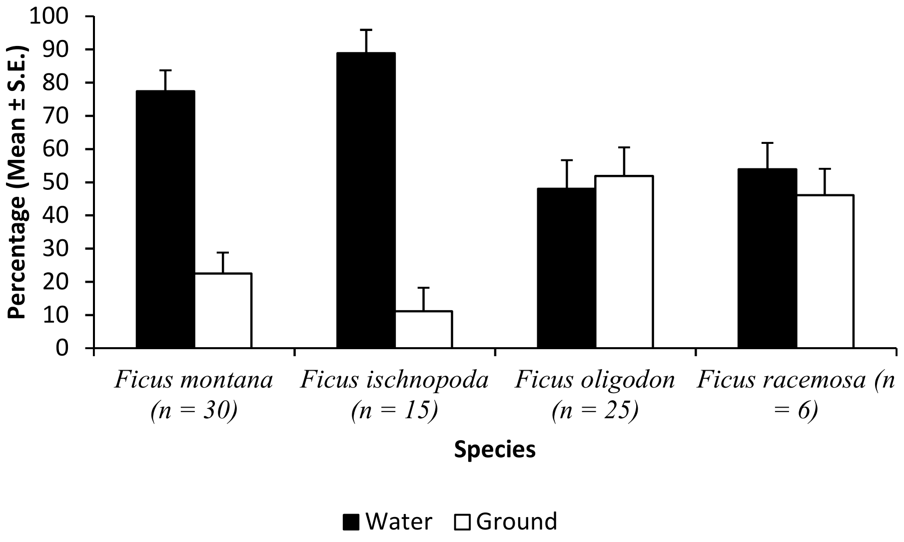

Fig. 3.1. Potential fig fall destinations of four different riparian *Ficus* species.

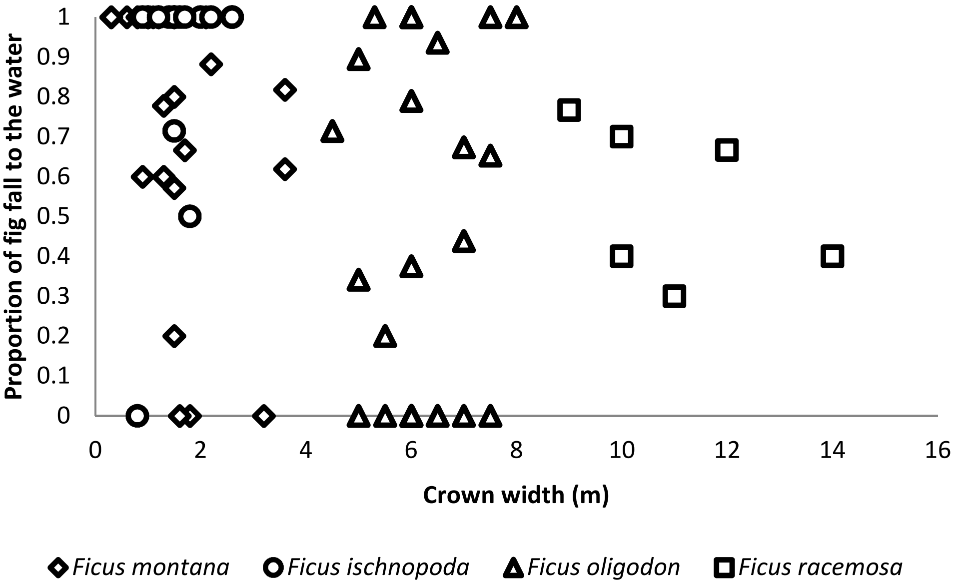

Fig. 3.2. The relationship between crown width and the proportion of figs that would have landed on the water if they fell vertically from four riparian *Ficus* species.

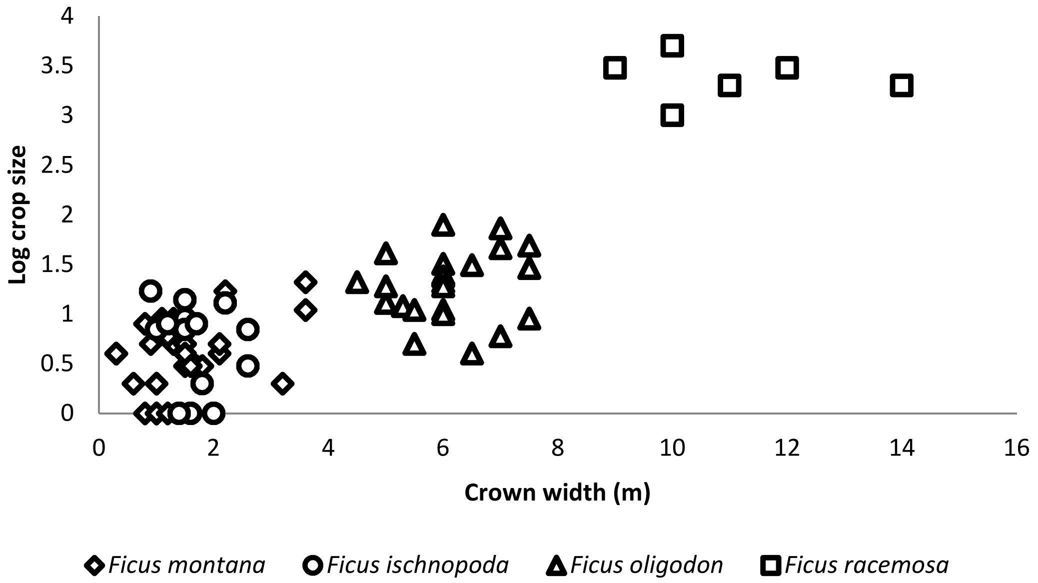

Fig. 3.3. The relationship between crown width and log crop sizes of four riparian *Ficus* species.

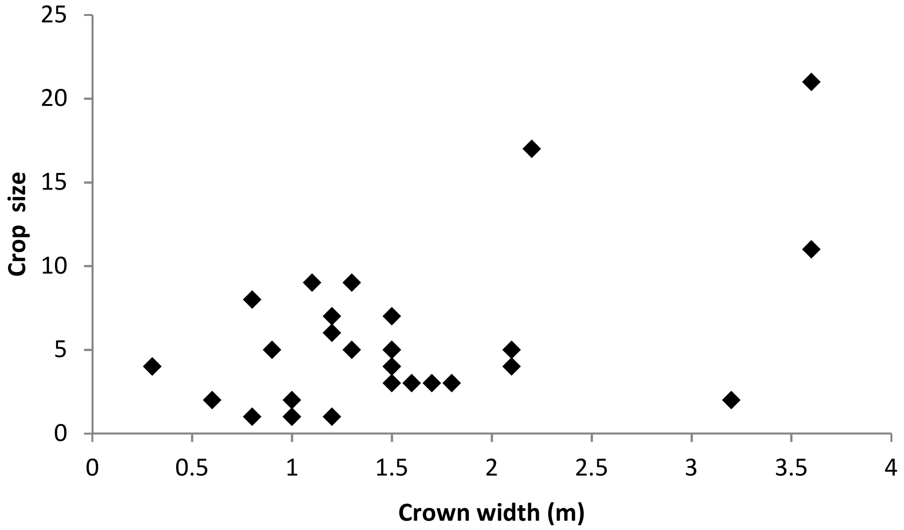

Fig. 3.4. The relationship between crown width and crop sizes of *F. montana.*

3.4.2 Frugivore assemblages

Figs that were not removed by frugivores could either fall down into the water, fall to the ground or rot in situ on the trees. Less than half of the *F. montana*, *F. ischnopoda* and *F. oligodon* trees were visited by any frugivores during the periods of observation or recording (Fig. 3.5, Tables 3.5 – 3.8). This is in contrast to *F. racemosa*, where all six crops were seen to be visited by frugivores (Fig 3.5).

When the observation periods of *F. montana* and *F. ischnopoda* crops were ended, the figs that had not been eaten by frugivores had mostly fallen into the water or ground below (Tables 3.5 – 3.6). However, there were four crops of *F. oligodon*, where figs still remained on the trees at the end of the observations, because these crops were directly observed for only relatively short periods (6 hours). Other crops of *F. oligodon* that were observed using camera traps for longer periods had no remaining figs and some crops had all their figs fall to the ground or water, without any being eaten by frugivores (Table 3.7).

Among *F. montana*, *F. ischnopoda* and *F. oligodon*, the frequency of crops seen to be visited by frugivores was not statistically different (Chi-square: $\chi^2 = 1.79$, df = 2, P = 0.41), though it should be noted that sampling effort was not uniform (see Methods). There was also no clear relationship between crop sizes and observed presence or absence of any frugivores during observation periods in *F. montana, F. ischnopoda* and *F. oligodon* (Figs. 3.6-3.8).

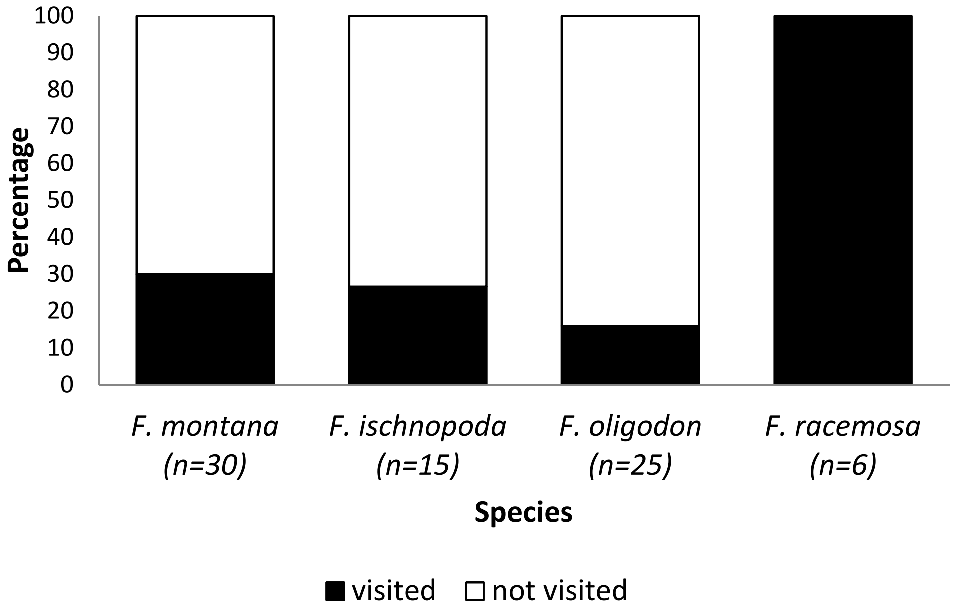

Fig. 3.5. The percentage of crops of four riparian *Ficus* species where any figs were observed to be consumed by frugivores.

Table 3.5. Observed crops of *F. montana*. Crops visited by frugivores are indicated in bold.

Crop	Method	Sampling Duration (Hrs)	Crown width (m)	Crop size (figs)	Frugivores visited? (Y/N)	Figs eaten	Fallen figs (water)	Fallen figs (ground)	Fig removal (%)	Figs eaten (Hrs^{-1})
1	**Direct observation**	**6**	**0.3**	**4**	**Y**	**4**	**0**	**0**	**100.0**	**0.667**
2	**Direct observation**	**6**	**0.6**	**2**	**Y**	**2**	**0**	**0**	**100.0**	**0.333**
3	Direct observation	6	1.0	1	N	-	1	0	-	-
4	Camera traps	72	0.8	1	N	-	1	0	-	-
5	Camera traps	72	1.0	1	N	-	1	0	-	-
6	**Camera traps**	**170**	**1.2**	**1**	**Y**	**1**	**0**	**0**	**100.0**	**0.006**
7	Camera traps	384	1.3	5	N	-	3	2	-	-
8	Camera traps	360	0.8	8	N	-	8	0	-	-
9	Camera traps	336	1.5	3	N	-	3	0	-	-
10	Camera traps	240	2.1	4	N	-	4	0	-	-
11	Camera traps	240	1.5	4	N	-	4	0	-	-
12	**Camera traps**	**240**	**1.2**	**7**	**Y**	**5**	**2**	**0**	**71.4**	**0.021**
13	**Camera traps**	**576**	**3.6**	**21**	**Y**	**16**	**0**	**5**	**76.2**	**0.028**
14	**Camera traps**	**72**	**1.5**	**4**	**Y**	**4**	**0**	**0**	**100.0**	**0.056**
15	**Camera traps**	**72**	**3.2**	**2**	**Y**	**2**	**0**	**0**	**100.0**	**0.028**
16	Camera traps	240	1.3	9	N	-	4	5	-	-
17	Camera traps	240	1.7	3	N	-	2	1	-	-
18	**Camera traps**	**144**	**2.2**	**17**	**Y**	**4**	**5**	**0**	**23.5**	**0.028**
19	Camera traps	48	1.0	2	N	-	2	0	-	-
20	Camera traps	72	0.3	4	N	-	4	0	-	-
21	Camera traps	312	3.6	11	N	-	7	4	-	-
22	Camera traps	312	1.5	7	N	-	4	3	-	-
23	Camera traps	312	1.1	9	N	-	9	0	-	-
24	Camera traps	288	1.5	5	N	-	4	1	-	-
25	Camera traps	336	2.1	5	N	-	5	0	-	-
26	Camera traps	336	1.5	4	N	-	4	0	-	-
27	Camera traps	264	1.8	3	N	-	0	3	-	-
28	Camera traps	264	0.9	5	N	-	3	2	-	-
29	Camera traps	240	1.2	6	N	-	6	0	-	-
30	Camera traps	240	1.6	3	N	-	0	3	-	-

Table 3.6. Observed crops of *F. ischnopoda.* Crops visited by frugivores are indicated in bold.

Crop	Method	Sampling Duration (Hrs)	Crown width (m)	Crop size (figs)	Frugivores visited? (Y/N)	Figs eaten	Fallen figs (water)	Fallen figs (ground)	Fig removal (%)	Figs eaten (Hrs^{-1})
1	Camera traps	120	0.8	3	N	-	0	3	-	-
2	**Camera traps**	**24**	**1.6**	**1**	**Y**	**1**	**0**	**0**	**100.0**	**0.042**
3	Camera traps	72	2.0	1	N	-	1	0	-	-
4	Camera traps	336	2.6	7	N	-	7	0	-	-
5	Camera traps	288	1.8	2	N	-	1	1	-	-
6	**Direct observation**	**6**	**1.4**	**1**	**Y**	**1**	**0**	**0**	**100.0**	**0.167**
7	Camera traps	240	1.0	7	N	-	7	0	-	-
8	**Direct observation**	**6**	**2.6**	**3**	**Y**	**3**	**0**	**0**	**100.0**	**0.500**
9	Camera traps	96	1.5	9	N	-	9	0	-	-
10	**Camera traps**	**336**	**0.9**	**17**	**Y**	**11**	**2**	**0**	**64.7**	**0.033**
11	Camera traps	240	1.5	14	N	-	10	4	-	-
12	Camera traps	72	1.5	7	N	-	7	0	-	-
13	Camera traps	72	2.2	13	N	-	13	0	-	-
14	Camera traps	240	1.7	8	N	-	8	0	-	-
15	Camera traps	240	1.2	8	N	-	8	0	-	-

Table 3.7. Observed crops of *F. oligodon.* Crops visited by frugivores are indicated in bold.

Crop	Method	Sampling Duration (Hrs)	Crown width (m)	Crop size (figs)	Frugivores visited? (Y/N)	Figs eaten	Fallen figs (water)	Fallen figs (ground)	Fig removal (%)	Figs eaten (Hrs^{-1})
1	**Direct observation**	**6**	**8.0**	**5**	**Y**	**1**	**N/A**	**N/A**	**20.0**	**0.167**
2	Direct observation	6	7.5	29	N	-	N/A	N/A	-	-
3	Camera traps	144	6.0	11	N	-	0	11	-	-
4	Camera traps	144	7.0	6	N	-	0	6	-	-
5	Camera traps	288	6.0	21	N	-	0	21	-	-
6	Camera traps	288	5.0	13	N	-	0	13	-	-
7	Camera traps	96	7.5	9	N	-	0	9	-	-
8	Camera traps	96	6.0	10	N	-	0	10	-	-
9	**Camera traps**	**288**	**5.5**	**5**	**Y**	**1**	**0**	**4**	**20.0**	**0.003**
10	**Camera traps**	**312**	**7.0**	**73**	**Y**	**32**	**0**	**41**	**43.8**	**0.103**
11	Camera traps	336	6.0	79	N	-	79	0	-	-
12	Camera traps	336	6.0	25	N	-	0	25	-	-
13	**Direct observation**	**6**	**5.3**	**12**	**Y**	**1**	**N/A**	**N/A**	**8.3**	**0.167**
14	Direct observation	6	4.5	21	N	-	N/A	N/A	-	-
15	Direct observation	6	6.5	4	N	-	N/A	N/A	-	-
16	Camera traps	288	5.0	41	N	-	14	27	-	-
17	Camera traps	288	7.5	49	N	-	32	17	-	-
18	Camera traps	288	6.0	24	N	-	24	0	-	-
19	Camera traps	240	6.0	32	N	-	32	0	-	-
20	Camera traps	240	5.0	19	N	-	17	2	-	-
21	Camera traps	240	7.0	46	N	-	31	15	-	-
22	Camera traps	312	5.5	11	N	-	0	11	-	-
23	Camera traps	312	6.0	24	N	-	9	15	-	-
24	Camera traps	312	6.0	19	N	-	15	4	-	-
25	Camera traps	264	6.5	31	N	-	29	2	-	-

Table 3.8. Observed crops of *F. racemosa.* Crops visited by frugivores are indicated in bold.

Crop	Method	Sampling Duration (Hrs)	Crown width (m)	Crop size (figs)	Frugivores visited? (Y/N)	Figs eaten	Figs eaten (Hrs^{-1})
1	**Direct observation**	**6**	**11.0**	**2000**	**Y**	**28**	**4.667**
2	**Direct observation**	**6**	**14.0**	**2000**	**Y**	**49**	**8.167**
3	**Direct observation**	**6**	**10.0**	**5000**	**Y**	**11**	**1.833**
4	**Direct observation**	**6**	**9.0**	**3000**	**Y**	**37**	**6.167**
5	**Direct observation**	**6**	**12.0**	**3000**	**Y**	**7**	**1.167**
6	**Direct observation**	**6**	**10.0**	**1000**	**Y**	**13**	**2.167**

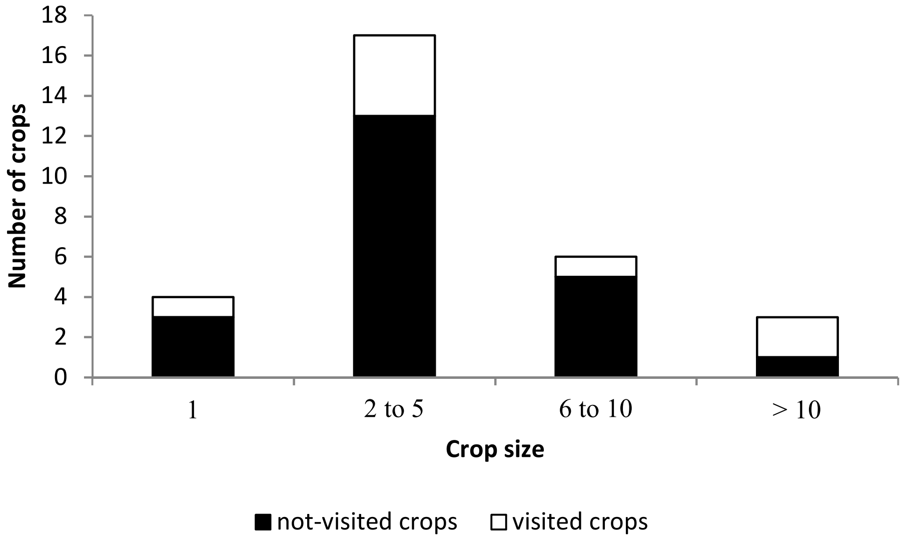

Fig. 3.6. The number of *F. montana* crops visited by frugivores in relation to crop size.

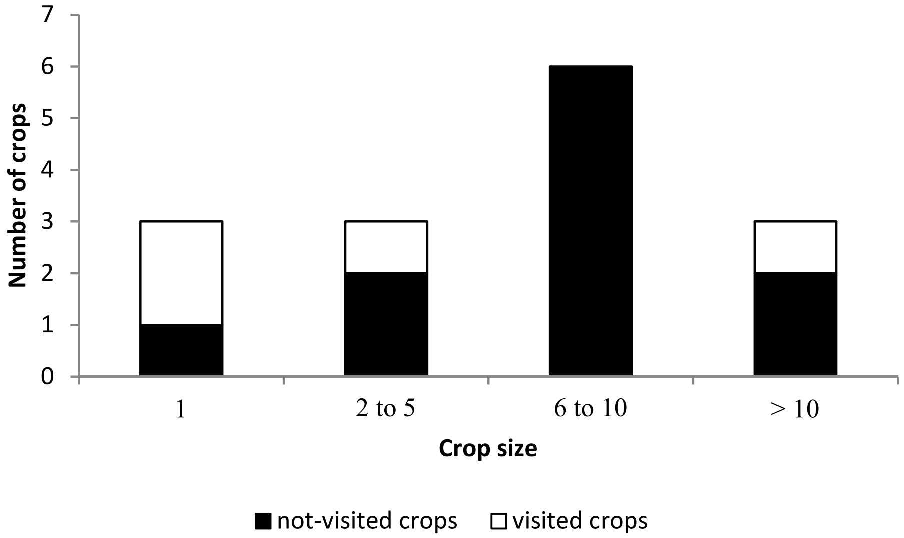

Fig. 3.7. The number of *F. ischnopoda* crops visited by frugivores in relation to crop size.

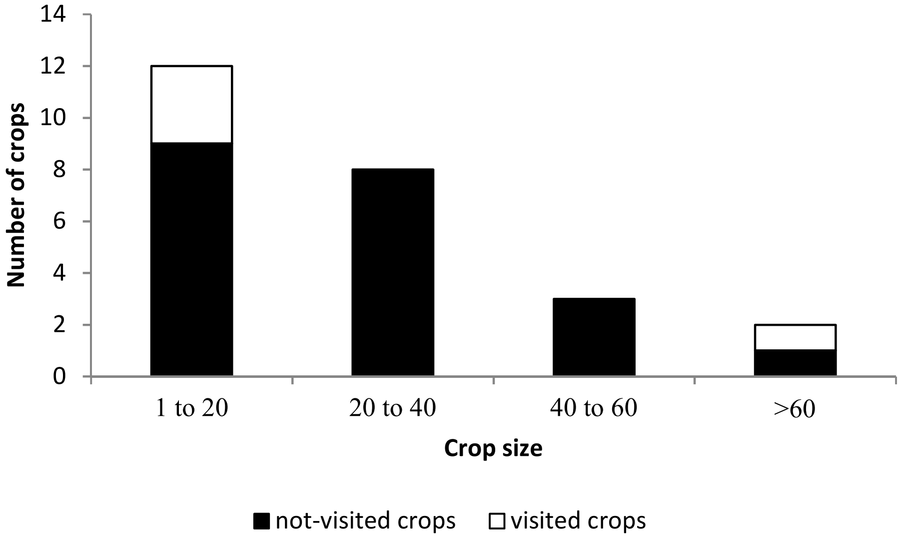

Fig. 3.8. The number of *F. oligodon* crops visited by frugivores in relation to crop size.

In *F. ischnopoda* and *F. oligodon*, the relationship between crop sizes and fig removal among trees visited by frugivores could not be examined due to low sample sizes. Within those crops of *F. montana* where some removal of figs by frugivores was observed, there was a negative relationship between crop size and percentage of figs removed, because the larger crops had retained more figs on the trees after visits by frugivores, which tended to eat a small number of figs and then depart (Spearman rank correlation: $r_s = -0.868$, $P = 0.005$, $N = 8$, Fig 3.9). The higher proportional removal rate from small crops was because in this species the crops of ripe figs were often so small that a visit by a single frugivore was all that was needed for all the available figs to be removed.

When only crops where frugivore visits were observed are compared, more than 75% of the figs present were removed from most crops of *F. montana* and *F. ischnopoda* (Figs. 3.10-3.11). In contrast, less than 25% of the figs were removed by frugivores from most crops of *F. oligodon*, a larger fig tree producing larger crops (Fig. 3.12). Equivalent estimates are not available for *F. racemosa*, which has far bigger crops than the other species.

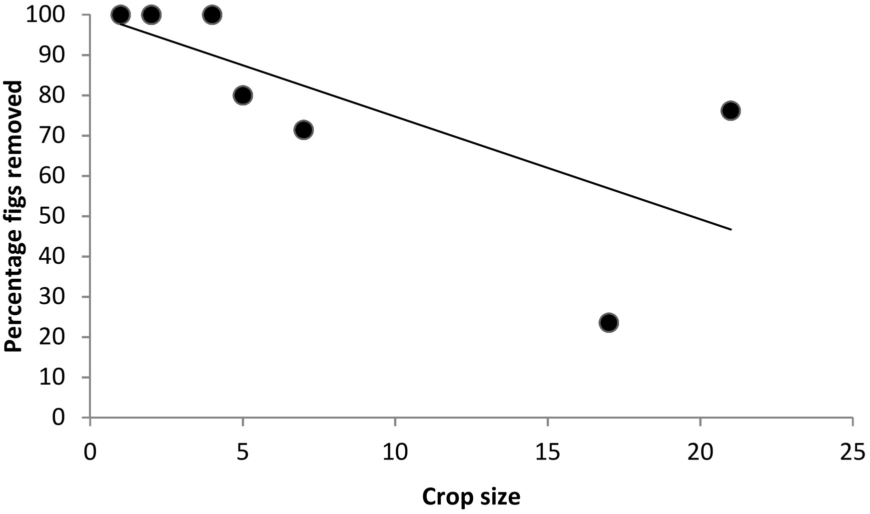

Fig. 3.9. The relationship between *F. montana* crop size and the percentage of figs removed by frugivores.

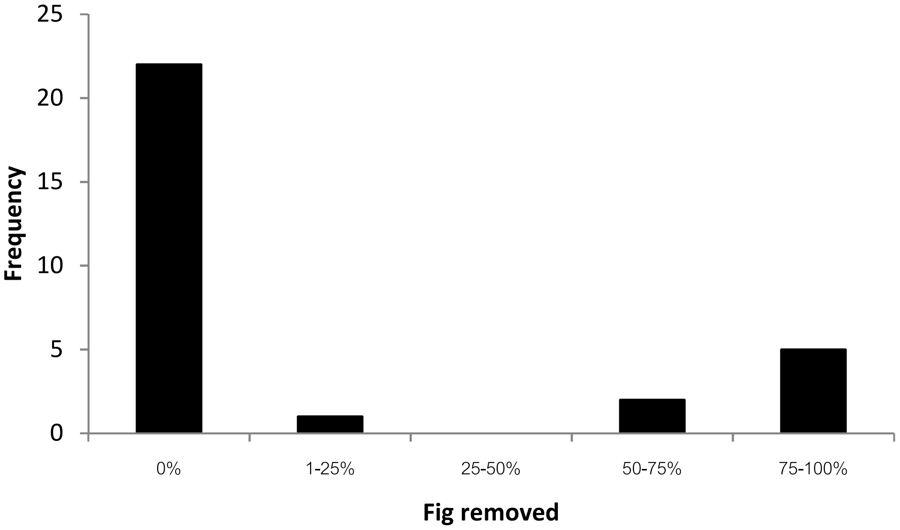

Fig. 3.10. The percentage of *F. montana* figs removed by frugivores.

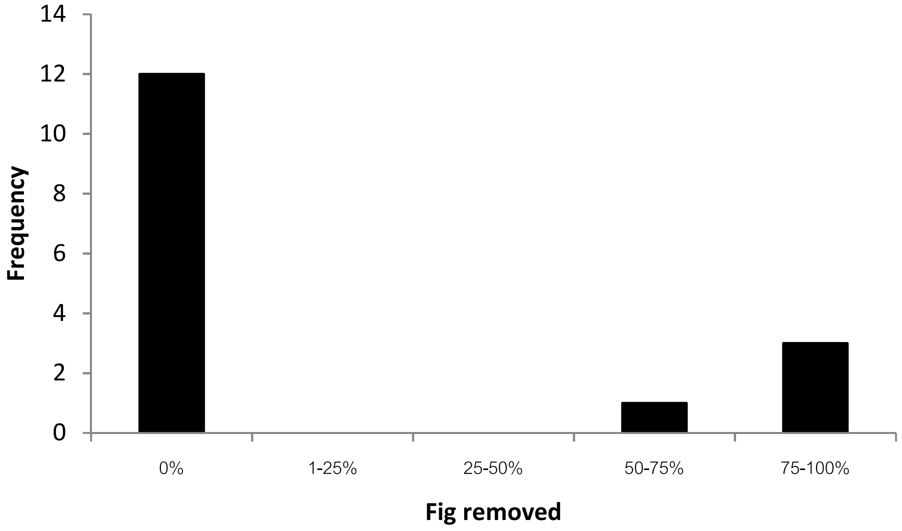

Fig. 3.11.The percentage of *F. ischnopoda* figs removed by frugivores.

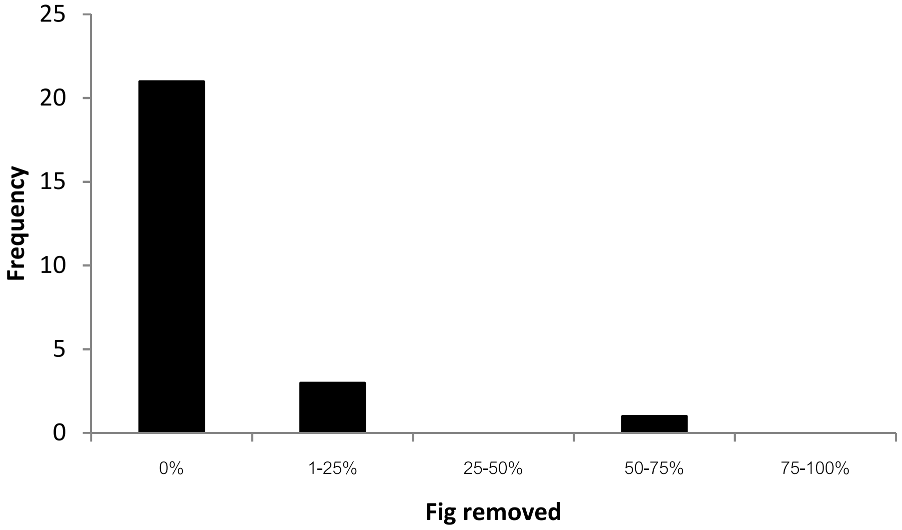

Fig. 3.12.The percentage of *F. oligodon* figs removed by frugivores.

In total, there were seven, four, three and eight frugivore species observed consuming figs of *F. montana*, *F. ischnopoda*, *F. oligodon* and *F. racemosa* respectively. Although only small numbers of frugivore species visited the crops of all four fig species, the species accumulation curves, based on the sequences in which crops of each species were observed, all reached plateaus, suggesting that further species were not likely to be recorded (Figs. 3.13 - 3.16). The majority of frugivores visiting *F. montana* and *F. ischnopoda* were birds, whereas mammals were the main visitors to *F. oligodon* and *F. racemosa* (Fig 3.17). Fig removal rates were: *F. montana* (mean ± S.E.: 0.146 ± 0.08 fig/hrs, range = 0.006 - 0.67 fig/hrs, N = 8), *F. ischnopoda* (0.185 ± 0.11 fig/hrs, range = 0.03 - 0.5 fig/hrs, N = 4) and *F. oligodon* (0.110 ± 0.04 fig/hrs, range = 0.003 - 0.17 fig/hrs, N = 4). These rates did not vary significantly between these three species (GLMs, $P > 0.05$). However, fig removal rates of *F. racemosa* (4.03 ± 1.13 fig/hrs, range = 1.83 - 8.17 fig/hrs, N = 6) was significantly higher than from the other three riparian fig species (GLM: *F. montana* v. *F. ischnopoda*, $Z = -0.877$, $P = 0.8168$; *F. montana* v. *F. oligodon*, $Z = 0.162$, $P = 0.9985$; *F montana* v. *F. racemosa*, $Z = -5.559$, $P < 0.0001$; *F. ischnopoda*v. *F. oligodon*, $Z = -0.619$, $P = 0.9259$; *F. ischnopoda* v. *F. racemosa,* $Z = 3.819$, $P < 0.001$; *F. oligodon* v. *F. racemosa*, $Z = 4.498$, $P < 0.0001$; Fig. 3.18).

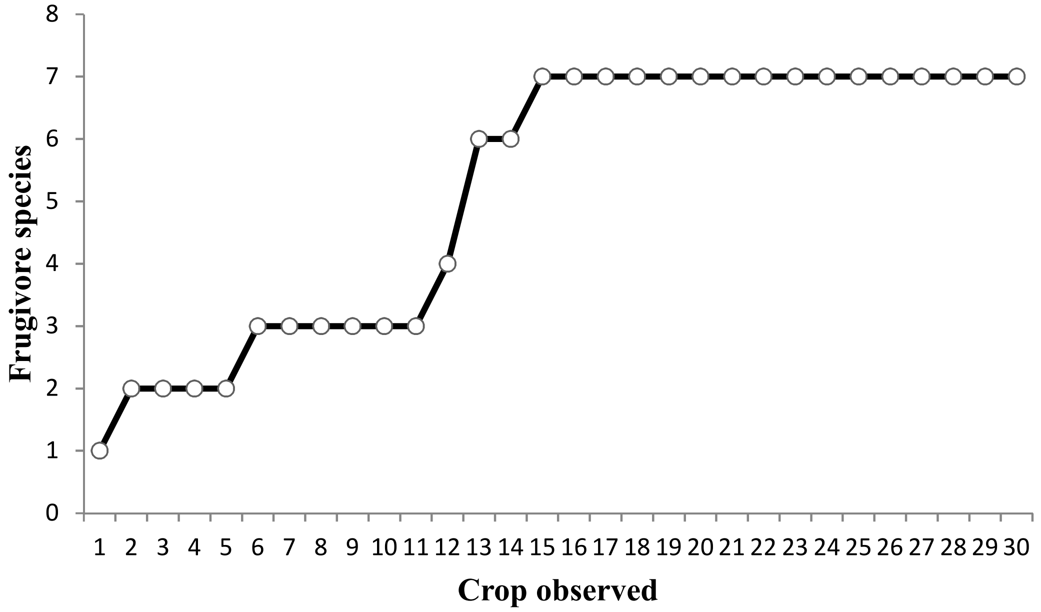

Fig. 3.13. Accumulative curve of frugivore species feeding on crops of female *F. montana* figs.

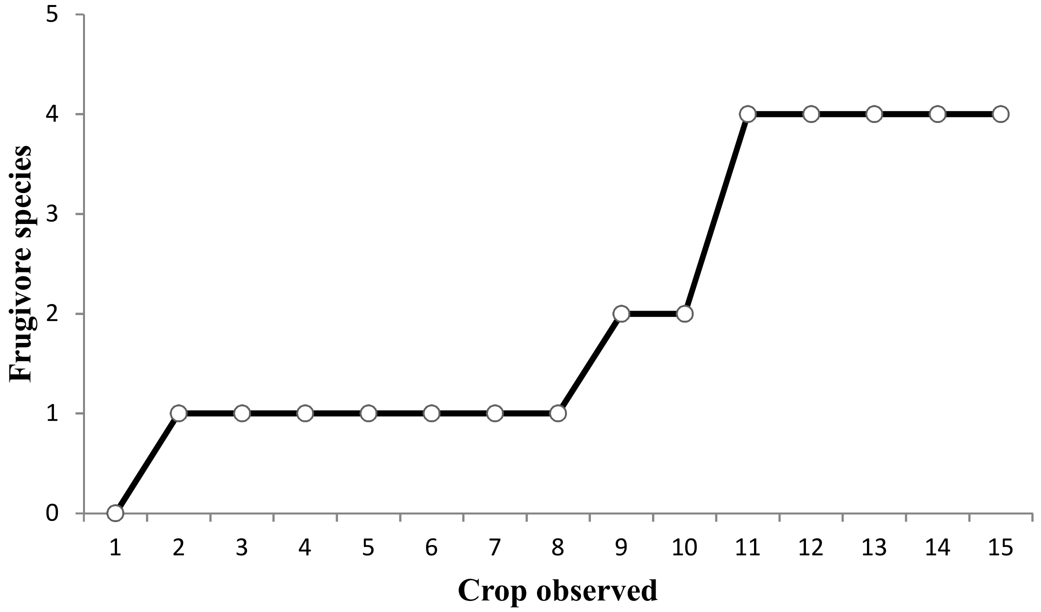

Fig. 3.14. Accumulative curve of frugivore species feeding on crops of female *F. ischnopoda* figs.

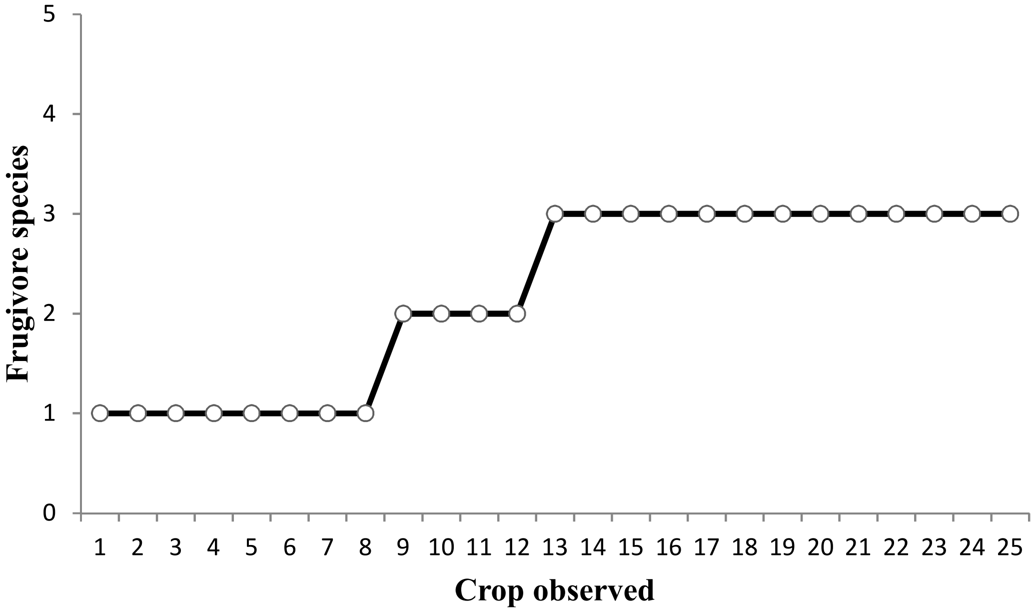

Fig. 3.15. Accumulative curve of frugivore species feeding on crops of female *F. oligodon* figs.

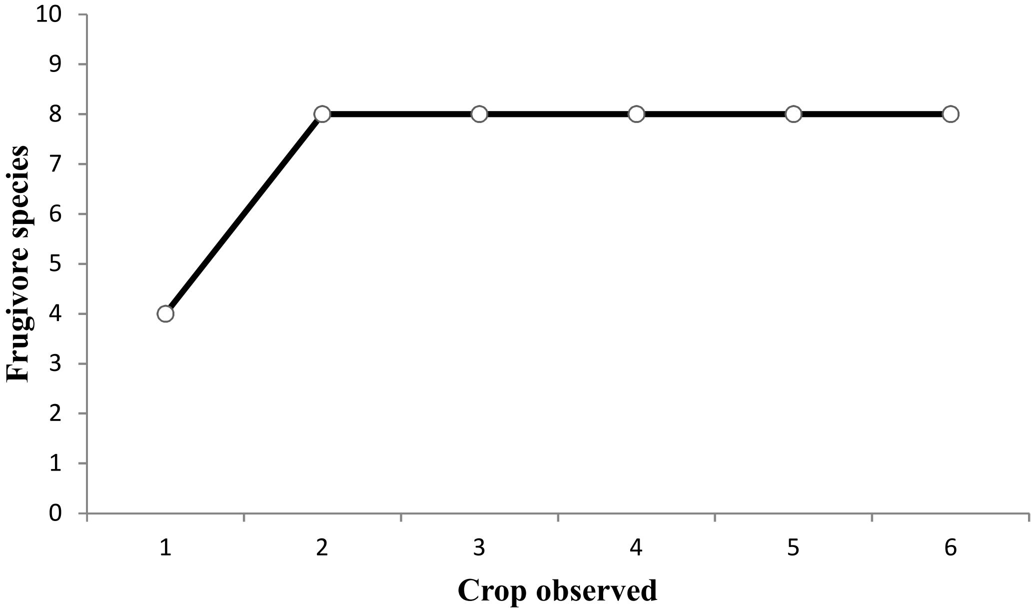

Fig. 3.16. Accumulative curve of frugivore species feeding on *F. racemosa* figs.

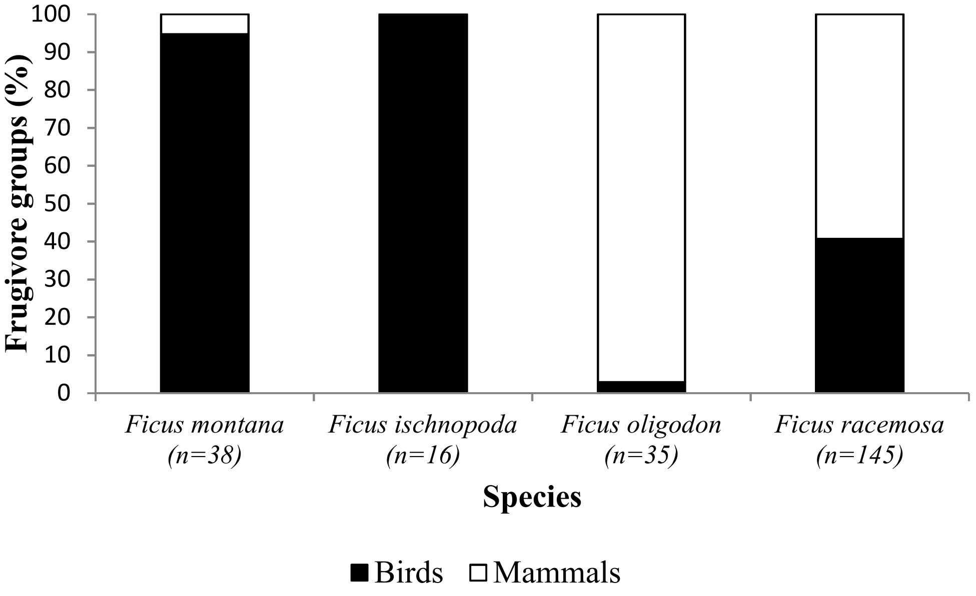

Fig. 3.17. The relative numbers of birds and mammals eating figs of four riparian fig tree species. The number of figs removed is indicated in parentheses.

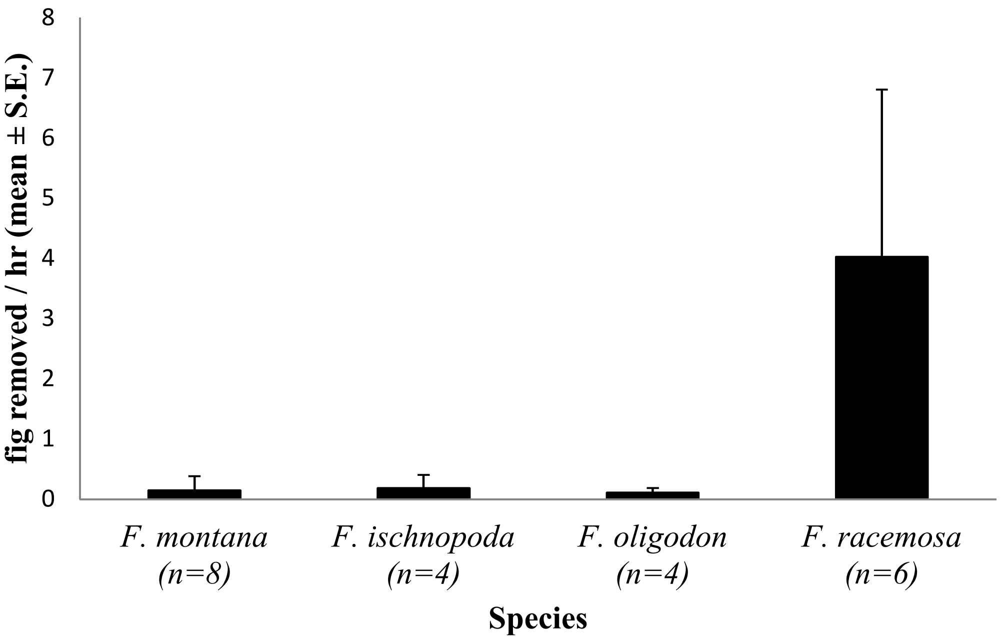

Fig. 3.18. Fig removal rates by frugivores from four riparian fig tree species. Crops where no frugivores were observed are excluded.

3.4.3 Frugivore feeding behaviours

3.4.3.1 *Ficus montana*

Seven frugivore species were recorded feeding on *F. montana* figs at Kratengjeng Waterfall, in Khaolaem National Park. Six were birds and there was one species of squirrel. The Black-crested bulbul (*Pycnonotus flaviventris,* Pycnonotidae) made the most visits and contributed most to fruit removal (Table 3.9, QR 3.1). The riparian specialist bird, Blue-whistling thrush (*Myophonus caeruleus,* Muscicapidae), occasionally fed on *F. montana* figs (QR 3.2). All the frugivore species recorded as consuming *F. montana* figs were diurnal (Table 3.10). There were long intervals between visits by frugivores and as a result figs were removed slowly from most of the crops, with ripe figs remaining on the trees for long periods (Table 3.11). For example, in crop number 13, which had 21 ripe figs present initially, the first fig removed was four hours after the start of observations and the last of the 21 figs was taken after 477 hours. At hour 477, 16 out of 21 figs had been removed, which was 76.2% of the initial total (Table 3.11, Fig. 3.19). Only crop numbers 1 and 2 were visited by any frugivores within 3-4 hours of the start of observations, and in each case all the figs present were removed the first time they were visited (Table 3.11). Black-crested bulbuls visited the crops singly or in pairs, whereas the other frugivore species only visited the crops singly. The bulbuls were observed visiting the crops on 26 occasions, but only stayed to feed 15 times. It is not clear how many individuals were involved.

QR 3.1

QR 3.2

The time spent by bulbuls at the fig crops was much longer if they stayed to feed: mean ± S.E. = 31 ± 2 seconds, range = 21-39 seconds, N = 15 birds, compared with birds that landed but did not feed: mean ± S.E. = 8.5 ± 1 seconds, range = 4-15 seconds, N = 11 visits (GLM: $\chi^2 = 11.45$, df = 1, $P < 0.0001$).

The mean time spent on fig crops by frugivores other than the bulbul (all species combined) that stayed to feed was 32 ± 6 seconds (mean ± S.E.), range = 17-51 seconds, N = 5. It was not significantly different to the time spent by feeding bulbuls (GLM: $\chi^2 = 0.00003$, df = 1, $P = 0.98$). The number of figs removed per visit by individual bulbuls was 1.87 ± 0.21 figs (mean ± S.E.), range = 1-3 figs, N = 15, which was also not statistically different from the numbers removed by other frugivores (mean ± S.E. = 2.80 ± 0.58 figs, range = 1-4 figs, N = 5; GLM: $\chi^2 = 1.46$, df = 1, $P = 0.227$). The feeding behaviours of the birds and squirrel were different. All the bird species swallowed entire *F. montana* figs after detaching them from the trees, but the squirrel held detached figs in its forelimbs and slowly nibbled and chewed the figs before swallowing them, which will have increased the chance that the seeds would be damaged.

Table 3.9. List of frugivore species that fed on four riparian *Ficus* species at four sites (KJ: Kratengjeng Waterfalls, PD: Phatad Waterfalls, EW: Erawan Waterfalls and PT: Phatart Cave). The proportion of figs removed by each frugivore species is shown in parentheses after the number removed. The 'n' refers to the total number of figs removed.

	Ficus montana	*F. ischnopoda*			*F. oligodon*			*F. racemosa*		
	KJ	PD	EW	All sites	KJ	PD	All sites	PT	EW	All sites
	(n=38)	(n=0)	(n=16)	(n=16)	(n=3)	(n=32)	(n=35)	(n=125)	(n=20)	(n=145)
Birds										
Stripe-throated bulbul (*Pycnonotus finlaysoni*)	2 (0.053)	-	3 (0.188)	3 (0.188)	-	-	-	-	-	-
Black-crested bulbul (*Pycnonotus flaviventris*)	17 (0.447)	-	7 (0.438)	7 (0.438)	1 (0.33)	-	1 (0.029)	7 (0.056)	2 (0.10)	9 (0.062)
Black-headed bulbul (*Pycnonotus atriceps*)	5 (0.132)	-	-	-	-	-	-	5 (0.040)	3 (0.15)	8 (0.055)
Sooty-headed bulbul (*Pycnonotus aurigaster*)	-	-	-	-	-	-	-	1 (0.008)	-	1 (0.007)
Black-hooded oriole (*Oriolus xanthornus*)	-	-	-	-	-	-	-	2 (0.016)	-	2 (0.014)
Red-throated barbet (*Psilopogon mystacophonos*)	-	-	-	-	-	-	-	1 (0.008)	-	1 (0.007)
Great hornbill (*Buceros bicornis*)	-	-	-	-	-	-	-	7 (0.056)	-	7 (0.048)
Oriental pied hornbill (*Anthracoceros albirostris*)	-	-	-	-	-	-	-	32 (0.256)	-	32 (0.221)
Blue whistling thrush (*Myophonus caeruleus*)	2 (0.13)	-	4 (0.250)	4 (0.250)	-	-	-	-	-	-
White-breasted waterhen (*Amaurornis phoenicurus*)	-	-	2 (0.125)	2 (0.125)	-	-	-	-	-	-
Green broadbill (*Calyptomena viridis*)	4 (0.105)	-	-	-	-	-	-	-	-	-
Asian fairy-bluebird (*Irena puella*)	3 (0.079)	-	-	-	-	-	-	-	-	-
Mammals										
Grey-bellied squirrel (*Callosciurus caniceps*)	2 (0.053)	-	-	-	1 (0.33)	28 (0.875)	29 (0.829)	70 (0.560)	15 (0.75)	85 (0.586)
Rat (*Rattus* sp. or *Maxomys* sp.)	-	-	-	-	1 (0.33)	4 (0.125)	5 (0.143)	-	-	-

Table 3.10. The timing of visits by frugivores to three species of riparian fig trees derived from camera traps and direct observations. Numbers refer to the number of visits.

	Ficus montana	Day (Hrs)													Night (Hrs)										
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	3	4	5
Birds	Stripe-throated bulbul (*Pycnonotus finlaysoni*)							1																	
	Black-crested bulbul (*Pycnonotus flaviventris*)				4	1	1	1	2	2	3	1													
	Black-headed bulbul (*Pycnonotus atriceps*)			1		2	2	3				1													
	Blue whistling thrush (*Myophonus caeruleus*)	1									1														
	Green broadbill (*Calyptomena viridis*)								1																
	Asian fairy-bluebird (*Irena puella*)				1																				
Mammal	Grey-bellied squirrel (*Callosciurus caniceps*)					1																			

	Ficus ischnopoda	Day (Hrs)													Night (Hrs)										
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	3	4	5
Birds	Stripe-throated bulbul (*Pycnonotus finlaysoni*)									1															
	Black-crested bulbul (*Pycnonotus flaviventris*)						4	1	1																
	Blue whistling thrush (*Myophonus caeruleus*)							1				1	1												
	White-breasted waterhen (*Amaurornis phoenicurus*)							2																	

	Ficus oligodon	Day (Hrs)													Night (Hrs)										
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	3	4	5
Birds	Black-crested bulbul (*Pycnonotus flaviventris*)									1															
Mammals	Grey-bellied squirrel (*Callosciurus caniceps*)	1	1	1		1	1	1	3		2	2	2	5											
	Rat (*Rattus* sp. or *Maxomys* sp.)																1	1		2	1	3	2	1	

Table 3.11. The frugivore visits and fig removal at each *F. montana* crop.

Crop number	Visit number	Total observed hours	Fig removal hours	Frugivore species	Figs available	Figs eaten	Removal (%)
1	1	6	4	Black-crested bulbul (*Pycnonotus flaviventris*)	4	4	100.0
2	1	6	3	Grey-bellied squirrel (*Callosciurus caniceps*)	2	2	100.0
6	1	170	163	Blue whistling thrush (*Myophonus caeruleus*)	1	1	100.0
12	1	240	24	Black-headed bulbul (*Pycnonotus atriceps*)	7	2	28.6
12	2	240	171	Black-crested bulbul (*Pycnonotus flaviventris*)	5	1	42.9
12	3	240	239	Black-crested bulbul (*Pycnonotus flaviventris*)	4	2	71.4
13	1	576	4	Black-crested bulbul (*Pycnonotus flaviventris*)	21	1	4.8
13	2	576	71	Black-headed bulbul (*Pycnonotus atriceps*)	20	1	9.5
13	3	576	171	Black-crested bulbul (*Pycnonotus flaviventris*)	19	2	19.1
13	4	576	193	Green broadbill (*Calyptomena viridis*)	17	4	38.1
13	5	576	195	Black-crested bulbul (*Pycnonotus flaviventris*)	13	1	42.9
13	6	576	212	Black-headed bulbul (*Pycnonotus atriceps*)	12	1	47.6
13	7	576	265	Black-crested bulbul (*Pycnonotus flaviventris*)	11	2	57.1
13	8	576	310	Black-crested bulbul (*Pycnonotus flaviventris*)	9	1	61.9
13	9	576	477	Asian fairy-bluebird (*Irena puella*)	8	3	76.2
14	1	72	53	Blue whistling thrush (*Myophonus caeruleus*)	5	4	80.0
15	1	72	72	Stripe-throated bulbul (*Pycnonotus finlaysoni*)	2	2	100.0
18	1	144	23	Black-crested bulbul (*Pycnonotus flaviventris*)	17	2	11.8
18	2	144	47	Black-headed bulbul (*Pycnonotus atriceps*)	15	2	23.5

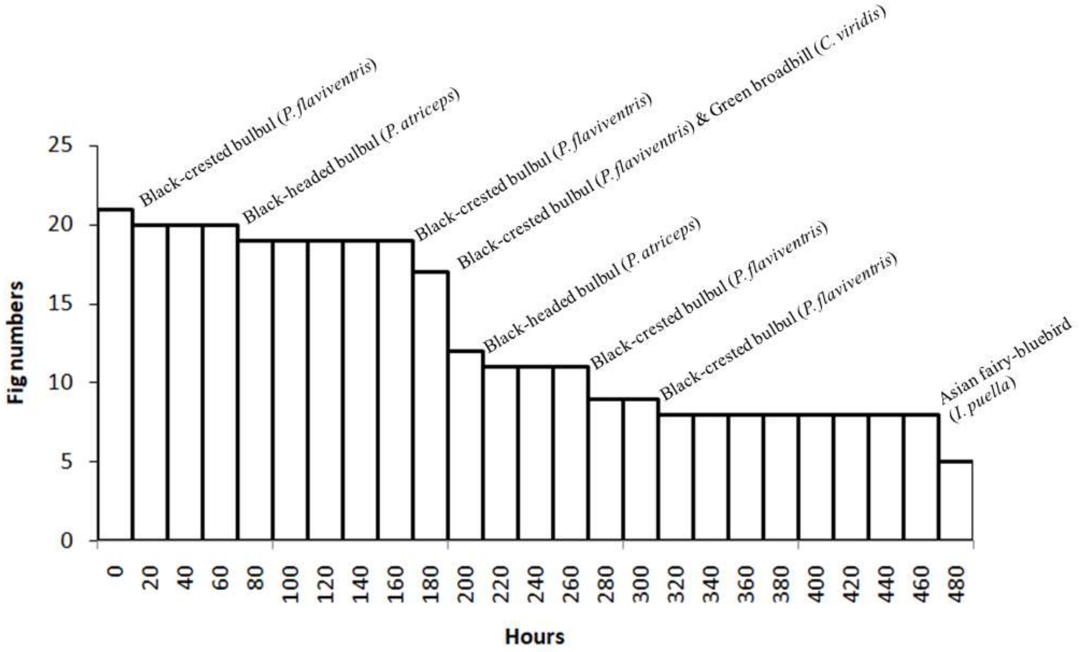

Fig. 3.19. The frequency distribution of 21 figs remaining on *F. montana* crop number 13 after removal by frugivores. Based on camera trap recording that began at 12.00 P.M.

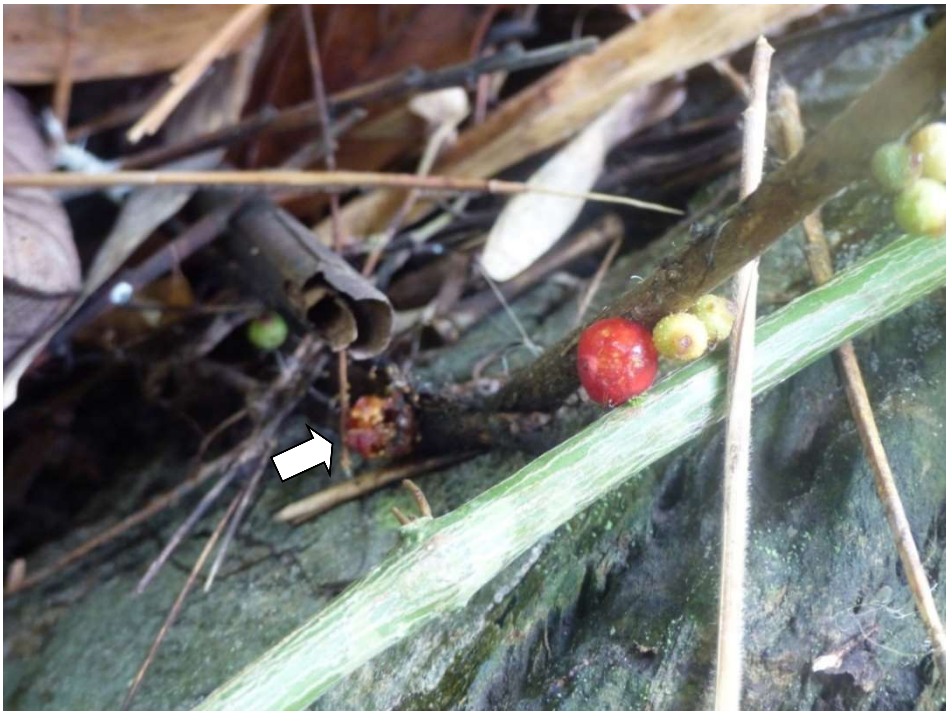

Fig. 3.20. Example of a fig of *F. montana* that remained without frugivore removal and became rotten. A ripe fig and several unripe figs are also present.

3.4.3.2 *Ficus ischnopoda*

Only four frugivore species interacted with *F. ischnopoda* fig crops at the Erawan Waterfalls study site in Erawan National Park during the periods of observation (Fig. 3.21), and no frugivores interacted with the trees at Phatad Waterfalls in Srinagarind Dam National Park.

QR 3.3

QR 3.4

QR 3.5

The Blue whistling thrush (*Myophonus caeruleus,* QR 3.3) and Black-crested bulbul (*P. flaviventris*, QR 3.4) were the most frequent visitors to the plants and eaters of their figs (Table 3.9). The frugivores recorded feeding on *F. ischnopoda* figs were all diurnal species (Table 3.10). All the crops where frugivore visits were recorded had interactions with frugivores within 3-6 hours after the start of observations (Table 3.12). The rarity of visits by frugivores is illustrated by crop number 10, where an initial feeding visit at hour three was followed by a period where there was no feeding on figs recorded until hour 142, and there were few fig removal events overall (Fig 3.22). As with *F. montana*, single individuals or pairs of this bulbul visited the fig crops, whereas only lone individuals of the other species were recorded. Figs were fed on during 75% of all visits by the bulbuls (N = 8 visits and 6 feeding events). All the figs present were removed during visits by Blue whistling thrushs (N = 3 visits). Two visits by White-breasted waterhen (*Amaurornis phoenicurus*, Rallidae, QR 3.5) were recorded, but only one of them resulted in feeding on the figs.

On the crops where figs were removed by the bulbul, the birds spent 35 ± 11.5 seconds per visit, range = 14-91 seconds, N = 6 visits, and Blue whistling thrush (*M. caeruleus*) spent 47 ± 14 seconds, range = 29-74 seconds, N = 3 visits.

Where crops were visited, but no figs were eaten, the bulbuls spent 9 and 12 seconds wandering around the fig crops (N = 2 visits), and the White-breasted waterhen spent 12 seconds at the fig tree (N = 1 visit). The number of figs removed per visit by bulbuls was 1.67 ± 0.33 figs, range = 1-3 figs, N = 6 visits. The other frugivores removed 1.50 ± 0.29 figs per visit, range = 1-2 figs, N = 4 visits. The White-breasted waterhen swallowed whole figs when foraging. The bulbul and Blue whistling thrush were also mainly swallowers, but both species were ‘biters’ sometimes, using their pecks to break open a whole *F. ischnopoda* fig, dividing it into smaller parts, and then swallowing the fig parts.

Fig. 3.21. ***F. ischnopoda*** **crop number 10 at Erawan waterfalls, Erawan National Park.**

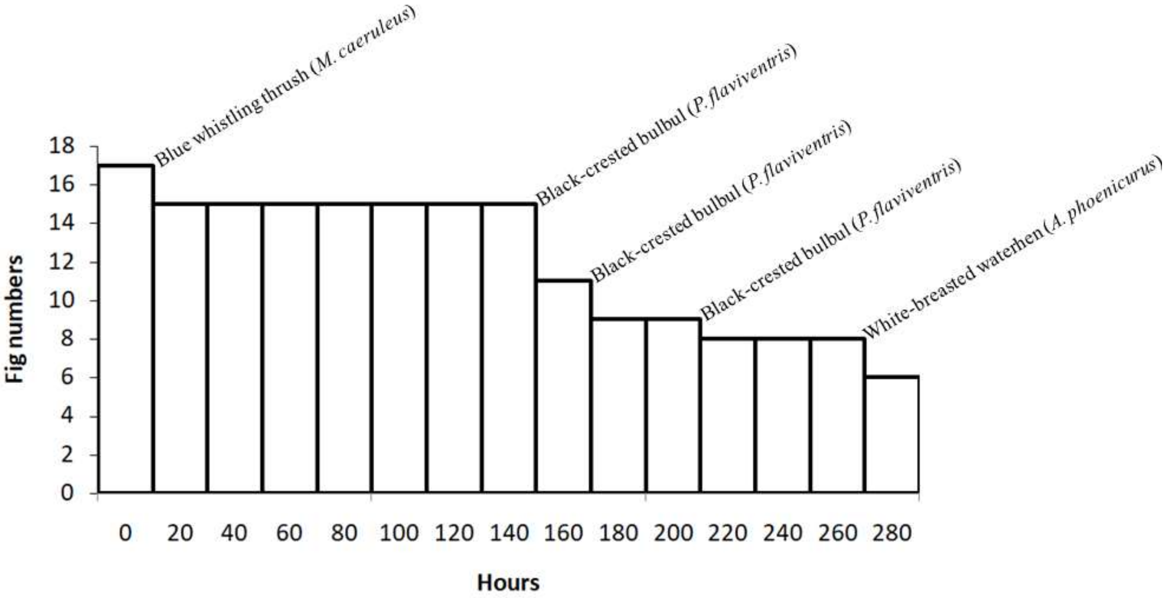

Fig. 3.22. The number of figs remaining on *F. ischnopoda* crop number 10. tree after removal by frugivores. Based on camera trap recordings that began at 10.00 A.M.

Table 3.12. Frugivore visits and fig removal at *F. ischnopoda* crops.

Crop number	Visit number	Total observed hours	Removal After (hours)	Frugivore species	Figs available	Figs eaten	Removal (%)
2	1	24	4	Blue whistling thrush (*Myophonus caeruleus*)	1	1	100.0
6	1	6	6	Blue whistling thrush (*Myophonus caeruleus*)	1	1	100.0
8	1	6	4	Stripe-throated bulbul (*Pycnonotus finlaysoni*)	3	3	100.0
10	1	336	3	Blue whistling thrush (*Myophonus caeruleus*)	17	2	11.8
10	2	336	142	Black-crested bulbul (*Pycnonotus flaviventris*)	15	1	17.7
10	3	336	144	Black-crested bulbul (*Pycnonotus flaviventris*)	14	3	35.3
10	4	336	166	Black-crested bulbul (*Pycnonotus flaviventris*)	11	1	41.2
10	5	336	167	Black-crested bulbul (*Pycnonotus flaviventris*)	10	1	47.1
10	6	336	214	Black-crested bulbul (*Pycnonotus flaviventris*)	9	1	52.9
10	7	336	263	White-breasted waterhen (*Amaurornis phoenicurus*)	8	2	64.7

3.4.3.3 *Ficus oligodon*

Only three frugivore species were seen to interact with crops of *F. oligodon*, across both sites. Grey-bellied squirrels (*Callosciurus caniceps*, Sciuridae, QR 3.6) were the most frequently recorded frugivore (Table 3.9). Only one feeding record of a Black-crested bulbul was recorded, involving a single ripe fig (at Kratengjeng waterfall). Mostly, single individuals of the squirrel visited crops, but they were occasionally seen in pairs. The bulbul and an unidentified rat (*Rattus* or *Maxomys* species, Muridae, QR 3.7) only visited fig crops as single individuals. The first fig removal by frugivores was generally recorded within 4-6 hours of the start of observations, except with crop number 9 where the first fig removal was recorded 128 hours after observations began (Table 3.13).With crop number 10, 52.1% of the total figs (38 out of 73 figs) were removed within 148 hours after the start of observations. However, the remaining figs were not removed by any frugivores from hour 148 until the end of observation at 312 hours, when all the ripe figs had disappeared, when they had fallen off the tree (Table 3.13, Fig 3.23).

QR 3.6

QR 3.7

A total of 32 visits to this fig tree species were recorded, with the squirrel providing 20 visits (62.5%), the rat 11 visits (34.4%) and the Black-crested bulbul just one visit (3.1%). The squirrel removed figs on 18 of its 20 visits, whereas the rat removed figs on only five of its 11 visits. The likelihood of visits by the squirrel and the rat resulting in fig removal were significantly different (Chi-square: $\chi^2 = 9.91$, df = 1, $P < 0.01$). The time spent by the squirrel on the figs if feeding occurred (297 ± 62 seconds, range = 60-900 seconds, N = 18 visits) was longer than when feeding behaviour was not observed (48.5 ± 11.5 seconds, range = 37-60 seconds, N = 2 visited). The rat spent 600 ± 204 seconds (range = 180-1080 seconds, N = 5 visits) when feeding, but only 250 ± 89 seconds, range = 60-720 seconds, N = 7 visits, when visits did not result in feeding. Although the rat tended to spend more time on the crops than the squirrel, there was considerable variation and the difference was not significant (GLM: $\chi^2 = 2.114$, df = 1, P = 0.114). There was also no significant difference in the time spent on the trees when no feeding took place (GLM: $\chi^2 = 2.663$, df = 1, P = 0.06).

The Grey-bellied squirrels removed 1.56 ± 0.18 figs per visit (range = 1-3 figs, N = 18 visits), whereas the rat always removed single figs (N = 4 visits). Both mammals are rodents, and their feeding behaviors were similar, in the way of nibbled feeding. Although the camera traps could not clearly capture fig removal behaviours of the squirrels, it was assumed that the feeding behaviours are as similar as when feeding on the *F. racemosa* figs. However, rats usually sniffed and nibbled the single ripe fig which was still on the trunk using their incisor teeth. The size of ripe *F. oligodon* figs was larger than the gape width of the bulbul, so this required the bird to peck the fig into smaller parts before swallowing them (Fig 3.24). The squirrel and bulbul were diurnal frugivores, but the rats were nocturnal, only feeding on the figs at night (Table 3.10). 70 % of the 20 visits by squirrels were recorded in the afternoon (12.00 – 18.00 p.m.), compared with 30% of the visits in the morning (06.00 a.m. – 12.00 p.m.). The frequency of visits by squirrels in the mornings and afternoons was not significantly different (Chi-square goodness of fit: $\chi^2 = 3.20$, df = 1, P = 0.074)

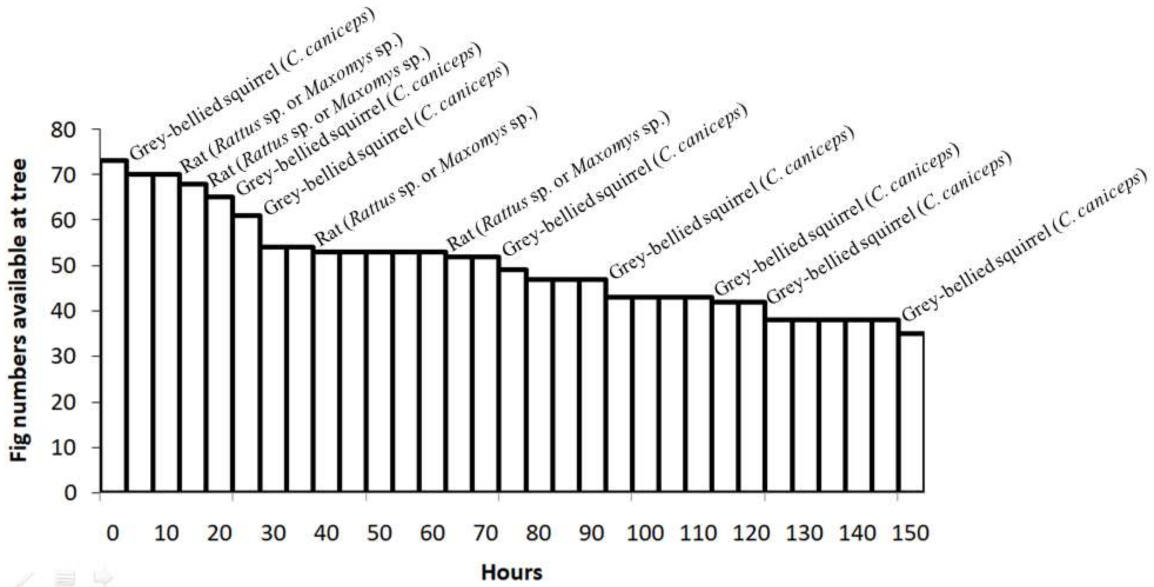

Fig. 3.23. The number of figs remaining on *F. oligodon* crop number 10. tree after removal by frugivores. Camera trap observations began at 13.00 P.M.

Fig. 3.24. A Black-crested bulbul (*Pycnonotus flaviventris*) feeding on a *F. oligodon* fig after removing it from the tree.

Table 3.13. Frugivore visits to *F. oligodon* crops.

Crop number	Visit number	Total observed hours	Removal times (hours)	Frugivore species	Figs available	Figs eaten	Accumulative Percentage (%)
1	1	6	6	Grey-bellied squirrel (*Callosciurus caniceps*)	5	1	20.0
9	1	288	128	Rat (*Rattus*sp.or *Maxomys* sp.)	5	1	20.0
10	1	312	5	Grey-bellied squirrel (*Callosciurus caniceps*)	73	1	1.4
10	2	312	5	Grey-bellied squirrel (*Callosciurus caniceps*)	72	1	2.7
10	3	312	5	Grey-bellied squirrel (*Callosciurus caniceps*)	71	1	4.1
10	4	312	11	Rat (*Rattus*sp.or *Maxomys* sp.)	70	1	5.5
10	5	312	12	Rat (*Rattus*sp.or *Maxomys* sp.)	69	1	6.9
10	6	312	17	Grey-bellied squirrel (*Callosciurus caniceps*)	68	1	8.2
10	7	312	19	Grey-bellied squirrel (*Callosciurus caniceps*)	67	1	9.6
10	8	312	19	Grey-bellied squirrel (*Callosciurus caniceps*)	66	1	11.0
10	9	312	21	Grey-bellied squirrel (*Callosciurus caniceps*)	65	1	12.3
10	10	312	21	Grey-bellied squirrel (*Callosciurus caniceps*)	64	1	13.7
10	11	312	22	Grey-bellied squirrel (*Callosciurus caniceps*)	63	1	15.1
10	12	312	24	Grey-bellied squirrel (*Callosciurus caniceps*)	62	1	16.4
10	13	312	26	Grey-bellied squirrel (*Callosciurus caniceps*)	61	1	17.8
10	14	312	26	Grey-bellied squirrel (*Callosciurus caniceps*)	60	1	19.2
10	15	312	29	Grey-bellied squirrel (*Callosciurus caniceps*)	59	1	20.6
10	16	312	29	Grey-bellied squirrel (*Callosciurus caniceps*)	58	1	21.9
10	17	312	29	Grey-bellied squirrel (*Callosciurus caniceps*)	57	2	24.7
10	18	312	29	Grey-bellied squirrel (*Callosciurus caniceps*)	55	1	26.0
10	19	312	38	Rat (*Rattus*sp.or *Maxomys* sp.)	54	1	27.4
10	20	312	63	Rat (*Rattus*sp.or *Maxomys* sp.)	53	1	28.8
10	21	312	72	Grey-bellied squirrel (*Callosciurus caniceps*)	52	1	30.1
10	22	312	75	Grey-bellied squirrel (*Callosciurus caniceps*)	51	1	31.5
10	23	312	75	Grey-bellied squirrel (*Callosciurus caniceps*)	50	1	32.9
10	24	312	76	Grey-bellied squirrel (*Callosciurus caniceps*)	49	1	34.3
10	25	312	77	Grey-bellied squirrel (*Callosciurus caniceps*)	48	1	35.6
10	26	312	94	Grey-bellied squirrel (*Callosciurus caniceps*)	47	1	37.0
10	27	312	95	Grey-bellied squirrel (*Callosciurus caniceps*)	46	1	38.4
10	28	312	95	Grey-bellied squirrel (*Callosciurus caniceps*)	45	1	39.7
10	29	312	95	Grey-bellied squirrel (*Callosciurus caniceps*)	44	1	41.1
10	30	312	113	Grey-bellied squirrel (*Callosciurus caniceps*)	43	1	42.5
10	31	312	123	Grey-bellied squirrel (*Callosciurus caniceps*)	42	1	43.8
10	32	312	123	Grey-bellied squirrel (*Callosciurus caniceps*)	41	1	45.2
10	33	312	125	Grey-bellied squirrel (*Callosciurus caniceps*)	40	1	46.6
10	34	312	125	Grey-bellied squirrel (*Callosciurus caniceps*)	39	1	48.0
10	35	312	148	Grey-bellied squirrel (*Callosciurus caniceps*)	38	1	49.3
10	36	312	148	Grey-bellied squirrel (*Callosciurus caniceps*)	37	1	50.7
10	37	312	148	Grey-bellied squirrel (*Callosciurus caniceps*)	36	1	52.1
13	1	6	4	Black-crested bulbul (*Pycnonotus flaviventris*)	12	1	8.3

3.4.3.4 *Ficus racemosa*

Observations of *F. racemosa* were only carried out during the day. Visitors to the trees were recorded at two sites, where a total of eight vertebrates were seen feeding on the figs: one mammal and seven birds. Fewer frugivore species were seen at Erawan than at Pratart cave, but the most frequent visitor at both sites was the Grey-bellied squirrel. This species provided 56–75% of the feeding records. The squirrel together with the Great hornbill (*Buceros bicornis*) and Oriental pied hornbill (*Anthracoceros albirostris*), Bucerotidae, removed the most figs - more than 50% of the total at each site (Table 3.9; 3.14).

The bulbuls usually visited the fig crops as single individuals, but sometime were in pairs or mixed species flocks. The hornbills and grey-bellied squirrel also visited the trees mostly as single individuals. In total, fig removal was recorded in 49 out of 55 (89.09%) of the visits by Grey-bellied squirrels, compared with 16 out of 22 visits (72.73%) by the bulbuls. Likelihood of visits resulting in feeding were similar (Chi-square: χ^2 = 3.199, df = 1, P = 0.074). Fig removal occurred during all the small number of visits to the trees made by other species (hornbills: N = 5 visits, other birds: N = 3 visits).

The average foraging times of the grey-bellied squirrels (471 ± 29 seconds, range = 150-1200 seconds, N = 49 visits) that fed on the figs was significantly higher than if they only visited the crops (175 ± 43 seconds, range = 60-350 seconds, N = 6 visits; GLM: χ^2 = 5.976, df = 1, P < 0.001). Likewise, bulbuls that fed stayed longer (105.53 ± 6.98 seconds, range = 65-150 seconds, N = 15) than if they did not feed (37.33 ± 10.84 seconds, range = 17-90 seconds, N = 6; GLM: χ^2 =

5.885, df = 1, P < 0.001), suggesting that bulbuls spent significantly more time to process fig before feeding on the fig trees. Among the other birds, Black-hooded orioles (*Oriolus xanthornus*, Oriolidae) spent 83 ± 29 seconds, range = 54-112 seconds, N = 2 visits, and a Red-throated barbet (*Psilopogon mystacophonos*, Megalaimidae) spent 135 seconds feeding, N = 1 visit. The mean foraging time of hornbills on the crops was 253 ± 31 seconds, range = 192-327 seconds, N = 5. When comparing foraging times among the three frugivore groups (bulbuls, hornbills, and squirrels), it was found that the foraging times were significantly different (GLM: bulbuls v. hornbills, Z = -4.526, P < 0.0001; bulbuls v. squirrel, Z = -13.243, P < 0.0001; hornbills v. squirrel, Z = -3.183, P < 0.001). Bulbuls, Black-hooded oriole and Red-throated barbet removed only one fig during each visit to the crops. However, hornbills removed significantly more figs (7.80 ± 0.86 figs, range = 6-11 figs, N = 5 visits) than Grey-bellied squirrel, (1.76 ± 0.11 figs, range = 1-3 figs, N = 49 visits; GLM: χ^2 = 47.15, df = 1, P < 0.0001). Due to their large gape size, hornbills were the only birds that could swallow whole figs of *F. racemosa*. The other birds were smaller and mashed ripe figs before swallowing small fig parts. The Grey-bellied squirrel foraging behavior was different from the birds and was similar to that when feeding on *F. oligodon* figs. The squirrels started by removing a fig from its attachment to the tree, and then held the fig using their forehands while nibbling and chewing it and then swallowing.

Thirty visits by birds were recorded, 16 in the morning session and 14 in the afternoon session. However, more than half the visits by the squirrel were in the afternoon (37 out of 54 visits, Fig 3.25). The visits by birds and the squirrel were associated with different sessions (Chi-square: χ^2 = 3.8609, df = 1, P < 0.05), and the frequency of visits by squirrels in the morning and afternoon was significantly different (Chi-square goodness of fit: $\chi^2 = 7.407$, df = 1, P = 0.006). In contrast, the frequency of visits by birds in the morning and afternoon was not significantly different (Chi-square goodness of fit: $\chi^2 = 0.133$, df = 1, P = 0.715).

Table 3.14. The timing of visits by frugivores to three *Ficus racemosa* crops, derived from direct observations. Numbers refer to the number of visits. Observation periods were from 7.00-11.00 and 14.00-18.00

Ficus racemosa		Times commencement							
		7	8	9	10	14	15	16	17
Birds	Black-crested bulbul (*Pycnonotus flaviventris*)			4		6			
	Black-headed bulbul (*Pycnonotus atriceps*)	3		2	1	3	4		
	Sooty-headed bulbul (*Pycnonotus aurigaster*)					1			
	Black-hooded oriole (*Oriolus xanthornus*)		1						
	Red-throated barbet (*Psilopogon mystacophonos*)			1					
	Great hornbill (*Buceros bicornis*)		1						
	Oriental pied hornbill (*Anthracoceros albirostris*)		2	1					
Mammal	Grey-bellied squirrel (*Callosciurus caniceps*)	3	3	5	6	5	5	11	16

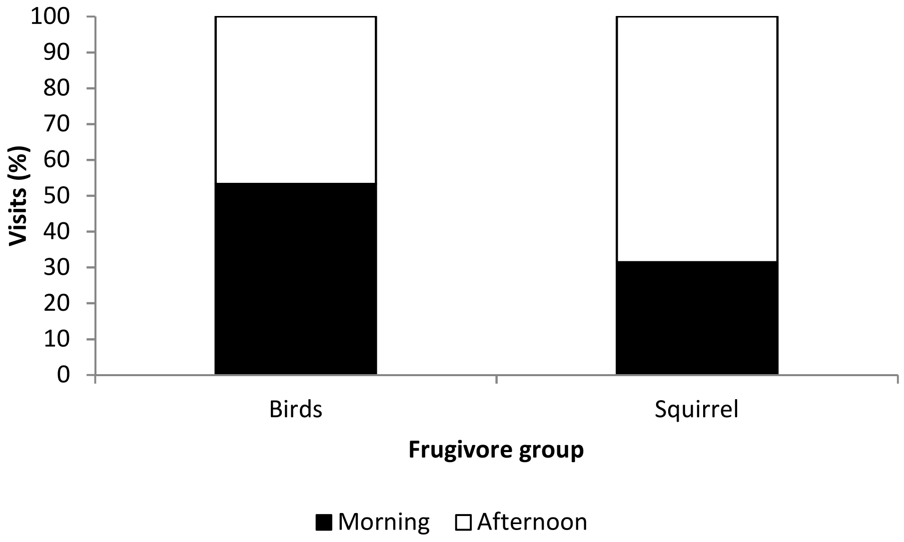

Fig. 3.25. The percentage of visits by birds and mammals to *F. racemosa* crops in the morning (07.00 - 10.00) and afternoon (14.00 – 17.00).

3.5 Discussion

Frugivores only fed on a small proportion of the figs and when the remaining figs fell from the trees some would fall into the water, where they are possibly dispersed by water. Although all four species grew in the streams or within meters of them, the figs of the smaller shrubby species (*F. montana* and *F. ischnopoda*) were more likely to fall into the water than those of the bigger fig trees (*F. oligodon* and *F. racemosa*). This was because their larger crowns extended further from the streams. Most of the fig crops produced by the two smaller species (*F. montana*, *F. ischnopoda*) were not visited by any frugivores, and the overall fig removal rates for these two fig species were correspondingly low. Figs which were not eaten by frugivores fell directly to the ground or water or began to rot in situ on the trees. Together with the locations of the figs on the trees, this meant that water dispersal may be more significant for these smaller species.

Both *F. montana* and *F. ischnopoda* were only seen to interact with diurnal frugivores, which are likely to be responding to the visual cues provided by the brightly coloured mature fruits (Gautier-Hion et al., 1985; Lomáscolo et al., 2010). The visitors to crops of *F. montana* and *F. ischnopoda* were present in small numbers and almost all were small birds. There may be several reasons why these small fig trees were almost ignored by frugivores. Firstly, they produced small fig crops which did not allow them to attract frugivores from long distances. Poor ‘advertisement’ was made worse because the figs were mostly presented close to the ground, and often hidden among other shrubs and ground flora. Shanahan & Compton (2001) and Kitamura et al. (2002) pointed out that most understorey trees are not likely to be visited by the frugivores that forage on canopy trees and these include major frugivore groups like pigeons, hornbills, squirrels and gibbons. Large terrestrial mammals, such as elephants and deer are also not likely to be attracted because the resources they offer are insignificant.

Bulbuls (Pycnonotidae) were the major frugivores removing figs from the smaller fig trees. They are small frugivorous birds distributed in a wide range of habitats and are considered as important seed dispersers across tropical East Asia (Corlett, 2002). They have a small gape width (Fukui, 1995) and only small fruit (less than 20 mm in diameter) are suitable for bulbuls to swallow whole, as was the case with the figs of *F. montana* and *F. ischnopoda*. Bulbuls are likely to be the most important seed dispersers of these and other small riparian fig trees in western Thailand and elsewhere in the region.

Although only small numbers of crops were visited by of the Blue whistling thrush (*M. caeruleus*), this riparian specialist species (del Hoyo et al., 2017) may be another important disperser of small riparian fig tree species, because of its habitat preferences and ground feeding behaviour. The thrush also swallowed whole figs, like the bulbuls, but it has a larger body and gape and fed on more figs during a single feeding bout than the bulbuls. In addition, because of its habitat preference, the thrush is likely to mainly defaecate fig seeds in riparian areas and along stream banks, at the sites that are most suitable for establishment by these fig trees. Therefore, the thrush may offer them better quality seed dispersal than the bulbuls, where the seed dispersal quality comprises of fruit handling by frugivores and the fate of seeds to disperse in suitable sites (Schupp et al., 2010).

The larger riparian fig tree *F. oligodon,* produced larger figs (30-50 mm in diameter) and larger crops than the two smaller riparian fig species. It was also less popular among frugivores and when crops were visited, if at all, it was largely by terrestrial mammals, not birds. As with *F. montana* and *F. ischnopoda*, no hornbills were recorded feeding on *F. oligodon*. They are canopy feeders (Shanahan & Compton, 2001) and like *F. montana* and *F. ischnopoda*, the figs of *F. oligodon* are mostly produced on or close to the ground, which makes them unavailable to this group of birds (CHAPTER 2). Based on its large figs, and where the figs are present, potential dispersal agents are large terrestrial species such wild boars, deer or elephants that feed directly from the trees or eat fallen fruits on the forest floor (Shanahan et al., 2001; Kitamura et al., 2002). However, these larger species are rare or entirely absent from the study areas, despite being located in national parks, and no interactions between *F. oligodon* and large terrestrial mammals were recorded. The most common species feed on its figs was the Grey-bellied squirrel (*C. caniceps*) and a nocturnal rat (*Rattus* or *Maxomys* species). These rodents are known as seed predators (Janzen, 1971; Corlett, 1998), especially for plant species with large seeds. Some of the small seeds in the figs may not be totally destroyed when these rodents are chewing on them, and rats can disperse small numbers of fig seeds (Wells et al., 2009; Staddon et al., 2010; Duron et al., 2017).

In contrast to the other three species, *F. racemosa* is a large fig tree with a large canopy and large crops. It interacted with more frugivore species. Fig trees with large crop sizes have been shown previously to interact with a wider range of frugivores species (Shanahan & Compton, 2001). Figs of *F. racemosa* are presented at a wide range of heights including the tree canopy along the rivers (more than 5 meters above the ground). It has been suggested that mammals are the main frugivorous group associated with *F. racemosa* (David et al., 2015), with fruit bats particularly important (David et al., 2012). In this study, observations were only made in the day time, so only recorded part of the likely range of dispersal agents associated with this tree. The most frequent diurnal frugivore removing *F. racemosa* figs was the grey-bellied squirrel (*C. caniceps*), the same species found eating the figs of *F. oligodon*. Figs, including *F. racemosa*, are important food resource for Indian hornbills (Balasubramanian et al., 2004). Hornbills were the second most important groups of diurnal frugivores. They removed large numbers of figs and were the only the frugivores that could swallow whole *F. racemosa* figs. It has been suggested that frugivores that swallow fruits whole provide a higher probability of seed dispersal for many plants as whole seeds enter into their gut, whereas biter and masher frugivores may drop some seeds during feeding (Schupp, 1993). Thus, as the swallowers, hornbills may be the top seed dispersers of the big fig trees. They also travel long distances, making long distance dispersal of the seeds more likely (Holbrook & Smith, 2000).

Despite having more visits by frugivores than the other species, the large crop sizes of *F. racemosa* meant that a low proportion of the figs were removed, and a majority of the figs were likely to fall down to the ground or into the water below. This contrasts with some Neotropical strangler fig trees, where it has been found that more than half (58-80%) of their ripe figs can be removed by the frugivores (Coates-Estrada & Estrada, 1986; Korine et al., 2002). There may be several explanations for the low animal dispersal of the trees. Some of the riparian areas in national parks, for example waterfalls and streams, are attractive to tourists and prone to disturbance. It is known that tourism can interfere with wildlife, and animals avoid areas with human activities (Green & Higginbottom, 2001).

Secondly, frugivores that are sensitive to forest fragmentation or human activity, for example, pigeons, civets, elephants, deer, bears and gibbons (Corlett, 1998), were absent. Conversely, the most frequently found frugivores were bulbuls and squirrels, two groups known to have high tolerance to humans and fragmented habitats (Corlet, 1998). Thirdly, hunting and poaching reduce frugivore populations. For example, half of the primate species and 85% of hornbill species have been annihilated from the Lambir Hills National Park, Borneo, Indonesia by hunting pressure (Harrison, 2011). Many protected areas in Kanchanaburi are also affected by local poachers and hunters, including some of the study sites, and it was reported that seed dispersal events decrease by more than a half as a result elsewhere (Wright et al., 2002; Holbrook & Loiselle, 2009).

Birds with a larger body size tend to stay longer on fig trees. The smaller visitors such as the bulbuls spent shorter time periods feeding on the riparian figs than the hornbills. Hornbills also consumed a higher number of figs than the smaller birds. By removing more figs at one visit, hornbills required more time to feed. Bulbuls stayed longer when feeding on the *F. racemosa* figs (mean = 105 seconds) than on the smaller fig trees (*F. montana* and *F. ischnopoda*; mean = 30 seconds). When feeding on smaller trees, the bulbuls swallowed whole figs and flew away from the trees. They could not do this when feeding on the large figs of *F. racemosa*, where the bulbuls searched for ripe figs, pecked and broke them down to smaller parts before swallowing them. Thus, bulbuls required more time to process the figs.

The small mammals spent longer in the trees than the birds, but the diurnal squirrel had shorter visiting times than the nocturnal rat. Smell is believed to be more important for attracting mammals than birds (Nakabayashi et al., 2016) and smellier fruits are more attractive to them (Borges et al., 2008). It was observed that the squirrel and rat always sniffed at the figs before choosing which to remove and eat. Sniffing may require more time to find ripe figs than the visual searching used by birds, and the mammals may be less nervous of attack by predators.

Frugivores visited the fig trees at different times during the day and night. Frugivorous birds are almost exclusively diurnal. The frequency of bird visits to the fig trees in the morning and afternoon was similar, but in other studies, it was found that birds are more active around *F. caulocarpa* trees in early morning as more new ripe figs are available at this time (Sreekar et al., 2010). The squirrels tended to visit in the afternoon, especially in the late afternoon before dusk. This high feeding intensity in late afternoon is similar to that of Red squirrels (*Sciurus vulgaris*) in September to October (Degn, 1974). The squirrel is less active during the middle of the day because it avoids the mid day temperature peak (Thompson, 1977). Also, the squirrel may need to maintain food in their stomach overnight (Thompson, 1977).

In conclusion, many of the crops produced by the small dioecious fig tree species were not visited at all by frugivores and fig removal rates were very low. Many of the uneaten figs in these riparian habitats were likely to fall down to the water and could be potentially aided by abiotic dispersal or dispersal by fish. Figs of the large monoecious *F. racemosa* were more frequently visited by frugivores, but many of its figs also remained uneaten and could enter the water. The trees attracted different species of vertebrates to their figs, but the diversity of dispersal agents was low. The frugivores showed different feeding behaviours which could affect their effectiveness as seed dispersers and the mammalian visitors are likely to be mainly seed predators.

Chapter 4 The effect of feeding and gut passage on seed survival and germination of *Ficus montana* when eaten by two cyprinid fish species, the Blue mahseer (*Neolissochilus stracheyi*) and the Red-tailed tinfoil (*Babonymus altus*)

4.1 Abstract

Frugivorous animals play an important role as seed dispersers for plant species in different ecosystems across the globe. The majority of seed dispersal research focuses on birds or mammals and aquatic animals like fish are rarely investigated. Many *Ficus* spp. (Moraceae) are riparian species that grow along the streams of South East Asia. Many ripe figs fall directly into the water, where they can be transported downstream. Minnows and carp (Cyprinidae) are common in many riverine systems in Thailand, where they consume plant and animal food. Two common cyprinid fish species in western Thailand, Blue mahseer (*Neolissochilus stracheyi*) and Red-tailed tinfoil, *Babonymus altus*, were seen to feed on figs that fell into the water. The former is found in fast-flowing streams and the later is more typical of larger, slower-flowing rivers. Fallen figs landing near shoals of both species were grabbed within seconds. The role of two fish species in the dispersal of seeds of the riparian fig tree (*Ficus montana*) were investigated. Seeds were retained in the digestive system for six to ten hours (Blue mahseer) and seven to ten hours (Red-tailed tinfoil). Most of the ingested seeds were destroyed and seed retrieval rates did not differ between fishes of different sizes and species. Intact seeds that survived gut passage had lower germination success but germinated faster than

control seeds. The results indicate that both fish species are mainly seed predators for this fig tree species but are also capable of dispersing some seeds upstream.

4.2 Introduction

The seed dispersal of tropical plants is mostly assisted by terrestrial vertebrates such as birds and mammals (e.g. Howe & Wesley, 1986; Kitamura et al., 2002; Corlett, 2002) and fish, amphibians and reptiles are less often considered as potential seed dispersal agents. However, fish may play an important role as seed dispersers in freshwater aquatic environments (Pollux et al., 2006). Based on the stomach contents of frugivorous fish and the results of field investigations, it can be concluded that fish feed on numerous plant species and that the number of seeds dispersed can vary according to fish species, season and geographical area (Kubitzki & Ziburski, 1994; Correa et al., 2007; Galetti et al., 2008). In particular, fish are widely reported as seed dispersal agents of riparian plants in the Neotropics (Gottsberger, 1978; Goulding, 1983; 1993; Kubitzki & Ziburski, 1994; de Souza-Stevaux et al., 1994; Galetti et al., 2008), but seem to be less significant as seed dispersal agents in the Palaeotropics (see Baird, 2007; Davis et al., 2010; Horn et al., 2011). Among riparian plant species, where any seeds that arrive in the water will be likely to be carried downstream, any up-stream transport of seeds by fish could be particularly important (Horn, 1997).

Barbs, minnows, and carp (Family Cyprinidae) are widespread and sometimes abundant constituents of river systems in Thailand (Beamish et al., 2006). Gut analysis of cyprinid fishes has revealed that plant materials, including leaves and seeds, can be a major part of their diet. Seeds from numerous plant species can be found in the guts of a single fish (Baird, 2007; Kulabtong et al., 2011). This suggests that cyprinid fishes could act as significant seed dispersal agents for several riparian plant species in tropical Asia. Although the quantity of seeds dispersed by fishes can be inferred from the number of seeds found in their digestive system, the quality of their dispersal depends on how they treat the seeds, and this is largely unknown in this region.

Fig trees (*Ficus* spp.) are known to interact with fish by acting as a food source (Ridley, 1930; de Souza-Stevaux et al., 1994; Horn, 1997; Baird, 2007). Unlike birds and mammals, fishes are considered as secondary seed dispersers as they cannot remove figs directly from the trees and can only feed on fallen figs floating on the water. Dispersal by water and fish could be important for riparian fig trees as these trees may rarely interact with terrestrial frugivores and most ripe female figs are likely to fall into the water or onto the ground (CHAPTER 3). Although figs are included in the diet of Asian fishes, the fate of fig seeds after passing through frugivorous fish guts is yet to be investigated.

The main objectives of this chapter are to (i) assess the annual pattern of riparian figs falling into the water body and how this relates to rainfall; (ii) assess shoal sizes of the common cyprinid fish, the Blue mahseer (*Neolissochilus stracheyi*), in two riparian systems in western Thailand; (iii) investigate the responses of Blue mahseer to fallen figs; and (iv) examine the effect on germination of *Ficus montana* seeds being ingested by Blue mahseer and a second common cyprinid fish species (the Red-tailed tinfoil, *Babonymus altus*). Both species had been observed feeding on figs that landed in the water.

4.3 Methods

4.3.1 Study species

The Blue mahseer (*Neolissochilus stracheyi*) is a member of the Cyprinidae family, which also includes minnows and carp. It is distributed across South East Asia, including India, Myanmar, Thailand, Laos PDR, Cambodia, and Southern Vietnam (Chaudhry, 2010; Hoang et al., 2015). The adult fish can grow to 60 cm in body length (Baird et al., 1999). *N. stracheyi* are often found living together in shoals of 20 to 30 individuals (Fig 4.1) in shallow flowing streams and often live with other cyprinids, such as *Poropuntius* spp. (Hoang et al., 2015).

The breeding biology of *N. stracheyi* is still relatively unknown although observations have been made in the Krong No River, Vietnam (Hoang et al., 2015). Adult individuals migrate to nutrient rich pools full of plant debris at the beginning of the rainy season (June/July) to aid their reproductive organ development (Hoang et al., 2015). Juvenile fish were found in the rainy season which is comparable with the closely related mahseers of the genus *Tor* in peninsular Malaysia where juveniles are also abundant in the rainy season (Hoang et al., 2015). In controlled aqua culture systems, the female fish can spawn eggs several times in one year (De Silva et al., 2004).

The Blue mahseer is an omnivorous fish that feeds on arthropods and plant material falling into water bodies and is also a detritus feeder (Rainboth, 1996). In Kanchanaburi, a big population with numerous shoals is present in riparian areas such as the Erawan waterfall, the Huey Mae Khamin waterfall, and streams in Tha

Thung Na. The Blue mahseer is commonly found in the stream along the riparian forest of western Thailand (Dumsrisuk, Y., pers. comm.).

Red-tailed tinfoil (*Barbonymus altus*, Cyprinidae) is distributed across several Southeast Asian river basins and can be found in the Maeklong river, Southeast Thailand (Vidthayanon et al., 1997), in the Srinakarind dam, and Kwai Yai river in Kanchanaburi (Chutmongkonkul, unpublished). The body length of adult fish can range from 15 – 25 cm. (Rainboth, 1996; Satrawaha & Pilasamorn, 2009). This fish species is found in medium to large river systems in shoals ranging from 10 to over 100 individuals (Fig 4.2). It is an omnivorous fish and has adapted to feed on organic matter disposed of humans along rivers (Rainboth, 1996). Not much is known regarding the reproductive biology of this fish. It has been reported that the juvenile fishes can be found in floodplain forests and then they migrate to large rivers as adults (Rainboth, 1996). Red-tailed tinfoils are often eaten by humans and are kept as ornamental fish (Rainboth, 1996).

Fig. 4.1. A Blue Mahseer (*Neolissochilus stracheyi*) shoal in the Erawan waterfall, Erawan National Park, Kanchanaburi, western Thailand.

Fig. 4.2. A Cyprinidae shoal including Red-tailed tinfoil (*Barbonymus altus*) in the Kwai Yai river, Kanchanaburi, western Thailand.

4.3.2 Shoal sizes of *Neolissochilus stracheyi* in natural habitats and responses of the fish to fallen figs

The shoal sizes of *N. stracheyi* were recorded by direct counting at two major sites in Kanchanaburi province, western Thailand between 18 and 23 February 2016. The first study site was the Erawan waterfall in Erawan National Park (14° 22'N/99° 08'E). The waterfall is connected directly to the Kwai Yai river and the accessible part was 3 km in length. It includes a stretch of moderately flowing water and seven separate falls. Limestone was found in this waterfall and dissolved Ca^{2+} was recognised by the calcareous covering of plant sediment found in the pools. Several riparian fig trees, including *F. montana, F. oligodon*, *F. racemosa*, *F. ischnopoda*, and *F. squamosa* are found in this riparian system.

The second study site was the Kratengjeng waterfall in Khaolaem National Park (15°02'N/98°58'E). This riparian system is approximately 6 km from the top of the watershed. It is part of the Kwai Noi river and the water flows directly to the Vajiralongkorn Dam in the west of the park. The major riparian fig trees found in this site are *F. oligodon* and *F. montana*. All *N. stracheyi* individuals in each pool were counted within a 10 m stretch of the stream's bank. The mature and sub-adult fish were defined by the dark blue colour of their fins and their large body sizes (often longer than 10 cm in adults, but lower than 10 cm in sub-adults). However, the adult and sub-adult individuals were grouped together as the counting was based on estimation. Juvenile fish was defined by the light blue colour in their fins and their small body sizes (often shorter than 5 cm). All shoals were mapped and counted along both riparian systems and the total number of fish individuals and the numbers in each shoal were recorded.

The largest shoals of *N. stracheyi* in each park were then observed between 20-23 March 2016 and 9-11 April 2016 at Erawan and Kratengjeng respectively. Fifteen mature figs of each of four local riparian fig tree species, *Ficus racemosa*, *F. oligodon*, *F. ischnopoda*, and *F. montana*, were provided to the fishes at Erawan, and they were provided with *F. oligodon* and *F. montana* figs at Kratengjeng. Whole figs were thrown in to the water and feeding behaviours were observed. The size of the figs was 1 cm (*F. montana*), 1.5 – 2 cm (*F. ischnopoda*) and 4 – 6 cm (*F. oligodon* and *F. racemosa*). *F. racemosa* is monoecious the others are dioecious, and only mature female figs (the ones that contain seeds) were used. The time the fish took to respond after throwing each fig into the water was recorded to the nearest second. The feeding behaviour of the fishes was also recorded, in particular whether the fishes swallowed the figs whole or first nibbled on them.

4.3.3 Fig fall destinations for four different riparian *Ficus* species

The sample sites and methods were the same as in the CHAPTER 2. In this study, only the female fig trees were chosen for further analysis as they contained seeds. During each visit all the figs of *F. racemosa* and female *F. oligodon*, *F. ischnopoda*, and *F. montana* were counted and separated into three categories: those that would fall directly into the water, figs that would fall on the ground within 1 m of the water and would often roll in the water, and figs that that would fall on the ground more than 1 m from the water. *F. racemosa* produced large fig crops of more than 1,000 fig/crops and the numbers of figs in each category were estimated as in the CHAPTER 2.

4.3.4 Feeding trials and seed germination

F. montana seeds were collected from a single female individual at the Kratengjeng waterfall (98° 36’ 29.99” E/15° 02’ 00.31” N) at most three days prior to the feeding trials. This female individual produced large fig crops (20-30 figs/crop) throughout the year and ripe female figs could be collected almost every month. All the collected *F. montana* figs were cleaned and the seeds were removed from the pulp by gently squeezing them in tap water and then dried.

Before conducting the experiment, the use of captive animals for scientific research was approved under the license issued by the Institute of Animals for Scientific Purpose Development, National Research Council of Thailand (License number: U1-04986-2559). Live fishes were bought at local aquarium shops in Nakhonpathom and Kanchanaburi Provinces, Thailand as they are used as food or ornamentals. The Blue mahseer (*N. stracheyi*) and Red-tailed tinfoil (*B. altus*) individuals were measured from the tip of the nose to the tip of the tail using measuring tape and separated into three size classes: 10-15 cm, 15-20 cm, and > 20 cm. The fishes were put individually into 20x50x25 cm^3 glass aquaria with hang-on water filter systems (a 45W water pump connecting to a mixture of filter media, including fine filter fibre, bioballs, and charcoal) and aeration was provided to maintain a suitable oxygen level for 24 hours under both light (0600h-1759h) and dark (1800h-0559h) conditions, which were created using a 40W white light with an automatic timer switch.

The water temperature of all the aquaria fluctuated between 25 and 27 degrees Celsius. The fish were fed by synthetic pellet food (CP 9932^{TM};

Herbivorous Fish Feeds; 15.5% of protein) twice a day (0800h and 1600h) for around 15 – 20 days to habituate them to the aquaria. For twenty-four hours before conducting the experiments the fish were not fed, thus increasing the possibility of feeding success when performing the trials (Fig 4.3). Twenty fresh *F. montana* seeds were mixed with a 3 mm diameter piece of dough made from corn and bread flour in a 1:1 ratio. The dough was then placed on the surface of the water of each aquarium for the fish to eat.

All the fish fed on the dough pellets immediately after they were thrown into the aquaria. The aquaria were monitored closely for the first thirty minutes after feeding and all spat out seeds were removed and counted. The fish was then monitored every twenty minutes for ten hours to observe any faeces on the bottom of the aquaria. Gut passage time was also recorded after detecting the faeces on the aquaria floor or when possible. After 10 hours of observation, the fish were retained in the experimental aquariums for 24 hours to ensure that all the ingested seeds had been defaecated.

Fish excrement was collected using a water siphon to investigate seed survival. Seeds were sorted from the fish faeces and seed retrieval numbers were counted. After that all retrieved seeds were germinated separately on moist filter paper in Petri dishes. After finishing the experiment all the fishes were transferred to a 4 m^3 concrete aquarium tank and cared for as pets by C. Kerdkaew.

To compare germination of ingested seed and non-ingested seeds, five control seed germination sets were prepared consisting of 100 *F. montana* seeds each. Controlled experimental seeds were prepared from several ripe female figs of the same crops. The seeds were mixed with dough pellets made from the same mixture used in the experiment. The dough pellets were then soaked in water from the fish tanks for 24 hours. The ingested and non-ingested seeds, including the control seeds and spat out seeds, were sown separately on filter paper in Petri dishes. The Petri dishes were labelled and kept at room temperature (25-35ºC) with a light cycle of 12 hours in a light condition (0600h-1759h) and 12 hours in a dark condition (1800h-0559h), which were created using a 40W light bulb with a timer switch.

The Petri dishes were watered with distilled water and observed every three days for 30 days. The germination of seeds was recorded when the two-cotyledon phase of the seedlings was clear of the surrounding seed. All the germinated seeds were removed immediately from the Petri dishes. Seed germination numbers were recorded for all Petri dishes and the first day of seed germination was also recorded. The median length of seed germination (MLG) was also recorded by calculating the day that 50% of seeds germinated.

4.3.5 Data analysis

A generalised linear model (GLM) was used to test the fig fall patterns in relation to the monthly rainfall amount (Quasi-binomial error), the different shoal sizes of Blue mahseers from two riparian sites (negative binomial error), the time that fish responded to fallen figs (Gamma error) and the proportion of *F. montana* seeds retrieved from different fish species and size classes (Quasi-binomial error). The first day of seed germination, the MLG (binomial error), and the seed germination proportion (Quasi-binomial error) at day 30 were also compared with the control germination set and all fish size classes were combined within the same fish species (binomial error). The error distribution (Poisson or binomial) was selected according to the criteria dictated by the data and the over-dispersion of data was examined. If over-dispersion occurred, a log or square root transformation was applied to the data, and the Chi-square terms were reported. If the data could not be transformed, other error distributions for each type of data were considered, e.g. Quasi-Poisson and Quasi-binomial, and F values were reported instead of the Chi square value. All statistic tests were performed in R 3.4.3.

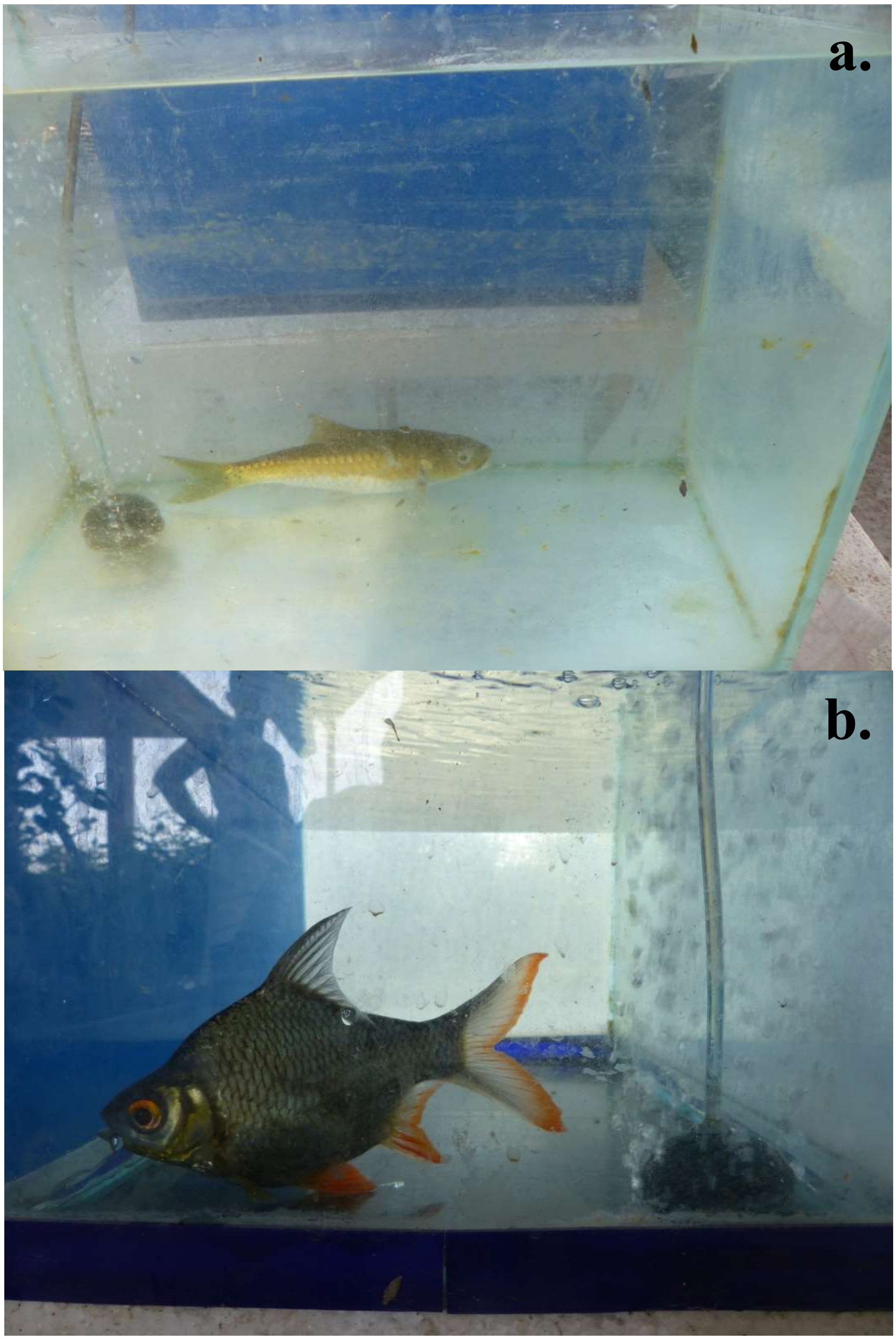

Fig. 4.3. (a) a Blue mahseer (*N. stracheyi*) and (b) a Red-tailed tinfoil (*B. altus*) housed in glass aquaria during the experiment.

4.4 Results

4.4.1 Seasonal fig fall variation in four riparian fig tree species

In *F. racemosa* and female *F. oligodon*, more than 50% of any figs that fell vertically from the trees would have landed in the water or within 1 m of the water during almost every month of the year. This percentage increased between August and October (Figs. 4.4 and 4.5). Most female *F. ischnopoda* figs would also have fallen into the water or within 1 m of the water throughout the year, except in March and April (Fig 4.6). *F. montana* female figs would have fallen mainly on the ground in January and between April and mid-May, but during the rest of the year, a majority would have fallen into the water or close to it (Fig 4.7). Therefore, there was the potential for large numbers of figs of all four species to be transported by water movement.

The likelihood of figs falling close to or in the water had a positive relationship with rainfall in the same month in *F. racemosa* (GLM : $F_{(1, 11)} = 26.22$, $P < 0.001$) and *F. oligodon* (GLM: $F_{(1, 11)} = 4.41$, $P < 0.05$). Figure 5.8 illustrates annual rainfall in the year of study. In contrast, the proportion of figs likely to end up in the water was not linked to rainfall (*F. ischnopoda*: GLM: $F_{(1, 11)} = 1.41$, $P = 0.25$, *F. montana*: GLM: $F_{(1, 11)} = 3.54$, $P = 0.07$).

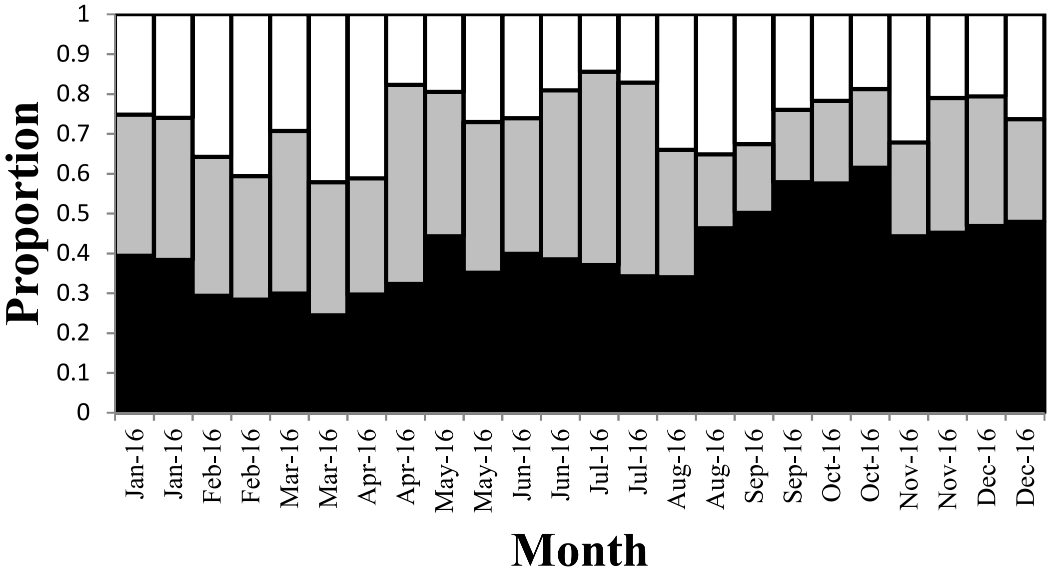

Fig. 4.4. The fig fall of-*F. racemosa* trees in 2016: water (black bars), < 1m (grey bars), > 1m (white bars).

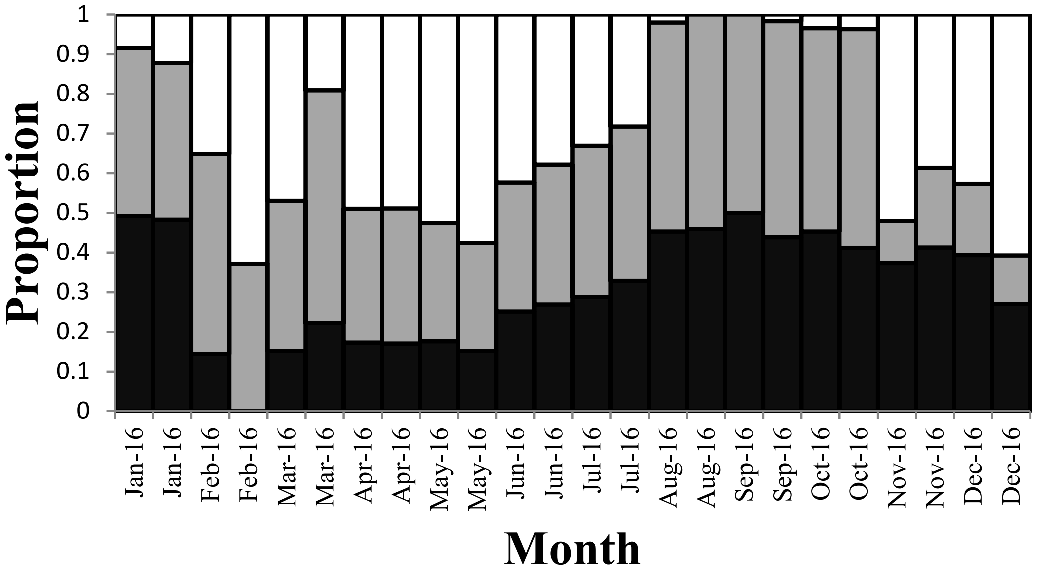

Fig. 4.5. The fig fall of female-*F. oligodon* trees in 2016: water (black bars), < 1m (grey bars), > 1m (white bars).

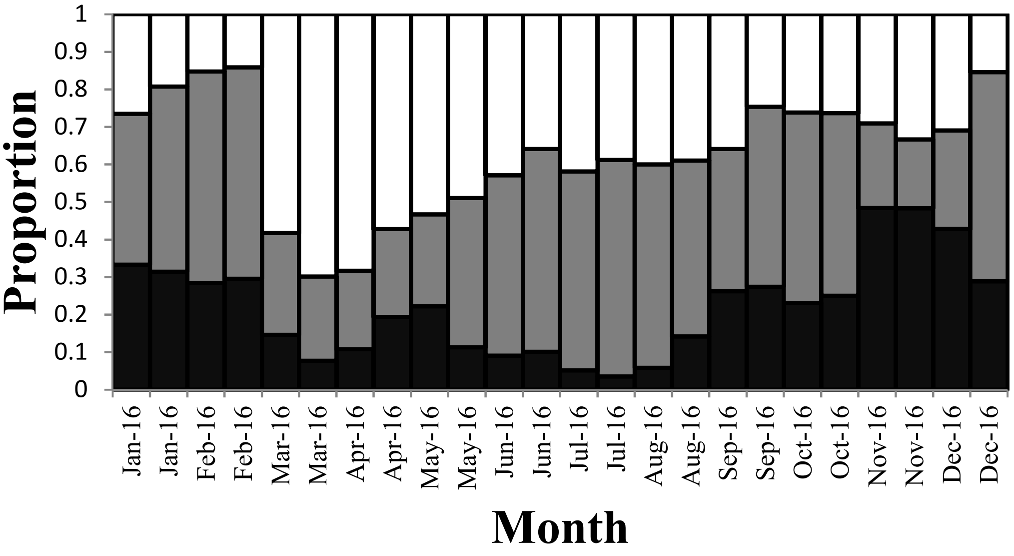

Fig. 4.6. The fig fall of female-*F. ischnopoda* trees in 2016: water (black bars), < 1m (grey bars), > 1m (white bars).

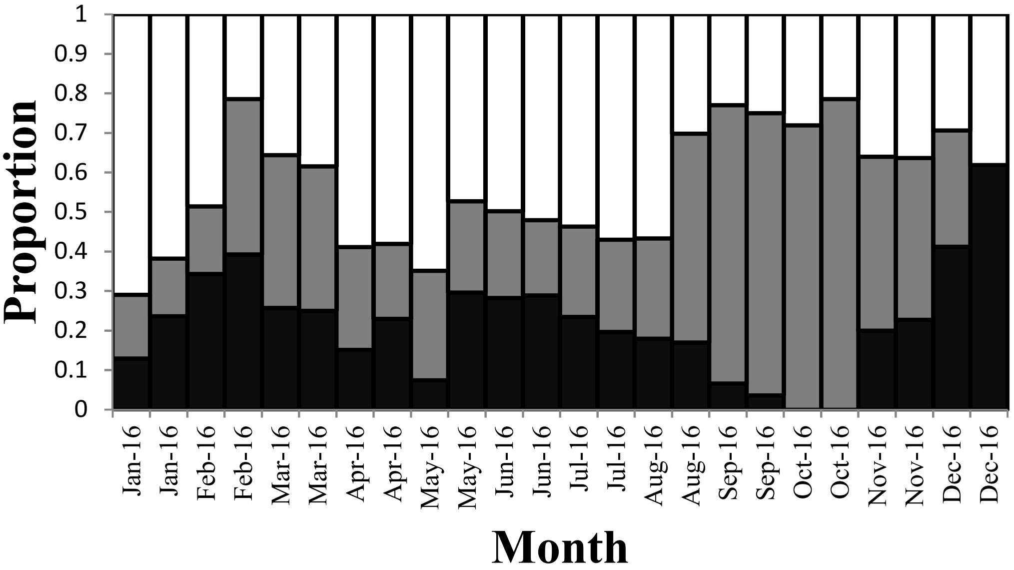

Fig. 4.7. The fig fall of female-*F. montana* trees in 2016: water (black bars), < 1m (grey bars), > 1m (white bars).

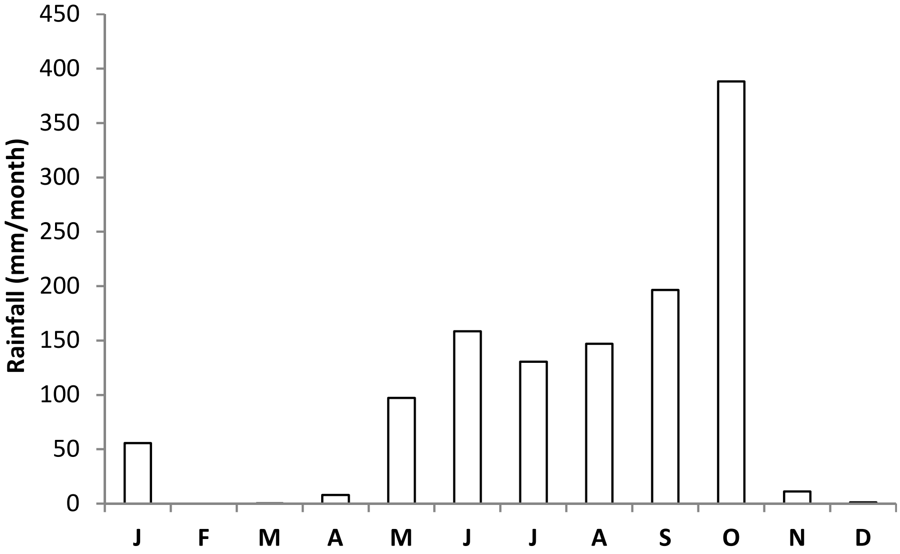

Fig. 4.8. Monthly rainfall (mm) at the Kanchanaburi Meteorological Centre from January to December 2016.

4.4.2 Blue mahseer responses to fallen figs in the water

In total, thirty-five shoals of Blue mahseer (*N. stracheyi*) were recorded at Erawan and twelve at Kratengjeng. The shoal sizes (mean ± SE) were 66 ± 9.43 (range: 12-318) and 26.92 ± 4.74 (range: 6-62) in the Erawan and Kratengjeng sites, respectively. The shoal sizes were significantly different between the two sites (GLM: $F_{(1,\ 46)} = 7.45$, $P < 0.01$). The densities of fish were at least 285 individuals/100 m and 22 individuals/100 m in the Erawan and Kratengjeng sites, respectively. Most individuals in both sites were the juveniles.

Female figs of the four species that were thrown into the water floated initially but were rapidly taken under the water by the fish (QR 4.1). The large individuals responded to all the thrown figs and swallowed whole floating figs, but the smaller individuals had limited gape widths and nibbled on the figs within five seconds of them being available (Table 4.1). There was no significant difference

QR 4.1

QR 4.2

between the speed of the fishes' responses to the figs in the water between sites and fig species (GLM, P > 0.05, Table 4.2). This suggests that the fishes will attempt to feed on the figs of a wide range of species, including other fruits, if they fall into the water (QR 4.2).

Table 4.1. The mean speed of the response by Blue mahseer (*N. stracheyi*) to the figs thrown into the water at Erawan waterfall and Kratengjeng.

Site	Shoal	Fig species	Feed on fallen figs (number)	Feeding (%)	Mean time response (second)
Erawan	1	*F. montana*	15	100.0	5.3 ± 0.2 [4-8]
	2	*F. montana*	15	100.0	5.9 ± 0.3 [4-8]
	1	*F. ischnopoda*	15	100.0	5.1 ± 0.6 [3-11]
	2	*F. ischnopoda*	15	100.0	5.5 ± 0.4 [3-9]
	1	*F. oligodon*	15	100.0	5.2 ± 0.3 [3-7]
	2	*F. oligodon*	15	100.0	5.2 ± 0.3 [4-9]
	1	*F. racemosa*	15	100.0	5.2 ± 0.3 [4-7]
	2	*F. racemosa*	15	100.0	5.2 ± 0.5 [3-8]
Kratengjeng	1	*F. montana*	15	100.0	5.6 ± 0.3 [4-8]
	2	*F. montana*	15	100.0	5.3 ± 0.2 [4-8]
	1	*F. oligodon*	15	100.0	5.1 ± 0.2 [4-7]
	2	*F. oligodon*	15	100.0	5.1 ± 0.3 [3-6]

Table 4.2. Differences in the speed of response of Blue mahseer (*N. stracheyi*) to figs of different species at Erawan and Kratengjeng (GLM).

	N (figs)	Degrees of Freedom	F-Value	P
Site	178	1	0.0919	0.7621
Shoal	177	1	0.3039	0.5822
Fig Species	174	3	0.9960	0.3962
Site*Shoal	173	1	1.3674	0.2439
Site*Fig Species	172	1	0.0000	1.0000
Shoal*Fig Species	169	3	0.1632	0.9210
Site*Shoal*Fig Species	168	1	1.1029	0.2951

4.4.3 Effect of feeding by Blue mahseer (*N. stracheyi*) and Red-tailed tinfoil (*B. altus*) on *F. montana* seed survival and germination

4.4.3.1 Seed handling

The Blue mahseer used in the experiments (N = 37) varied in length between 10.4 and 33.5 cms. They mostly swallowed whole pellets, indicating a generally 100% seed ingestion rate, but with the small-sized individuals there were two trials where seeds were spat out two minutes after the pellets were eaten (Table 4.3). Seed passage times could not be precisely recorded, but seeds and debris were found from six to ten hours after feeding, which suggests a range of gut passage time for all fish size classes of six to ten hours. It was clear that most of the seeds that passed through the fish guts were badly damaged or destroyed, regardless of fish size, and seed retrieval proportions were lower than 0.1 for all three size categories (Table 4.3). There was no significant difference in seed retrieval success between fish size categories (GLM: $F_{(2, 36)} = 0.5689$, $P = 0.571$).

The Red-tailed tinfoil used in the experiments (N = 15) varied in length between 10.6 and 23.0 cms. They swallowed all the dough pellets without any spitting behaviour. The gut passage time could not be precisely recorded, but all the seeds were defecated within seven to ten hours after ingestion based on the seeds and debris that were detected within this period. Similar to the Blue mahseer, only small numbers of seeds were retrieved after being defecated by the fishes (Table 4.3). There was no significant difference in seed retrieval success between size categories (GLM: $F_{(2, 14)} = 0.6278$, $P = 0.550$).

When comparing fish species and sizes, no statistical differences of seed retrieval were detected (GLM: between fish species: $F_{(1, 51)} = 1.3539$, $P = 0.251$; among fish sizes: $F_{(2, 51)} = 0.4152$, $P = 0.663$; interaction between fish species and sizes: $F_{(2, 51)} = 0.7638$, $P = 0.472$).

Table 4.3. ***F. montana*** **seed passage, spitting, and retrieval rates when eaten by** ***N. stracheyi*** **and** ***B. Altus*** **of varying size. Means ± SE are provided and [ranges].**

Fish species (length)	Body length (cm)	N (fish)	Seed passage rate	Seed spitting rate	Seed retrieval rate
N. stracheyi (10-15 cm)	11.71 ± 0.98 [10.4-14.0]	15	0.97 ± 0.02 [0.70-1.00]	0.03 ± 0.02 [0-0.30]	0.08 ± 0.02 [0-0.21]
N. stracheyi (15-20 cm)	16.70 ± 1.08 [15.2-19.0]	15	1	0	0.05 ± 0.02 [0-0.30]
N. stracheyi (>20 cm)	29.47 ± 1.99 [27-33.5]	7	1	0	0.09 ± 0.05 [0-0.35]
B. altus (10-15 cm)	12.86 ± 1.38 [10.6-14.0]	5	1	0	0.06 ± 0.05 [0-0.15]
B. altus (15-20 cm)	16.47 ± 1.19 [15.2-18.0]	6	1	0	0.12 ± 0.06 [0-0.35]
B. altus (>20 cm)	22.38 ± 0.51 [21.8-23.0]	4	1	0	0.14 ± 0.05 [0-0.25]

4.4.3.2 Seed germination

In total there were 32 germination trials of *F. montana* seeds involving eight treatments, including the controls (Table 4.4). Small numbers of seeds were used in the germination trials involving both fish species (less than five seeds per trial) due to low seed retrieval rates from the faeces (Table 4.3). Over half the seeds that were defaecated by the fish germinated (Table 4.4). Among the seeds that appeared intact after gut passage there were no significant differences in proportion of seed germination success between the two fish species and three size categories (GLM: between fish species: $F_{(1, 24)} = 0.024$, $P = 0.843$; among fish sizes: $F_{(2, 24)} = 0.017$, $P = 0.986$; interaction between fish species and sizes: $F_{(2, 24)} = 2.37$, $P = 0.163$). Overall, the germination probability for the control seeds was significantly higher than the germination probability of those treated by the guts of both fish species (Table 4.4, Fig 4.9) (GLM: control v. *N. stracheyi* (all size classes): $F_{(1, 31)} = 11.48$, $P < 0.0001$; control v. *B. altus* (all size classes): $F_{(1, 31)} = 8.77$, $P < 0.01$). The first day of seed germination did not differ significantly between fish species and sizes (GLM: between fish species: $\chi^2 = 0.09$, df = 1, $P = 0.467$; among fish sizes: $\chi^2 = 0.33$, df = 2, $P = 0.385$; interaction between fish species and sizes: $\chi^2 = 0.26$, df = 1, $P = 0.465$). Seeds that had survived gut passage germinated as early as three days after defaecation, whereas the first control seeds germinated after five to six days.

The first day of seed germination was significantly shorter for seeds eaten by the two fish species (GLM: control v. *N. stracheyi* (all size classes): $\chi^2 = 2.76$, df =1, $P < 0.05$; control v. *B. altus* (all size classes): $\chi^2 = 1.07$, df =1, $P < 0.05$). The median time to germination for all treatments was shorter than for the control seeds (Table 4.4, Fig 4.9) (GLM: control v. *N. stracheyi* (all size classes combined): $\chi^2 =$

5.53, df =1, $P < 0.001$; control v. *B. altus* (all size classes): $\chi^2 = 0.437$, df =1, $P < 0.05$). This suggests that the seeds that survived gut passage through both species had reduced seed germination times. The median time to germination did not differ significantly between fish species and size classes (GLM: between fish species: $\chi^2 = 0.04$, df = 1, $P = 0.618$; among fish sizes: $\chi^2 = 0.09$, df = 2, $P = 0.753$; interaction between fish species and sizes: $\chi^2 = 0.40$, df = 1, $P = 0.301$).

Table 4.4. *F. montana* germination trials with seeds eaten by two fish species of varying size. Median time to germination = MLG. Means ± SE are provided and [ranges]

Treatments	N (Trials)	Seed numbers	First day of germination	MLG (days)	Germination proportion [range]
Control	5	100	5.8 ± 0.2 [5-6]	11.2 ± 0.49 [10-12]	0.89 ± 0.04 [0.84-0.94]
N. stracheyi (Spat out seeds)	2	5 ± 1.41 [4-6]	3	3	1
N. stracheyi (10-15 cm)	9	2.56 ± 0.88 [1-4]	4 ± 1.5 [3-6]	4.33 ± 1.58 [3-6]	0.70 ± 0.24 [0.33-1]
N. stracheyi (15-20 cm)	4	3.50 ± 1.91 [1-4]	5.25 ± 4.25 [3-12]	5.25 ± 4.25 [3-12]	0.69 ± 0.24 [0.5-1]
N. stracheyi (>20 cm)	3	4 ± 2.65 [2-7]	3	3	0.63 ± 0.11 [0.5-0.71]
B. altus (10-15 cm)	3	2 ± 1 [1-3]	4 ± 1.73 [3-6]	4 ± 1.73 [3-6]	0.83 ± 0.29 [0.5-1]
B. altus (15-20 cm)	3	4.67 ± 2.52 [2-7]	5 ± 1.73 [3-6]	5 ± 1.73 [3-6]	0.56 ± 0.05 [0.5-0.6]
B. altus (>20 cm)	3	3.67 ± 1.54 [3-5]	4.33 ± 1.15 [3-5]	4.33 ± 1.15 [3-5]	0.71 ± 0.08 [0.67-0.8]

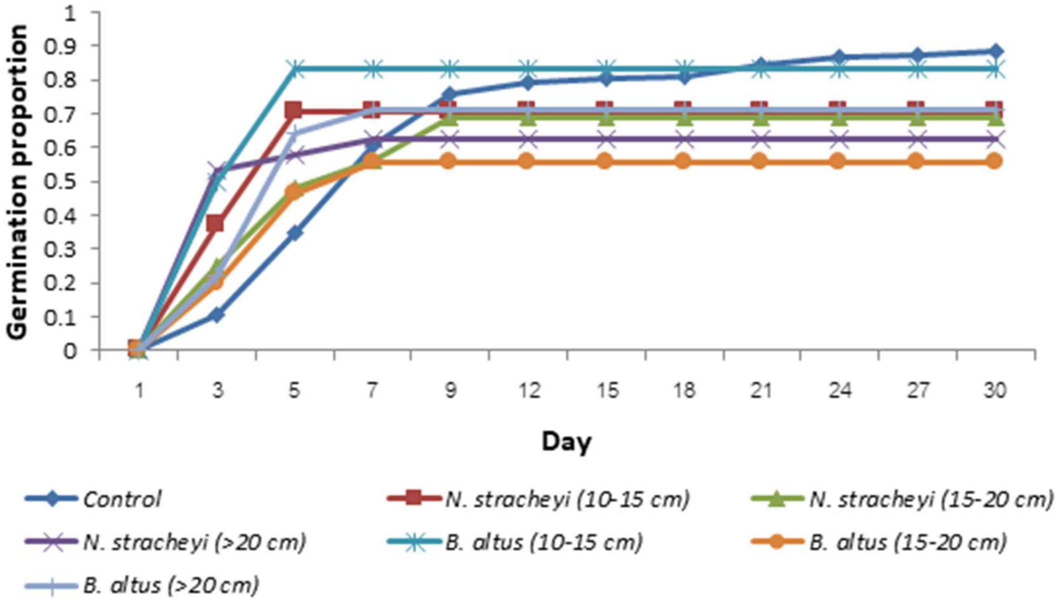

Fig. 4.9. Probability curves of seed germination over time for the trials of *F. montana* seeds.

4.5 Discussion

Many mature figs of all four riparian fig tree species are not dispersed by frugivores and eventually fall from the trees (CHAPTER 3). Many of these figs are produced above water, or close to it, and when they fall are potentially dispersed by water movements or frugivorous fish in the water (Fig 4.10). Figs are also buoyant and this might be an adaptation for water dispersal and ichthyochorous seed dispersal (Compton, S. G., pers. comm.). Figs are reported as an important food item for South East Asian fishes (Baird, 2007). More clear-cut adaptations for dispersal by water are present in some specialist riparian species such as *F. squamosa* in SE Asia, for example, in riparian forest of Northern Thailand (Berg & Corner, 2005; Pothasin et al., 2016).

In the case of the larger fig tree species (*F. oligodon* and *F. racemosa*), the likelihood of falling into the water varies seasonally and is positively associated with the amount of rainfall. The number of figs produced by the trees is also high during the rainy season (CHAPTER 2), which increases further the number of figs likely to reach the water. This pattern is not clear for the smaller fig trees *(F. ischnopoda* and *F. montana*), as these small shrubby species often grow on rocks in the water or on the stream banks, which means the figs are less likely to be located above the water.

Shoals of the Blue mahseer were larger at Erawan than Kratengjeng. It is recognised that a major cause of declining fish populations is commercial and recreational fishing (Cooke & Cowx, 2004) and field site observations found that (illegal) fishing activities were taking place at Kratengjeng (Fig 4.11). Conversely, tourists feeding fish can also alter their populations and behaviours (Hémery & McClanahan, 2005; Milazzo et al., 2005) and recreational fish feeding by tourists has been reported at Erawan (Dumsrisuk, Y., pers. comm.). In 2016, 691,721 tourists visited the Erawan waterfalls, but only 35,295 tourists visited the Khaolaem National Park, which is where the Kratengjeng waterfall is located (Department of National Parks, Wildlife and Plant Conservation, 2017). This large number of tourists visiting the Erawan waterfall increases the chance that fish will be fed there and may have allowed their populations to be unnaturally high.

At both sites the Blue mahseer responded immediately to the figs after they were thrown into the water. There is intense competition within the shoals and this forces the fish to grab any potential food items before they are taken by others. This suggests that all plant materials falling into the water are attractive and may be fed upon by the Blue mahseer. The smaller fish nibbled on the figs as they had limited gape sizes, but the bigger fish swallowed the figs whole. The figs of *F. montana* and *F. ischnopoda* were totally swallowed by the adult fishes, but sometime the larger figs of *F. oligodon* and *F. racemosa* were also nibbled into smaller pieces before swallowing those parts. A previous study reported that fallen *F. racemosa* figs were eaten by many fish species, especially Cyprinidae, along the Mekong River of Lao PDR and suggested that fig trees are one of the most important food sources for fishes (Baird, 2007). In Kanchanaburi town, figs of *F. microcarpa* falling into the River Kwai are very attractive to *B. altus* and large shoals containing hundreds of fish can gather beneath trees where figs are falling into the water (Compton, S. G., pers. comm.). As with *N. stracheyi* the fallen figs are taken within seconds.

Fig. 4.10. Fallen *F. racemosa* figs floating on the water at Phatad waterfall, Kanchanaburi, western Thailand.

Fig. 4.11. A poacher's fishing net found in the stream connected to the Kratengjeng waterfall, Kanchanaburi, western Thailand.

Multiple factors are known to influence seed survival when they pass through the guts of frugivores, including both the animal species involved and seed morphology (Traveset, 1998). The majority of the *F. montana* seeds were destroyed after being ingested by the two fish species, suggesting that these fishes play a largely seed predator role rather than a seed disperser role. More than 80% of the ingested *F. montana* seeds were also destroyed after passage through the digestive tract of Scissor-tailed rasbora (*Rasbora trilineata*, Cyprinidae), a species that has also been observed eating *F. montana* figs in Thailand streams (Kerdkaew T., unpublished). Two species of Cyprinidae fishes, *Tor tambroides* and *Leptobarbus hoeveni*, are similarly recognised as seed predators in the Mekong River, Lao PDR, but again some plant seeds are not destroyed in these fishes' digestive tracts (Baird, 2007). This suggests that Cyprinidae in SE Asian rivers may in general act as both seed predators and to lesser extent seed dispersers, especially for small-seeded plants like the genus *Ficus* (Baird, 2007).

Elsewhere, the common Eurasian carp (*Cyprinus carpio*, Cyprinidae) is also known to destroy almost all ingested seeds of the submerged macrophyte, *Najas marina* (Hydrocharitaceae) (Agami & Waisel, 1988). Species of the family Cyprinidae have pharyngeal teeth to crush ingested food (Boedeltje et al., 2015), which allows food to be masticated and is the likely cause of seed destruction. Other families of fish such as the characins (Characidae) in the Neotropics have grinding teeth, and they are also largely seed predators (Goulding, 1983). In contrast, some catfishes (Pangasiidae) in South East Asia have less developed teeth and most seeds ingested by these fishes are not destroyed (Baird, 2007).

Fish size could impact the seed dispersal of aquatic plants as different feeding behaviours can result in different seed handling. Fish characteristics, such as body weight and length and gape width have been correlated with the number of viable seeds in their guts (Galetti et al., 2008). For example, small-bodied catfishes (*Ictalurus punctatus*, Ictaluridae) show different fruit handling behaviour to larger adults when feeding on *Forestiera acuminate* (Oleaceae) fruits. The smaller fish consume the fruit pulp and ignore swallowing the seeds, whereas the larger fish which having wider gape width swallow the fruits whole, resulting that seeds ingested by smaller fishes may have low chance to disperse and are likely to deposit close to their sources because of spitting behaviours (Adams et al., 2007). Likewise, seeds of aquatic plants ingested by large *Colossoma macropomum* (Serrasalmidae) in the riparian forests of Northern Peru had higher viability, 1.89 times higher than the seeds consumed by the juvenile fishes, as these adult fishes swallow the seeds whole and also have higher gut volume which can be able to hold larger number of seeds, whereas the majority of the seeds ingested by the smaller fishes are masticated (Anderson et al., 2009). In contrast, larger carp (*C. carpio*) have a stronger bite than the smaller individuals, causing lower seed survival rates in the former, and individuals that are less than 15 cm in length are more likely to disperse viable seeds (Boedeltje et al., 2015). In this study, we found that seed retrieval and survival rates did not differ between size categories for both cyprinid fish species. However, as the largest fishes used in the experiment were only 33.5 cm (Blue mahseer) and 23 cm (Red-tailed tinfoil), it is possible that a difference in seed retrieval rates may have been detected if larger fish (> 40 cm) had been used.

It has been suggested that the hardness of a seed’s coat can affect its survival after it has been ingested by a fish, with the harder the seed, the more likely it is to survive (Agami & Waisel, 1988; Pollux et al., 2006; 2007). Agami & Waisel (1988) found that the hard seeds of aquatic plants (*N. marina*, Hydrocharitaceae) have a higher probability of seed retrieval after fish gut passage compared to softer seeds. Likewise, the seeds of *Sparganium emersum* (Typhaceae), a species with a hard seed coat, have a higher seed survival rate than those of *Sagittaria sagittifolia,* Alismataceae, (which has a softer seed coat) after being ingested by common carp, although the ingestion rate of harder seeds is also lower than for softer seeds (Pollux et al., 2006). The hardness of seeds appears to be a crucial factor for surviving digestion by common carp, whereas a mucilaginous covering only seems to be a minor factor affecting seed survival (Boedeltje et al., 2015). Elongated and hard seeds, light weight and an absence of a mucilaginous layer were found to be traits affecting seed survival after being ingested by tilapia (*Oreochromis mossambicus*, Cichlidae) (Boedeltje et al., 2015).

F. montana seeds had a low retrieval rate (< 20%) and high ingestion rate (> 90%). These results are similar to the survival and ingestion rates recorded for *S. sagittifolia* (Alismataceae) seeds eaten by the common carp (*C. carpio*) (Pollux et al., 2006). *F. montana* seeds passed through the Blue mahseer and Red-tailed tinfoil digestive tracts within 6 to 10 hours. This is similar to the amount of time seeds take to pass through the gut of the common carp (Pollux et al., 2007). This long digestion time allows the fish to be long-distance seed dispersers, and the maximum seed dispersal distance provided by the common carp was estimated to be up to 27 km (Pollux et al., 2007) and longer than 5 km in *Colossoma macropomum* (Characidae) (Anderson et al., 2011). However, a shorter seed dispersal range inferred from radiotelemetry data was reported for the Neotropical *Brycon guatemalensis* (Characidae), which only moves up to 1 km upstream over 1 – 2 weeks (Horn, 1997). The ranging behaviours of the Blue mahseer and Red-tailed tinfoil are still not known, but it is suggested that migratory movement could occur in cyprinids (Lucas & Baras, 2008). Therefore, these two cyprinid fish species could operate as long-distance seed dispersers for riparian plants.

Seeds moving through frugivore digestive tracts are treated mechanically and chemically and this can negatively or positively affect seed germination rates (Traveset, 1998). For example, the germination of aquatic plant seeds ingested by grass carp (*Ctenopharyngodon idella*, Cyprinidae) and tilapia (*Oreochromis* sp.) was found to be higher than control sets (Agami & Waisel, 1988), whereas germination rates of ingested *S. sagittifolia* (Alismataceae) seeds, which have soft seed coats, decreased by 47.3% compared to controls (Pollux et al., 2006). Although most of the ingested *F. montana* seeds were masticated after being eaten by the two fish species, the intact *F. montana* seeds retrieved from the faeces of both fish species germinated faster than the control seeds. Passing through the fish’s gut may break the dormancy of the *F. montana* seeds by scarifying their seed coats and removing a narrow layer of mucilage that surrounds them.

In summary, our results indicate that the two species of Cyprinidae fishes are mainly predators of fig seeds that fall into the water, but they can also disperse a small proportion of the seeds of these riparian trees in western Thailand. The fish therefore could be responsible for upstream movements of these plants species, whereas seeds in the water that are not eaten will mostly be carried downstream. Seeds that have passed through the fish germinated more rapidly, which may also be beneficial to the plants. Figs of the four *Ficus* species are also eaten by a wide range of terrestrial birds and mammals, which also provide dispersal services, but feeding by fish can complement their activities because the seeds may be more likely to be deposited at stream edges, in microsites that are suitable for plant establishment. This study is the first investigation into the seed dispersal role of fishes within western Thailand. Further investigation is needed to generalise the role of fish in the seed dispersal of riparian plants, for example, comparing other groups of plants and other groups of fish.

Chapter 5 Germination inhibition, not frugivore reward, is the likely function of the jelly that surrounds the seeds of *Ficus oligodon*

5.1 Abstract

Figs of several *Ficus* species produce jelly-like layers covering their seeds, but the roles of these structures in relation to seed dispersal and germination are still poorly known. Here, we examine possible functions of the extensive jelly-like substance that can fill the interior of female figs of *Ficus oligodon* and exude onto the fig surface. *F. oligodon* is a riparian species, distributed across SE Asia. In western Thailand a majority of its figs fall directly to the ground where they may enter adjacent streams. Ants visiting the figs fed on the fleshy pulp but not the jelly. This suggests that the jelly does not function as a reward for dispersal agents. Seeds with the surrounding jelly intact failed to germinate within three months when kept moistened with distilled water, but when the jelly was removed after three months most of the seeds germinated quickly. Germination rates among seeds with the jelly removed were far lower among seeds that were moistened with an extract of local soils. This confirms that the jelly inhibits germination and also provides protection from pathogens. It will have the effect of extending the time over which the figs germinate, making dispersal more extensive and less likely to occur beneath parent trees.

5.2 Introduction

The fleshy fruits of plants have evolved to facilitate dispersal of the seeds they contain by animals (Shanahan, 2000; Lomáscolo et al., 2010). They typically display visual and olfactory signals to attract suitable dispersers and provide nutritional rewards to encourage their return to eat further fruits (Janson, 1983; Lomáscolo et al., 2010; Nakabayashi et al., 2016). In tropical and sub-tropical regions, the fleshy compound fruits (figs) of fig trees (*Ficus* spp., Moraceae) are eaten by a wider range of species than any other plants (Shanahan et al., 2001). Reflecting the wide variety of dispersal agents favoured by different *Ficus* species, mature figs vary in diameter from less than 1 cm to over 10 cm, and can be located among the leaves, on leafless branches, on the trunk or even underground. After figs ripen, they usually consist of a large number of small seeds (each a fruit in the strict botanical sense) surrounded by a soft and colourful or scented exocarp, which attracts fruit-eating dispersers and also provides a nutritional reward. Based on the nutritional analysis of fresh *F. carica* figs, it is suggested that 100 g of fresh fig consists of 79-83% water, that it is rich in fibre (2.9 g) and sugars (16.26 g), and provides a good source of minerals, for example, potassium, calcium and iron (Vinson et al., 2005; USDA, 2014).

Pollination of fig trees depends on the entry of tiny fig wasps (Agaonidae) into the figs. They enter receptive figs to lay their eggs inside the flowers that line the figs' inner surfaces. Flowers that are pollinated but not oviposited into by the fig wasps can each produce a single seed. *Ficus* species with a monoecious breeding system have figs where fig wasp offspring develop side by side with the seeds, whereas in dioecious species figs on functionally male trees develop no seeds (and are not attractive to frugivores), whereas figs on female trees contain only seeds.

Mucilage occurs around the seed coats (pericarp) in plant species from at least 50 plant families throughout the world (Western, 2012). The production of mucilage by secretory cells has been studied in detail in *Arabidopsis thaliana* (Brassicaceae) (Western et al., 2000; Young et al., 2008). The mucilage is hydrophilic and can absorb water from the environment. It consists mainly of polysaccharide-like hemicelluloses and also pectins (Western, 2012). Based on studies on several plant species from arid areas, it is suggested that the mucilage layers may have multiple roles in plant survival and can also aid reproduction by promoting seed hydration, seed germination or seed dispersal (see Grubert, 1974; Ryding, 2001; Western, 2012). In figs, mucilage is commonly present in a thin layer around the seeds (Berg & Corner, 2005). One proposed function is to protect fig seeds from digestive enzymes during passage through the guts of dispersers such as fruit bats (Reiter, 2002). It has also been suggested that the exocarp of *F. microcarpa* contains lipid-rich compounds which could be attractive to ants (Kaufmann et al., 1991). Other functions revealed in other plants, such as promoting or inhibiting seed germination, and seed disperser attraction, have not been studied in *Ficus*.

A feature of some lineages of dioecious *Ficus* is that their figs become filled with liquid during the period when seeds and pollinator offspring are developing (Janzen, 1979). The liquid may have an antibiotic function, and although it is largely resorbed by the time that pollinator offspring emerge, it has generated specialized adaptations among the plants' associated pollinators that reduce the risk of drowning

(Rodriguez et al., 2017). Liquid is not resorbed inside female figs of a small number of Asian *Ficus* species, and when these figs mature they become filled with a mucilaginous jelly that fills the central cavity and can exude out onto the surface of the figs, via the ostiole (Fig. 5.1). Species where this jelly is produced by the pericarp include *F. awkeotsang* (Grubert, 1974), where it forms the basis of a small commercial drink industry in Taiwan (Huang et al., 1980), *F. oligodon* and *F. rosulata* (Compton, S. G., pers. comm.). The role of this jelly has not been examined, but its restriction to female figs suggests a role in seed dispersal or post-dispersal germination.

F. oligodon is one of the *Ficus* species that can produce conspicuous amounts of jelly in its female figs. The aims of this chapter are to investigate the role of the mucilaginous jelly produced in female figs of *F. oligodon*. Specific questions are: (i) Does the jelly inhibit seed germination and protect seeds from pathogens? (ii) What is the effect of removal of the jelly on germination? (iii) And is the jelly attractive to ants?

5.3 Methods

5.3.1 Study species

Ficus oligodon is a dioecious fig tree, with stoliniferous and cauliflorous figs. It is widespread in SE Asia and grows along streams in riparian habitats in Kanchanaburi Province, western Thailand (Berg & Corner, 2005). The figs are produced from ground level up to several metres above the ground (CHAPTER 2).

Female trees produce figs that reach 3-4 cm or more in diameter, and develop a red to purple colour when ripe (Berg et al., 2011). The figs ripen in the normal way, with the outer wall becoming soft and sweet. This provides a reward for frugivores. The few published records of seed dispersal agents of *F. oligodon* (Shanahan et al., 2001) comprise the Asiatic Black Bear (*Ursus thibetanus*, Ursidae; Shanahan et al., 2001), rats (*Rattus* sp. or *Maxomys* sp., Muridae), Grey-bellied squirrels (*Callosciurus caniceps*, Sciuridae) and Black-crested bulbuls (*Pycnonotus flaviventris*, Pycnonotidae) were also found to consume the figs in riparian areas of western Thailand (CHAPTER 3). Because they grow in and near streams, many figs fall into the water (CHAPTER 4). The blue mahseer (*Neolissochilus stracheyi*, Cyprinidae) also feeds on fallen *F. oligodon* figs floating on the water surface (CHAPTER 4). Within the figs, seeds become enveloped within the jelly (Fig. 5.1), which does not taste sweet to the human tongue (Kerdkaew, T. & Compton, S. G., pers. obs.). The birds and mammals that visit its ripe figs have not been observed to eat the jelly. Several arboreal ant species also forage on this fig tree species, and can be seen around the figs. They may interact with the fig jelly.

5.3.2 Jelly volumes

Figs were collected from two female *F. oligodon* individuals growing along a stream located in evergreen rain forest at Khaolaem National Park, Kanchanaburi, western Thailand (Table 5.1). The trees were located at 98°36' E-15°01'N (Tree 1, sampled 1st August 2016 and 25th November 2016) and 98°35'E-15°01'N (Tree 2, sampled 15th August 2016 and 25th November 2016). The widths and lengths (from ostiole to stalk) of the figs were measured using vernier calipers. The volume of jelly they contained was estimated after they were cut in half by removing the jelly using a spoon and filling in a 1 ml capacity graduated Eppendorf tube (Table 5.1, Fig. 5.2). The estimated volumes included both the jelly and the seeds within it. Not all the jelly could be removed, so the volumes recorded are minimum estimates.

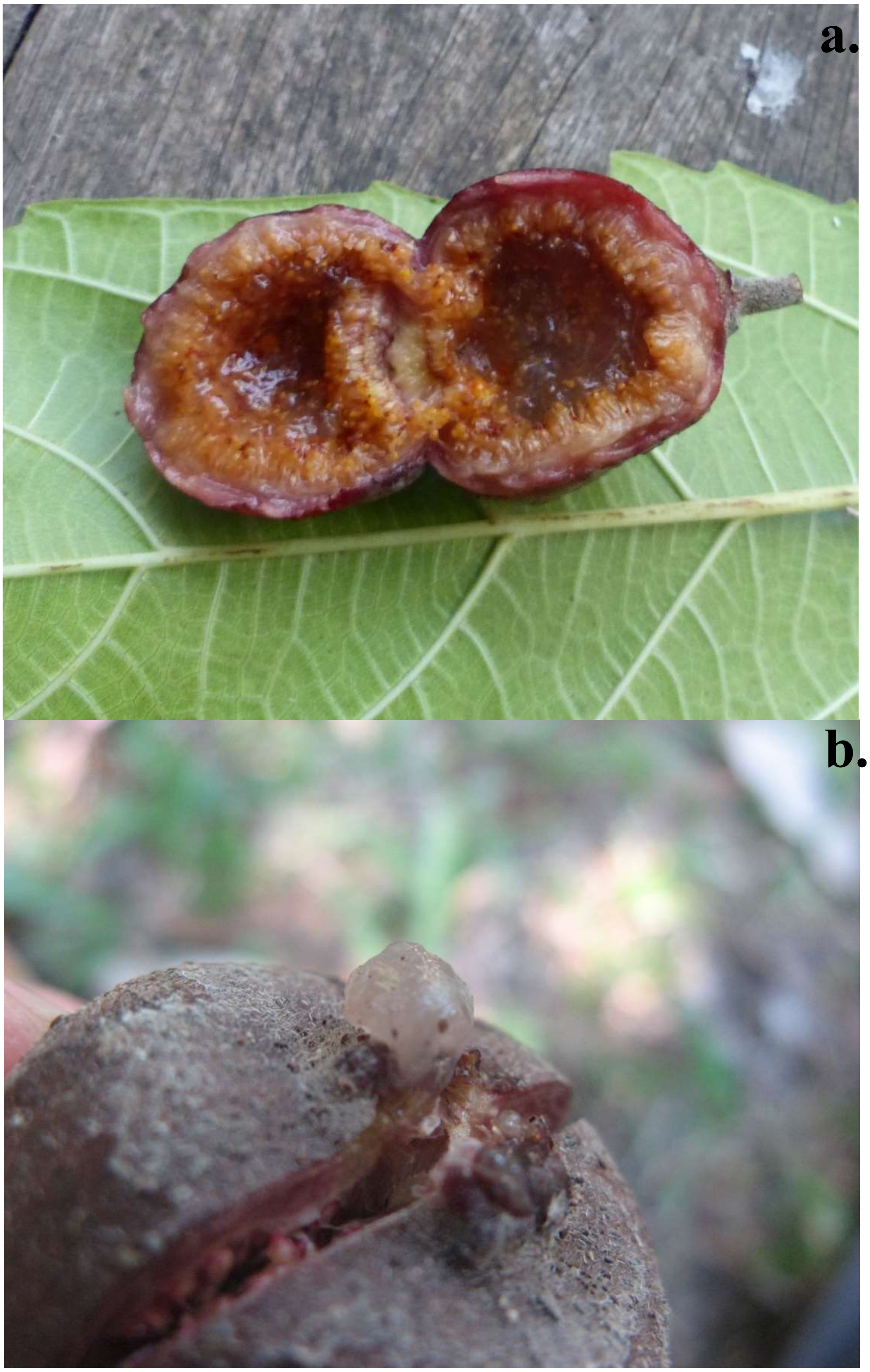

Fig. 5.1. The mucilaginous jelly inside a ripe female *F. oligodon* fig (a.), and an example of the jelly exuding from a female fig via the ostiole (b.)

5.3.3 Germination trials

Female figs collected from the first samples of both trees were used to examine the effect of the jelly on seed germination. After the jelly volume measurements, 2 ml of seeds and their surrounding jelly from one half of each fig was transferred onto filter paper in sterile Petri dishes. This gave a total of 10 Petri dishes containing seeds from 10 figs. Jelly was removed from the remaining seeds which were then treated in the same way. The jelly was removed from the seeds by stirring gently in distilled water until the jelly was totally removed. Then the volume of cleaned seeds was measured to 0.1 ml using graduated Eppendorf tubes, and seed numbers were counted. Extracted seeds from each fig were germinated separately on filter paper in Petri dishes.

The trials ran for 108 days. All the Petri dishes were kept in an indoor greenhouse which provided a 12/12 hours light (0600h-1759h) and dark (1800h-0559h) cycle. Light was provided by a 40W white light bulb with a timer switch. Mid-day temperatures ranged from 25-35°C. These were recorded by a digital thermometer at 1300h at the same times as seed germination was monitored (every three days). The filter paper was kept moist by adding 3-5 ml of distilled water when necessary or the sign of dry on the germination medium was appeared. Seed germination was monitored at three day intervals, and seeds were recorded as having germinated when they were two cotyledon stage seedlings. They were then removed. The first day that germination was found in each Petri dish was recorded and the day that most seeds germinated under each set of experimental conditions was also calculated.

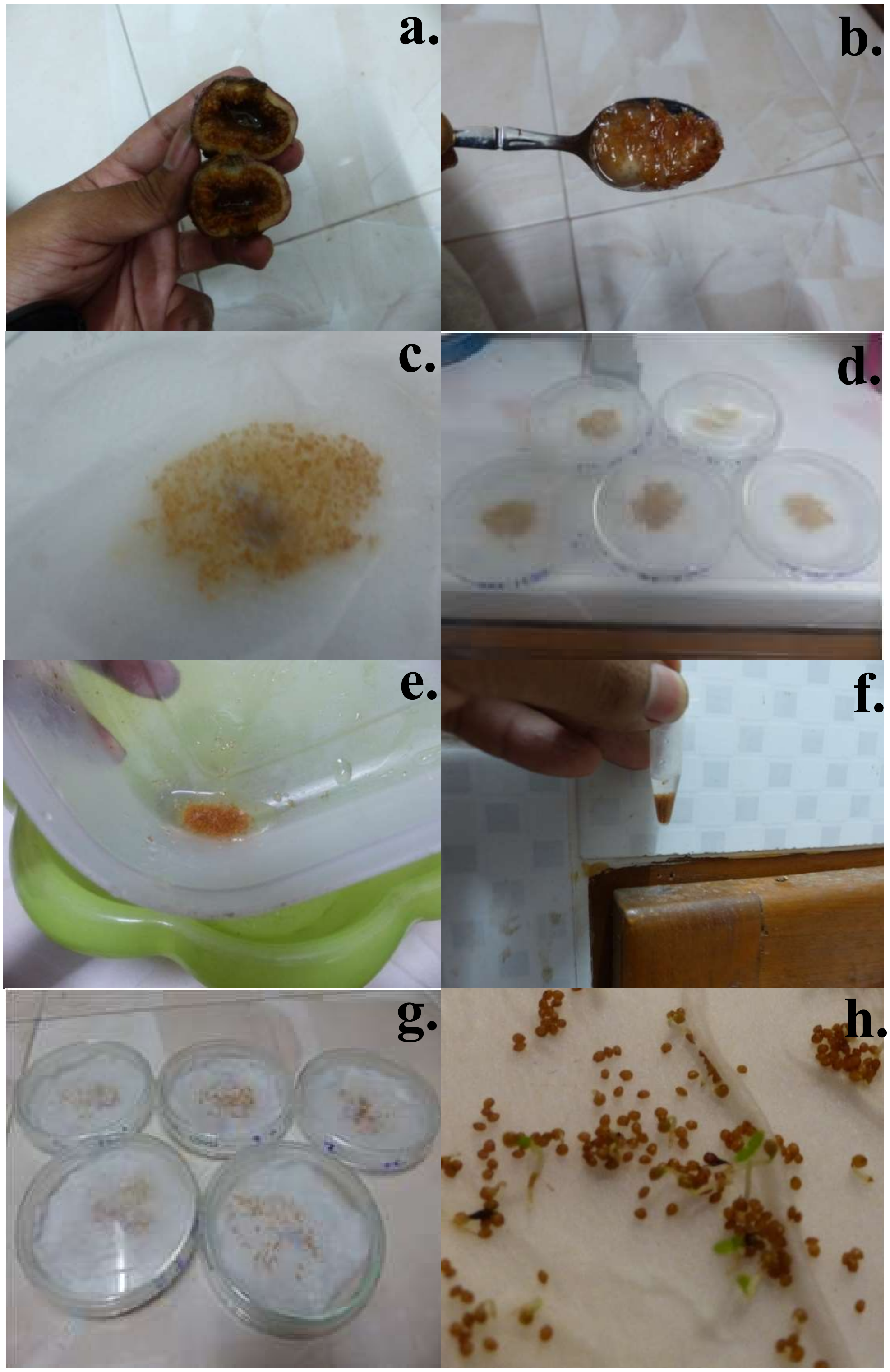

Fig. 5.2. Jelly extraction from ripe female figs of *F. oligodon (*a. and b.), the seeds germinating together with surrounding jelly (c. and d.), the process to clean up the jelly from seeds using water (e. and f.) germination trials with cleaned seeds (g.), and seedling germination in the control trial in which jelly was removed (h.).

After the experiment had been running for 108 days any un-germinated *F. oligodon* seeds from the plus-jelly treatment were cleaned to remove the surrounding jelly as before. The seeds were then transferred onto moist filter paper in a Petri dish and kept damp with distilled water and monitored for a further 90 days.

Some of the figs collected on the second sample date from both trees (Table 5.1) were germinated under more natural conditions. Seeds with and without surrounding jelly were moistened using water contaminated by soil from where the parent trees were growing. Ten kilograms of soil was collected from the Kratengjeng waterfall, Khaolaem National Park on 25th November 2016 under tree number 1 (98°36' E-15°01'N). The soil from the forest was kept in a flowerpot and watered daily by distilled water to maintain soil humidity. When the Petri dishes needed moisture, 10 g of the soil was then mixed with 100 ml of distilled water until the soil and water were mixed together, and the soil was then filtered through tissue paper and filter paper. In total, one third of the seeds from seven figs were placed in 3 x 7 Petri dishes. The treatments were (1) seeds with jelly removed and moistened with distilled water, (2) seeds with jelly and distilled water and (3) seeds with jelly removed and moistened with soil-treated water. The trial ran for 108 days and experimental conditions were as in the first germination trials.

5.3.4 Fig jelly and ants

Ants (Formicidae) foraging on the bark and figs of *F. oligodon* trees were collected from Kratengjeng and Phatad waterfalls, and sent to the Prince of Songkla University Natural History Museum, Hatyai, Thailand for identifying by entomologists (Dr. Abdullah Samoh and Dr. Nawee Noon-anant). Single species belonging to the genera *Crematogaster*, *Pheidole* and *Philidris* could only be identified to genus. A species of weaver ant, *Oecophylla smaragdina*, was also found foraging under the *F. oligodon* trees in an open area close to the streams (Figs. 5.3-5.6).

To assess whether the ants were attracted to the jelly, ripe figs where jelly was exuding were routinely monitored in the field for ant visitation and their behavior on the figs was observed. Jelly was also placed in five open Petri dishes beneath the trees. Each Petri dish contained 1 cm^3 of jelly spread out thinly across the dish bases (the volume was measured as before). They were placed under five female *F. oligodon* trees at Kratengjeng waterfall where ants were present on 14th of January 2017. The jelly had been collected from ripe figs on the same trees where each Petri dish was placed. The Petri dishes and figs were monitored every 15 minutes for 5 hours, from 1000h to 1500h. Ant visitors were identified and counted and their interactions with the jelly were recorded.

Fig. 5.3. ***Crematogaster*** **sp. worker from a female** ***F. oligodon*** **tree.**

Fig. 5.4. ***Pheidole*** **sp. worker from a female** ***F. oligodon*** **tree.**

Fig. 5.5. ***Philidris* sp. worker from a female *F. oligodon* tree.**

Fig. 5.6. ***Oechophylla smaragdina* worker from a female *F. oligodon* tree.**

5.3.5 Data analysis

Differences among fig sizes and jelly volumes from the two fig tree individuals were tested separately using Mann-Whitney U as non-normality and non-homogeneity of variances was detected. Generalized linear models (GLM) tested the effects of different treatments on seed germination proportions with binomial or Quasi-binomial error distribution due to overdispersion. GLMs also compared first day of seed germination and the day that most seeds germinated at day 108 in jelly and control sets treated with distilled and soil-treated water and at day 90 after the removal of jelly at day 108 with Gamma error distributions as variances increased with the mean. All statistical calculations were performed in R 3.4.3.

5.4 Results

5.4.1 Jelly volumes

The figs were roughly spherical and between three and four centimetres in diameter (Table 5.1). They each contained over 3 ml of jelly including seeds. As not all the jelly could be removed, these are slight underestimates of the true volumes. Figs collected on the first sampling dates from tree 1 and tree 2 had fig widths, lengths and jelly volumes that did not differ significantly (Width: Mann-Whitney U-test: U = 8.50, N = 10, P = 0.395; Length: Mann-Whitney U-test: U = 4.50, N = 10, P = 0.093; Jelly Volume: Mann-Whitney U-test: U = 10.00, N = 10, P = 0.589). Figs collected on the second sampling dates from the two trees also did not differ significantly (Width: Mann-Whitney U-test: U = 4.50, N = 7, P = 0.578; Length: Mann-Whitney U-test: U = 5.00, N = 7, P = 0.721; Jelly Volume: Mann-Whitney U-test: U = 6.00, N = 7, P = 1.00).

Table 5.1. The size of mature female *Ficus oligodon* figs obtained from trees growing at Kratengjeng waterfall, Khaolaem National Park, Kanchanaburi, with estimates of the minimum volume of jelly (and included seeds) they contained.

Trees & (Samples)	N figs	Fig size (Mean ± SE) [range] (cm)		Jelly volume (Mean ± SE) [range] (ml)
		Width	Length	
1 (1)	5	3.60 ± 0.26 [3.2 - 3.9]	3.62 ± 0.39 [3.2 - 4.2]	3.36 ± 0.31 [2.9 - 3.7]
2 (1)	5	3.74 ± 0.18 [3.5 - 3.9]	4.04 ± 0.11 [3.8 - 4.2]	3.48 ± 0.20 [3.3 - 3.8]
1 (2)	3	3.63 ± 0.23 [3.5 - 3.9]	3.83 ± 0.15 [3.7 - 4]	3.47 ± 0.06 [3.4 - 3.5]
2 (2)	4	3.68 ± 0.17 [3.5 - 3.9]	3.85 ± 0.25 [3.5 - 4.1]	3.58 ± 0.10 [3.5 - 3.7]

5.4.2 *F. oligodon* seed germination

The Petri dishes each contained about 275-400 seeds (Table 5.2). In trial one, where seeds were moistened only with distilled water, the seeds that still had jelly around them had all failed to germinate when the experiment was terminated at day 108 (Trial 2, Table 5.2). In contrast, the seeds that had been cleaned of jelly started to germinate after only three days and about half the seeds had germinated by the end of the experiment. The day that most seeds germinated was about 44 days. When the seeds with jelly, that had all failed to germinate, had the jelly removed at day 108 and were then placed back under the same conditions (trial three), some responded by germinating within three days and over one third had germinated after the experiment was terminated after a further 90 days. After jelly removal, median length of time to germination was about 37 days. The first day of seed germination between trials number one and three was not significantly different (GLM: $\chi^2 = 4.57$, df = 1, $P = 0.10$), but the day that most seeds germinated (GLM: $F_{(1,18)} = 10.41$, $P < 0.01$) and germination proportion was significantly different (GLM: $F_{(1,19)} = 7.83$, $P = 0.011$), with a higher proportion of seeds germinating in trial one but with a significantly longer duration that most seeds germinated than in trial three.

In contrast to the seeds that were moistened with distilled water, germination rates were low among the seeds with their surrounding jelly removed that had been watered with the soil extract (trials five and six, Table 5.2). They also started to germinate slightly later than similar seeds moistened with distilled water, and their MLG was slightly longer, but because the trials were not run simultaneously, the different speeds of germination may reflect different temperatures. The seeds that did not germinate in trials five and six were likely to have been infected by mould as their seed coats were blackened. As with seeds moistened with distilled water, no germination was recorded within the duration of the experiment among seeds in soil water where their surrounding jelly was present (trial 6, Table 5.2). These seeds responded as before to having jelly removed after 90 days and moistening with distilled water (trial 7; Table 5.2). Germination was first observed after three days, and almost one third of the seeds had germinated when the experiment was terminated. First day of seed germination were significantly different among all trials except numbers four and seven. (Overall GLM: $\chi^2 = 5.28$, df = 2, $P < 0.001$; Trial 4 v. Trial 5: $Z = -3.361$, $P < 0.01$; Trial 4 v. Trial 7: $Z = 0.700$, $P = 0.764$; Trial 5 v. Trial 7: $Z = 4.061$, $P < 0.001$). The day that most seeds germinated was significantly different only between trials five and seven (GLM: $F_{(2, 18)} = 89.58$, $P < 0.001$; Trial (4) v. Trial (5): $Z = 1.147$, $P = 0.485$; Trial (4) v. Trial (7): $Z = 2.196$, P

= 0.07; Trial (5) v. Trial (7): Z = 3.344, P < 0.01). The germination proportion in trials 4-7 were all significantly different (Overall GLM: $F_{(2, 20)}$ = 89.58, P < 0.001; Trial (4) v. Trial (5): Z = -10.759, P < 0.001; Trial (4) v. Trial (7): Z = 4.646, P < 0.001; Trial (5) v. Trial (7): Z = -7.740, P < 0.001).

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Table 5.2. *Ficus oligodon* seed germination, day that most seeds germinated and probability of seed germination in different treatments. All data are reported as means ± S.E. and [range].

Treatments	N figs	Seed numbers	First day of germination	Day that most seeds germinated (days)	Germination proportion
Trials 1-3					
(1) Jelly-free seeds + Distilled water	10	317.00 ± 14.48 [265-409]	7.50 ± 0.92 [3-12]	45.00 ± 0.77 [42-48]	0.45 ± 0.02 [0.35-0.57]
(2) Seeds + Jelly + Distilled water	10	313.40 ± 15.81 [269-424]	-	-	0
(3) Cleaned (from trial 2) + Distilled water	10	276.50 ± 10.51 [237-354]	5.40 ± 0.98 [3-12]	37.50 ± 2.01 [30-51]	0.36 ± 0.03 [0.20-0.46]
Trials 4-7					
(4) Jelly-free seeds + Distilled water	7	304.29 ± 22.07 [239-396]	8.14 ± 0.86 [6-12]	42.43 ± 1.53 [39-48]	0.49 ± 0.03 [0.41-0.59]
(5) Jelly-free seeds + Soil water	7	400.29 ± 32.50 [248-519]	25.71 ± 6.74 [6-60]	48.43 ± 5.13 [33-75]	0.05 ± 0.02 [0.01-0.12]
(6) Seeds+Jelly + Soil water	7	365.14 ± 16.57 [321-452]	-	-	0
(7) Cleaned (from trial 6) + Distilled water	7	348.43 ± 15.64 [304-432]	6.86 ± 0.86 [3-9]	34.71 ± 1.44 [30-39]	0.30 ± 0.02 [0.22-0.37]

5.4.3 *F. oligodon* jelly and ants

None of the five controlled dishes placing under the trees with jelly were visited by ants, despite ants being present nearby. Three ant individuals were present on the edge of one Petri dish one hour after it was placed under the tree, but all ants did not come closer to the jelly spread on the centre of the Petri dish.

More than one hundred visits by ants to ripe female figs were observed. The ants that visited the figs always fed on the soft fig pulp only and avoided the jelly exudates. Observations for five hours of 12 figs with jelly exudates recorded very small numbers of visits by ants (Table 5.3). All three ant individuals fed on the outer surface of the ripe female figs but ignored the jelly. Therefore, there is no evidence that ants have any interest in the jelly exudates of female *F. oligodon* figs.

Table 5.3. Visits by ants to figs of *F. oligodon* with jelly exudates during five hours of observations at Kratengjeng.

Tree number	Location	Figs observed (N)	Figs visited by ants (N)
1	N15.03324°, E98.60836°	1	1
2	N15.03304°, E98.60839°	2	0
3	N15.03309°, E98.60847°	5	0
4	N15.03351°, E98.60826°	1	0
5	N15.03353°, E98.60864°	3	2

5.5 Discussion

The ants on female figs and on the trees also showed no interest in the jelly. The jelly surrounding the seeds of *F. oligodon* is produced in much larger quantities that the mucilage around seeds of *F. microcarpa* that is known to act as an ant-attracting elaisosome, and many of the seeds are surrounded by jelly that makes them not readily accessible to ants. Secondary seed dispersal of *F. oligodon* by ants, once most of the jelly is removed, might nonetheless occur, because the thin mucilaginous exocarp of *F. microcarpa* passes through bird guts and the seeds can then be secondarily transported by ants (Kaufmann et al., 1991). Similarly, leaf-litter ants (*Pheidole* sp.) will collect seeds from bird faeces and move them to refuse piles where some seeds could gain benefits from being dispersed by the ants (Byrne & Levey, 1993). A role of the jelly in secondary seed dispersal cannot therefore be ruled out.

Observations of *F. oligodon* trees where birds and mammals were present (CHAPTER 3) suggest that the jelly produced by mature female *F. oligodon* figs does not currently function as a reward for seed dispersers because the species visiting the figs show no interest in it (Compton, S. G., pers. comm.). The size and position of *F. oligodon* figs, and its riparian habitat, suggest larger mammals may be the main natural dispersers of this species, supplemented by water transport, but larger species have been eliminated from much of the range of the plant, including the study sites. Possibly species such as pigs, deer or bears might find the jelly attractive, but macaques (*Macaca* sp., Cercopithecidae) show no interest in it at Erawan (Compton, S. G., pers. comm.) and the fig pulp provides a reward that is both sweeter and available in much bigger quantities.

Several other fig tree species with their seeds covered with jelly-like compounds have been reported (Utzurrum & Heideman, 1991; Kaufmann et al., 1991; Reiter, 2002). These studies proposed that the gelatinous layer covering the fig seeds promoted survival when seeds passed through frugivore guts, especially those of fruit bats (Utzurrum & Heideman, 1991; Reiter, 2002). Fruit bat feeding on *F. oligodon* figs has not been confirmed. *Ficus oligodon* is a riparian species and many of its figs fall into the water, where the seeds might be eaten by fish (CHAPTER 4). However, preliminary trials using *F. oligodon* seeds with a jelly coating showed they were of no interest to the Blue mahseer (*Neolissochilus stracheyi*, Cyprinidae), and no seeds were ingested by the fish. Therefore, the effect of a gelatinous coating on the survival of *F. oligodon* seeds in the fish gut could not be investigated (Kerdkaew, T., unpublished).

In contrast to having no apparent role in seed dispersal by animals, the presence of jelly around the seeds of *F. oligodon* has a dramatic impact on the speed of germination. After the jelly was washed from the *F. oligodon* seeds most seeds germinated by around 40 days. A previous study of a different variety of the same species by Kuaraksa & Elliot (2013) found that the median length of seed germination in sand, rice husk and charcoal medium was only 20 days, and that the seed germination rate was approximately 40%. This was slightly faster and more successful than in the current study. Their treatment of the seeds (with sieving through a net) and the medium they used may have enhanced germination, and their (unspecified) temperatures may also have been higher.

Our study found that *F. oligodon* seeds coated by the surrounding jelly always failed to germinate within the first three months, and that this inhibition of germination is removed once the jelly coating is removed. This suggests that the jelly blocks factors that could break seed dormancy, such as humidity and oxygen. The coating by jelly delays germination, at a cost of slightly reduced seed viability. In some plant species, such as *Blepharis persica* (Acanthaceae) and *Spinacea oleracea* (Amaranthaceae), that have a mucilage layer covering their seeds plays role as an oxygen barrier to inhibit seed germination (Heydecker & Orphanos, 1968; Witztum et al., 1969). Seed coat mucilage could promote seed hydration in seeds deposited in severe environments, such as under arid conditions or high salt concentrations (Western, 2012). For example, under high salt conditions, germination of *Artemisia sphaerocephala* (Asteraceae) seeds covered by mucilage layers was significantly higher than in seeds where the mucilage layer were removed, suggesting that the mucilage structure could promote seedling survival in this environment (Yang et al., 2010). Moreover, the mucilage in *A. sphaerocephala* could promote the DNA repair process and promote higher seed viability (Huang et al., 2008). Another crucial function of mucilage layers around seeds is to prevent water loss during seedling development by absorbing water as for example in *Cavanillesia platanifolia* (Bombacaceae) (Garwood, 1985). An alternative function has been suggested for the sticky viscid layer around seeds of *Salvia columbariae* (Lamiaceae). It may reduce seed predation by attaching to the soil and camouflaging them from seed predators (Fuller & Hay, 1983). Mistletoe seeds are also very sticky and help attach these parasitic plants on to host trees (Roxburgh, 2007), but the jelly in the figs of *F. oligodon* is not sticky and so cannot have a similar function.

The benefit of covering seeds with a jelly layer may be to protect them from pathogens. Many *F. oligodon* seeds were still viable after being kept moist for more than 100 days and germinated when the jelly was cleaned off. An anti-fungal chitinase has been extracted from the jelly of *F. awkeotsang* which inhibits spore germination by the fungus *Colletotrichum gloeosporioides* (Li et al., 2003). It seems likely that some antifungal compounds may be found in the jelly of *F. oligodon* also.

It was found that *F. oligodon* seeds without surrounding jelly that were treated by soil-mixed water had low germination success and delayed seed germination times. In contrast, the *F. oligodon* seeds covered with the jelly were resistant to the soil-treated water and once the jelly was removed could still germinate at similar rates as the *F. oligodon* seeds previously moistened by distilled water. This suggests that jelly could protect seeds from factors that damage the seeds and inhibit seed germination. Along with damage from pathogens, the *F. oligodon* seed germination might have been be inhibited by allelopathic substances accumulated in the soil. It was reported that seed germination of several plant species was delayed when germinating on the soil that used to grow Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) (McEwan et al., 2010). In Kratengjeng waterfall, one of the common plant species is the banana (*Musa* sp., Musaceae). It has been found that chemical compounds extracted from banana rhizomes, roots, pseudostems and leaves can inhibit seed germination of many crop species (Roy et al., 2006). In *Ficus*, chemicals extracted from leaves of *F. benghalensis* have alleopathic effects on seed germination of *Vigna radiata* (Fabaceae) (Jayakumar et al., 1998), *Zea mays* (Poaceae) and *Helianthus annuus* (Asteraceae) (Mohsin et al., 2016). Therefore, it is possible that the soil at Kratengjeng waterfall is contaminated by alleopathic chemicals from one or more source species and that these inhibit *F. oligodon* seed germination. This may have been acting in combination with pathogenic infection of seeds by microbes from the soil.

In summary, the major findings of this chapter are (i) there is no evidence that ants are interested in the jelly around *F. oligodon* seeds. (ii) *F. oligodon* seeds covered with the jelly did not germinate, but most remained viable, (iii) after removing the jelly from the seeds, nearly half of the seeds could still be germinated, (iv) Soil extracts from under a parent tree greatly reduced germination success.

Chapter 6 Population genetics and gene flow of a dioecious fig tree, *Ficus montana*, in riparian forest of western Thailand

6.1 Abstract

Fig trees (*Ficus* spp.) are widely recognised as keystone species that provide food for wildlife in a wide variety of habitats. This significance depends on the obligatory mutualism between fig trees and pollinator fig wasps (Agaonidae). Gene flow of plants is achieved by the movement of pollen and seeds. Pollen of fig trees is carried by fig wasps that can be transported by wind currents, but long distance pollen flow may only be typical of free standing tall monoecious fig trees, not smaller dioecious species. Seed dispersal distances depend mainly on the behavior of the animals that transport their seeds, but riparian fig tree species may also be dispersed by water. We investigated gene flow in *Ficus montana*, a small shrubby dioecious species with figs eaten mainly by birds, in riparian forest of western Thailand using nuclear and chloroplast markers. Most genetic variation was within populations (95%), but with significant isolation by distance (IBD) in most pairs of populations. Extensive gene flow was detected, achieved largely by pollen flow. Gene flow by seed dispersal appears very limited, although occasional dispersal by water currents can be inferred by strong genetic differentiation of chloroplast DNA and lower haplotypic richness in populations downstream. Movements of seeds by water may contribute to gene flow in this riparian species, but long distance movement of *F. montana* pollinators may be the source of gene flow assisted by wind currents.

6.2 Introduction

Ficus (Moraceae) is a large genus of woody plants with more than 830 species distributed in a wide range of habitats across warmer regions of the world (The Plant List, 2018). The genus is characterized by its unique inflorescence – the fig (syconium). Fig trees are known for their mutualism with obligate pollinator fig wasps (Agaonidae) (Weiblen, 2002; Machado et al., 2005). Most fig wasps are host specific and each fig tree species typically supports one or a small number of pollinator species (van Noort & Rasplus, 2018). Female agaonids enter figs to lay their eggs inside the tiny flowers that line the inner surface of figs. The interaction has a very long history, possibly longer than 34 - 60 million years ago (Rønsted et al., 2005; Compton et al., 2010). After, emerging from their natal figs, female fig wasps start searching for their specific host figs using cues based on volatile compounds produced by receptive figs (Proffit et al., 2008). Two different sexual systems, monoecious and dioecious, can be recognized in fig trees. About half the species are monoecious and produce fig wasp offspring and seeds within the same figs. Fig wasps lay their eggs and gall mostly shorter styled flowers, with the ovules of flowers with longer style lengths mainly developing into seeds (van Noort & Rasplus, 2018). In functionally dioecious fig trees, which are the predominant group in Asia, pollen-loaded fig wasps and seeds develop in figs on different trees. Flowers inside male figs have shorter style lengths than the ones in female figs and facilitate egg laying by the fig wasps that enter. Although fig wasps cannot lay their eggs in female figs, female figs are still pollinated by the fig wasps (Raja et al., 2008).

Fig trees are particularly important parts of tropical ecosystems. Due to factors such as their abundance, easily eaten fruits and often all-year fruiting, fig trees provide food resources for more than 1900 vertebrate frugivore species throughout the world (CHAPTER 7). This large number is also a result of the variation between figs, which vary in size, location, colour and smell (Shanahan et al., 2001; CHAPTER 7). Frugivores are also usually mutualists with the trees because they disperse seeds away from parent plants and so reduce density dependent mortality due to competition, pathogens or seed predators under the parent trees (Howe & Smallwood, 1982; Schupp et al., 2010).

Gene flow, natural selection and genetic drift can all shape the genetic structure of plant populations (Loveless & Hamrick, 1984). Gene flow in flowering plants reflects the dispersal of pollen and seed across a range of spatial scales (Chen et al., 2008). Gene flow can be affected by many features of heterogeneous habitats, such as geographical characteristics, climate or biological factors (Wiens, 1997; Turner et al., 2001). In *Ficus* species, some monoecious species have extremely extensive gene flow as a result of pollinators being carried long distances by the wind (Ahmed et al., 2009). More restricted gene flow patterns are documented in some dioecious species, with local isolation by distance detected (Chen et al., 2011; Liu et al., 2015), but others have extensive gene flow between isolated populations (Chen et al., 2008; Yu et al., 2010; Wang et al., 2018). Seed dispersal distances also shape gene flow in plants. Figs attract a diverse range of frugivores which vary in feeding behaviours and the quality and quantity of the seed dispersal services they provide (Shanahan et al., 2001; CHAPTER 3). For example, small birds tend to move seeds for short distances than larger species, and some fruit bats can disperse seeds over very long distances, but typically move them more locally (Shanahan et al., 2001). The dynamic and complex interactions between frugivores and fig trees are likely to have varying effects on gene flow, but where the extent of gene flow has been compared, pollen flow has been found to be more extensive than seed dispersal (Yu et al., 2010).

In riparian systems some fig tree species are adapted for seed dispersal by flowing water. An extreme example is the rheophytic shrub *Ficus squamosa*, which has flowers in female figs that have long persistent styles with numerous hairs that may assist seeds floating in the water by attaching them to hard substrates such as rocks (Berg et al., 2011; Pothasin et al., 2016). More widely, the cavity inside figs gives them buoyancy that can also aid seed dispersal for long distances by allowing figs to float on a water body and if entering moving water be carried downstream. Seed dispersal by water flow has been inferred from the genetic structure and gene flow patterns in several riparian plant species (Imbert & Lefèvre 2003; Mitsui et al., 2010), and bidirectional gene flow has been detected in some riparian trees (Yan et al., 2016). Although unidirection gene flow in some riparian trees could be hardly detected, weak isolation by distance patterns between populations was found (Hevroy et al., 2017). The downstream populations showed higher genetic or haplotype diversity than the upstream populations (Russell et al., 1999; Akimoto et al., 1998; Mitsui et al., 2010). Less marked isolation by distance among some riparian plant populations also highlights that long distance seed flow can occur in these species (Kudoh & Whigham, 2001; DeWoody et al., 2004).

Ficus montana is a functionally dioecious fig tree with a wide range in South East Asia, from Southern Myanmar to Borneo (Berg & Corner, 2005). It is a small shrub, producing 1 cm red (female) or yellow (male) mature figs in the leaf axils 0-1 m above the ground (CHAPTER 2). In western Thailand, *F. montana* bears figs all year round, with fruit production peaking from April to July in both sexes. The crop sizes of this fig tree are small, mostly less than 20 to rarely nearly 100 figs present at any one time. Only around one-third of crops are synchronous within trees, so mature figs can be produced over extended periods (CHAPTER 2). *F. montana* is pollinated by *Kradibia* (previously called *Liporrhopalum*) *tentacularis* (Agaonidae) (Zavodna et al., 2005a). The small ripe female figs are eaten by small birds such as bulbuls, and also squirrels, but most figs are not consumed by frugivores and fall down to the water or ground (CHAPTER 3; 4). If figs fall down into the water, fish such as the Blue mahseer (*Neolissochilus stracheyi*, Cyprinidae) swallow floating figs and could offer upstream dispersal services, but they destroy most of the seeds they eat (CHAPTER 4).

This population genetic study examined populations of *F. montana* in nine riparian areas within Kanchanaburi province, western Thailand. The aims of this study were to: (i) investigate genetic diversity and differentiation among populations (ii) examine the isolation by distance among populations and also the extent of differences within and between different river systems (iii) to estimate gene flow among populations and whether it was related to shared river systems.

6.3 Methods

6.3.1 *Ficus montana* sampling

From 2011 to 2014, leaves of *F. montana* were collected from several riparian sites in Karnchanaburi and Supanburi by S. G Compton, Y. Chen, Y. Tarachai and P. Pothasin. These were from Erawan (E) (N14°36'/E99°14'), Hueymaeaekhamin (H) (N14°63'/E98°98'), Phatad (PT) (N14°65'/ E98°77'), Phasawan (PW) (N14°68'/ E98°83'), Takientong (TKT) (N15°30'/ E98°45'), Daichongtong (DCT) (N14°98'/ E98°62'), Kratengjeng (KTJ) (N15°03'/ E98°60'), Tapernkeeyai (TY) (N14°98'/ E99°31') and Tapernkeenoi (TN) (N14°96'/ E99°29') waterfalls (Fig. 6.1; Table 7.3). All sampled trees were marked and mapped by GPS, and their sexes were recorded for those individual where figs were available. All collected samples were dried and sealed in bags with silica gel and then transferred and stored in Mianyang Normal University, China for genetic analysis.

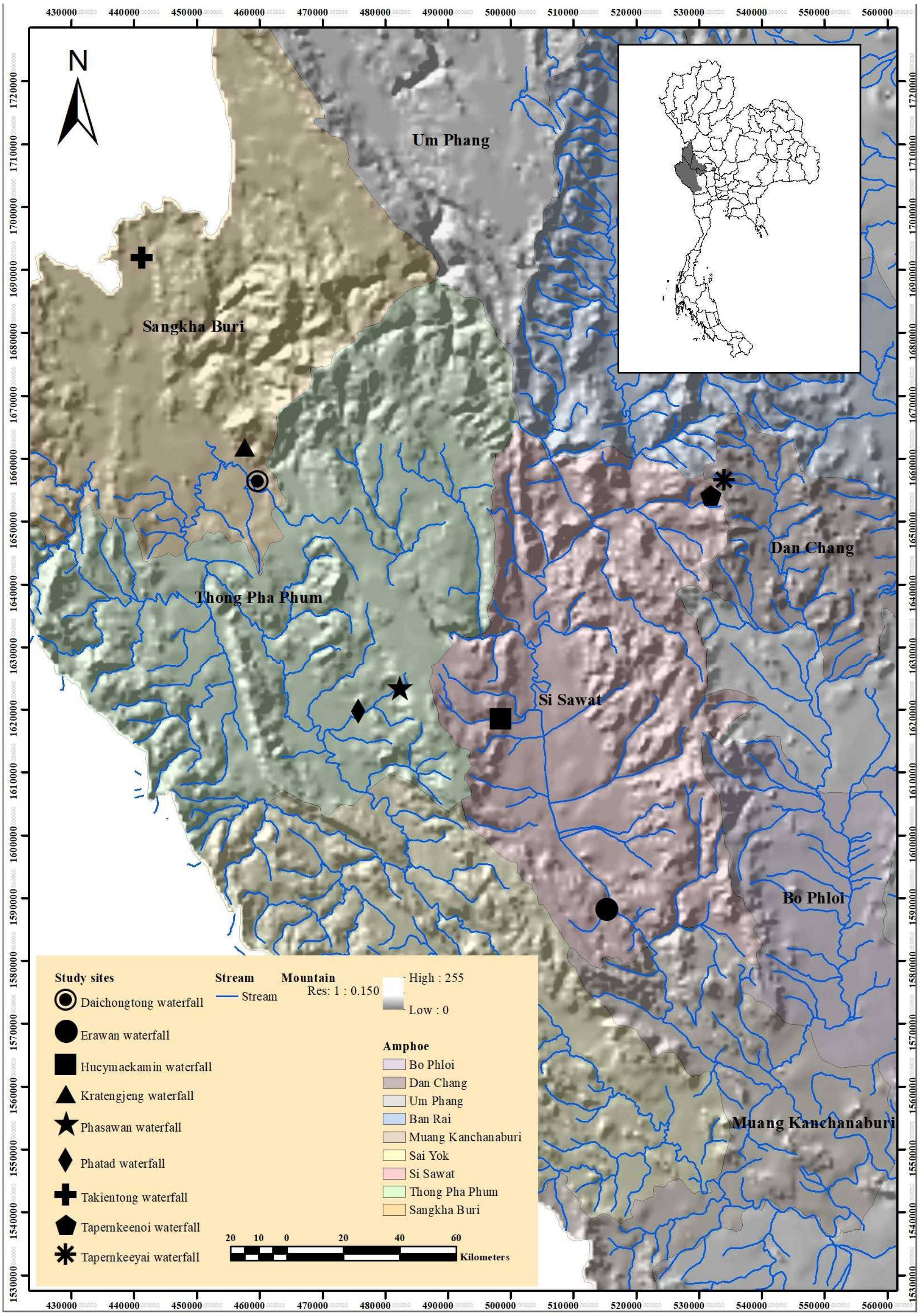

Fig. 6.1. Map of sampling location of the nine populations of *F. montana* in western Thailand. The different symbols identify the names of the locations, Note: Amphoe = district.

6.3.2 Microsatellite loci screening and genotyping

Field collected dried leaves were investigated for genomic DNA quality following PCR using TIANGEN^{TM}, an instant plant DNA extraction kit (Tiangen Biotech co.ltd. Beijing, China). The extracted DNA was visually quantified with 1% agarose gel electrophoresis (AGE).

Ten randomly selected *F. montana* individuals from all populations were preliminary screened using published five, two and eight microsatellite markers from *F. montana* (FM4-15, FM4-18, FM1-27, FM3-64 and FM4-70; Zavodna et al., 2005b), *F. septica* (FS4-11 and FS3-31; Zavodna et al., 2005b) and *F. insipida* (FinsI12, FinsJ10, FinsM5, FinsN1, FinsN3, FinsQ5, FinsQ6 and FinsH5; Vignes et al., 2006), respectively in 8% PAGE (Polyacrylamide gel electrophoreses) to ensure that these primers could be amplified with *F. montana* extracted DNA. These nuclear microsatellite markers allowed us to detect genetic structure and estimate gene flow in *F. montana*.

To address seed dispersal mediated gene flow, ten cpDNA microsatellite markers, ccmp1-ccmp10, (Weising & Gardner, 1999), and thirty six markers, NTCP2-NTCP40 (Bryan et al., 1999) were tested with PCR in *F. montana*. Although these chloroplast microsatellites markers were obtained from tobacco (*Nicotiana tabacum*) chloroplast sequences, it has been suggested that these markers can be applied to many plant species (Weising & Gardner, 1999). Also, all the chloroplast DNA sequences from *Ficus* spp. in the GenBank database were used to design chloroplast microsatellite primers. If there was the same locus sequence from numerous *Ficus* species, one sequence from this locus was randomly chosen when designing the primer. The same loci of chloroplast DNA sequences had more than 90% nucleotide similarity. Those sequences from every locus were searched for tandem repeated mono and dinucleotides. Then the primers of each sequence were designed using Primer Premier 5 software under these criteria (1) primer lengths ranging between 16-24 base pairs, with the most preferable primer size of 18-22 bp. (2) Hairpin and false priming must be prevented, and dimers among or within primers must be avoided. (3) T_m should range from 45 -65°C, with 55°C the best value. (4) The difference in T_m between forward and reverse primers should not be higher than 5°C. (5) The GC percentage must be 40-60%, with 50% optimal. (6) The maximal differences of GC percentage among sense and anti-sense primers should not be higher than 10%. (7) The length of PCR products amplified by these designed primers should be 100-300 bp. The highest scoring primer at each location in any repeat motif was chosen. Based on these criteria the 34 highest scoring primers were screened in this study.

All primers were tested for their suitable T_m and DNA amplification quality. To investigate suitable T_m for all nuclear and chloroplast SSR primers, 20 uL of PCR mixture, including DDH_2O 12.6 uL, blended Taq buffer 2 uL (1 U), dNTP 0.4 µL (0.4µM), forward and reverse nuclear SSR primers 0.2 µL (0.2 µM) were combined with 50 ng of extracted *F. montana* genomic DNA. Each primer pair was tested with DNA extracted from two *F. montana* individuals with ten T_m intervals ranging from 45-65°C. The PCR conditions for testing nuclear SSR primers (FinsI12, FinsJ10, FinsM5, FinsN1, FinsN3, FinsQ5, FinsQ6 and FinsH5) were as follows. The first step was to denature DNA at 94°C for 3 minute, following by 35 cycles of 30 seconds of initial denaturation at 94°C, annealing gradient at 45-65°C for 45 seconds, extension at 72°C for 30 seconds and elongation at 72°C for 5 minutes (Vignes et al., 2006). The PCR conditions for FM4-15, FM4-18, FM1-27, FM3-64, FM4-70, FS4-11 and FS3-31 nuclear SSR primers was DNA denaturation at 94°C for 5 minutes, followed by 30 cycles of 30 seconds of initial denaturation at 94°C, annealing gradient at 45-65°C for 45 seconds, extension at 72°C for 30 seconds and elongation at 72°C for 5 minutes. The PCR condition for all chloroplast SSR primers was DNA denaturation at 94°C for 5 minutes, following by 30 cycles of 60 seconds of initial denaturation at 94°C, annealing gradient at 45-65°C for 60 seconds, extension at 72°C for 60 seconds and elongation at 72°C for 8 minutes. All PCR reactions were done in Eppendorf AG™. The PCR products were quantified by running in 1% AGE (Agarose gel electrophoresis: 0.6g agarose, 60 ml 0.5 TBE buffer, 4.5 uL Ethidium Bromide) together with a 100bp DNA ladder for 15 minutes at 130 volts, and the pieces of gel were photographed by BIORAD Universal Hood II™ with Image Lab 4.0. The density of PCR products was shown in each T_m, and the highest T_m value that gives a clear DNA band was chosen. Three *F. montana* individuals were randomly selected from each of a total of ten sites, for DNA extraction for testing primers quality and polymorphism. All PCR conditions were the same as described previously except the gradient T_m was changed to the exact T_m temperature gathered from the optimal T_m investigation. All primers giving amplification products were examined for polymorphism in 8% PAGE (Polyacrylamide gel electrophoreses) with a 50bp DNA ladder stained with silver nitrate.

After screening of nuclear loci, all screened loci showed polymorphism, but there were only eight loci that could be reliably scored, FM1-27, FS4-11, FinsI12, FinsJ10, FinsM5, FinsQ5, FinsQ6 and FinsH5. Because these primers provided clear bands of amplified DNA product and showed clear DNA bands, these primers were selected for the population genetic analysis (Table 6.1). For Chloroplast SSR, in total, there were only five polymorphic loci which could be used to assess maternally inherited DNA, ccmp2, NTCP9, FC13, FC29 and FC34 (Table 7.2). These polymorphic primers were tagged with a fluorescent marker, and all PCR products with these primers were analysed by an automated sequencer (ABI 3730 Genetic Analyzer, Applied Biosystems^{TM}, California). All alleles were scored with GeneMarker HID v.2.05 (Holland & Parson, 2011). Individuals from all populations which showed unclear peaks or low concentrations of DNA products were reamplified twice and compared to previous amplified DNA products to avoid scoring errors.

Table 6.1. Eight polymorphic nuclear loci used for examining population genetic structure of *F. montana* in riparian forest of western Thailand. bp = base pair, N_a =Number of alleles.

Locus	Primer sequence (5'-3')	T_m (°C)	Repeat	Product length (bp)	N_a
FM1-27	F: GTGATTTGCGATGGCGTGGTTTA R: TCTTCGCTTGCTCGTCAGTGTCC	55	$(GA)_{19}$	314	22
FS4-11	F: AAGGCAACGGGGATAAAGTATTCA R: CTCCGAGAGCAACTCCATCACG	55	$(CGA)_6$	277	14
FinsI12	F: GAACCTTCAACCTCAATCAA R: CTCCCCTTTCCTAGTCCTTA	55	$(TC)_5(CT)_{11}$	144-157	14
FinsJ10	F: AGGTGGAATGAGGAGAGAGT R: AAACATCCTTTCTGGACTTG	54	$(TC)_{11}$	163-170	6
FinsM5	F: ATGAATGGTGAAATCCTGAA R: CATGGCCTCAACTTAGAAAC	55	$(TC)_{13}$	176-182	4
FinsQ5	F: CATGTCAGGAGGTGTCTAGG R: CTCCAAATGGGTATGTCAAG	55	$(GA)_{12}$	149-156	15
FinsQ6	F: TTCTCCAATTAAACCTCCAA R: CATGAAATCACCTTCCTCAT	55	$(TG)_7AG(TG)_5$	98-107	3
FinsH5	F: GACCGTATAGATGATTTGGG R: CATCCTGTGAACGACACTT	54	$(AT)_5GTAT(GT)_{11}$	262-272	17

Table 6.2. Five polymorphic chloroplast SSRs used for examining population genetic structure of *F. montana* in riparian forest of western Thailand. bp = base pair, N_a: Number of alleles.

Locus	Region	Primer sequence (5'-3')	T_m (°C)	Repeat	Product length (bp)	N_a
ccmp2	5' to trnS	F: GATCCCGGACGTAATCCTG R: ATCGTACCGAGGGTTCGAAT	60	$(A)_n$	189	2
NTCP9	trnG/trnR intergenic region	F: CTTCCAAGCTAACGATGC R: CTGTCCTATCCATTAGACAATG	55	$(T)_n$	237	2
Fc13	atpB-rbcL	F: ATAAATGGGCGTTAGCACT R: GAGCCGATGAGATAGAAAA	55	$(A)_n$	286	2
Fc29	rps16	F: TGTGGTAAAAAGCAACGTGCGACT R: TTCTGCCCGAGCTCCATCATGTAT	60	$(T)_n$	196	3
Fc34	clpP	F: GAGACCCATTTCAGCGT R: TGATCCAACAACCACCC	60	$(A)_n$	255	3

6.3.3 Data analysis

All nuclear loci were examined using LOSITAN v.1.0 (Antao et al., 2008) to ensure that the loci were neutral. Any locus that displayed positive or negative selection was excluded from further analysis to prevent the effects of non-neutrality of loci on fixation index estimation. Linkage disequilibria for all pairs of nuclear loci were tested using FSTAT v.2.9.3 and linked loci were excluded from the analysis (Goudet, 1995). The presence of any genotypic errors due to stuttering, large alleles dropout and null alleles were examined using Micro-checker v.2.2.3. (van Oosterhout et al., 2004).

Deviation from Hardy-Weinberg equilibrium (HWE) was tested among all loci from all populations with the multi loci exact test in GENEPOP v.4.0 (Rousset, 2008). Genetic diversity parameters, such as number of alleles (Na), observed (H_O), unbiased expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) in each population were estimated using FSTAT 2.9.3 (Goudet, 1995). Allelic richness (Ar) and private allelic richness (P_A) after rarefaction were estimated using HP-RARE v.1.1 because of unequal sample size in each population (Kalinowski, 2005).

The analysis of chloroplast genetic diversity was investigated by combining genetic length variation to build haplotype, because of its maternal inheritance. The haplotype richness (R_h), genetic diversity (H), haplotype number per population (A), number of private haplotypes (P), effective number of haplotypes (N_e) and the global fixation index of chloroplast DNA ($F_{ST(C)}$) were calculated by HAPLOTYPE ANALYSIS v1.05 (Eliades & Eliades, 2009).

To examine the possibility of population declines and bottlenecks in the past, the signal of heterozygosity excess or deficiency was examined in BOTTLENECK v1.2.02. This software was used for nuclear loci only as they reflect overall gene flow (Cornuet & Luikart, 1996). The Wilcoxon sign test was selected under the two-phases model of mutation (TPM) with 90% and 10% of single and multiple step mutations and 1000 repetitions, because assumptions of this model are appropriate for hyper variable markers like microsatellites (Wang et al., 2018).

Genetic differentiation between the nine *F. montana* populations was estimated in term of fixation indices (F_{ST}). The F_{ST} values (Weir & Cockerham, 1984) for all pairs of populations were calculated and significant values were estimated for each pair of populations using FSTAT 2.9.3 (Goudet, 1995). Because the F_{ST} values can underestimate genetic differentiation among populations based on hyper variable microsatellite loci, the standardized F_{ST} values were also estimated. The standardized F_{ST} values were estimated by the original F_{ST} divided by the $F_{ST(MAX)}$, where the $F_{ST(MAX)}$ values were calculated in RECODEDATA v.0.1 (Meirmans, 2006) and FSTAT 2.9.3 (Goudet, 1995). Overall gene flow (N_em) was estimated for each pair of populations using the standardized fixation indices (F'_{ST}) under the Wright (1978) equation which quantifies genetic differentiation between organism populations based on their allele frequencies;

$$F'_{ST} = \frac{1}{4N_em + 1}$$

The N_em term in the equation stands for the multiplication of effective population size (N_e) and migration rate (m). When selection is not found and the population is at Hardy-Weiberg Equilibrium, genetic differentiation between populations is inversely related to gene flow rates between populations.

The gene flow in such plant species can be estimated by the relationship between F_{ST} and parental mediated gene flow from both seed (Nm_{seed}) and pollen (Nm_{pollen}) by the following equation (Wright, 1949).

$$\mathrm{F_{ST(nuclear)}} = \frac{1}{4\mathrm{Nm_{seed}} + 2\mathrm{Nm_{pollen}} + 1}$$

Chloroplast and Mitochondrial DNA markers have been used to estimate the seed mediated gene flow (Nm_{seed}) in various plant species. Assuming that a 1:1 sex ratio occurred in such population of a dioecious plant species and seed migration is relatively low, the fixation index calculated from Chloroplast DNA markers can be related to seed mediated gene flow as follow: F_{ST}(chloroplast) = $1/(Nm_{seed}+1)$ (Hamilton & Miller, 2002; Liu et al., 2015). The pollen-to-seed ratio (*r*) of *F. montana* can be calculated by:

$$r = \frac{m_p}{m_s} = \frac{\left(\frac{1}{F_{ST(nuclear)}} - 1\right)(1 + F_{IS}) - 4\left(\frac{1}{F_{ST(chloroplast)}} - 1\right)}{2\left(\frac{1}{F_{ST(chloroplast)}} - 1\right)}$$

The variation of genetic differentiation was tested across all nine populations and also within populations to discover the source of genetic differentiation using the analysis of molecular variances (AMOVA). The test was applied in GenAlEx v.6.5 with 1000 randomisations (Peakall & Smouse, 2012).

To detect the relationship between genetic differentiation derived from nuclear loci and geographical distances, the Mantel test was applied in R v.3.4.3 with the package Vegan (Oksanen et al., 2013), with 10000 permutations in order to detect any isolation by distance (IBD). The analysis was based on the regression of

F_{ST} by $F_{ST}/(1-F_{ST})$ and F'_{ST} by $F'_{ST}/(1-F'_{ST})$ against the geographical ranges of each population. The pairwise geographical distances were calculated based on the straight line. The Mantel tests were separated into the populations in the same river systems (Kwai Yai River: TY, TN, H and E, Kwai Noi River: TKT, DCT, KTJ, PW and PT) and grouping all populations together to detect within river system and global IBD respectively.

To reveal the distinct genetic clusters among nine *F. montana* populations, a Bayesian approach simulation was applied for the nuclear loci dataset using the STRUCTURE v.2.3.4 with varying numbers of populations (K) (Pritchard et al., 2000). The 20 independent runs with the range of K value between 1 to 9 was set together with 100000 burn-in length and 200000 MCMC repetitions. The estimated LnP(D) values for each K for 20 runs was then used to calculate the most likely number of genetic groups, using the STRUCTURE HARVESTER program (Earl, 2012). Then the most suitable ΔK value was assigned to the K groups with 1000000 burn-in length and 2000000 MCMC repetitions.

The migration rates for each pairwise population were also estimated to reveal the current migration among populations using BAYESASS v.1.3 for the nuclear DNA under the Bayesian inference by the Markov Chain Monte Carlo simulation (MCMC) (Wilson & Rannala, 2005). The simulation required no linkage disequilibrium, but populations with departure from Hardy-Weinberg equilibrium could be accepted (Wilson & Rannala, 2005). Each run had 10000000 generations, with 10000 burn-in and sampling every 100 generations. The allele frequency, migration and inbreeding delta terms were set as 0.03, 0.05 and 0.05, respectively, with the acceptance percentage ranged from 20 to 60 percent.

6.4 Results

In total, there were 254 and 277 *Ficus montana* samples that were used in nuclear and chloroplast genetic assignment, respectively (Table 6.3; Table 6.7).

Overall, positive or negative selection was not detected from any of the eight used nuclear loci (Fig 6.2). Linkage disequilibrium was not detected in any pair of nuclear loci. Null alleles were detected from some loci from some populations (Table 6.3). Null alleles were detected at the FM1-27 locus in all populations. Therefore, for further analysis, the FM1-27 locus was excluded from the dataset.

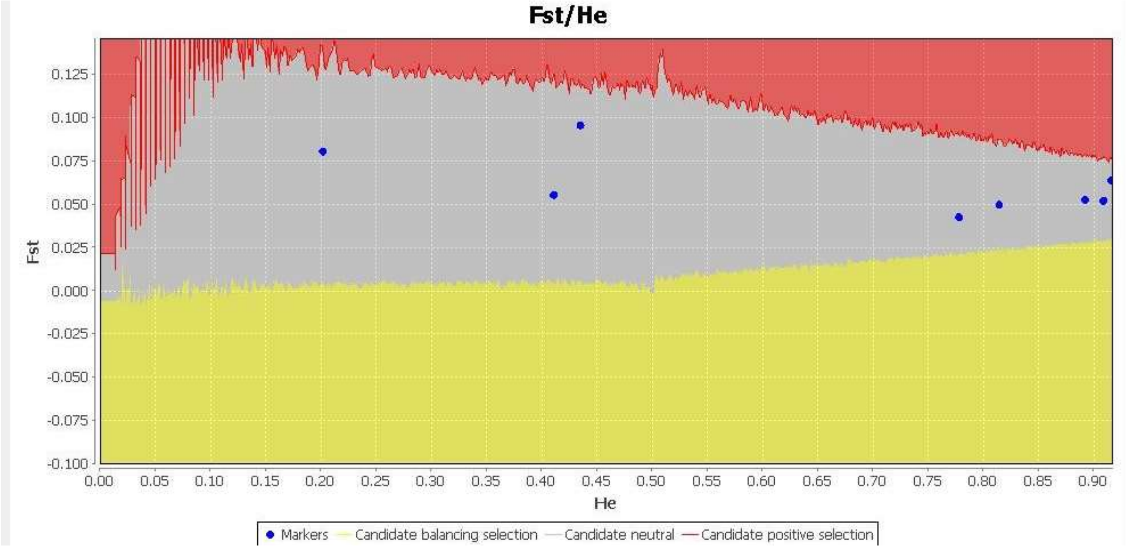

Fig. 6.2. Neutrality assignment for the eight nuclear microsatellite loci in this study.

6.4.1 Genetic diversity

In nuclear DNA, the mean number of alleles per locus (N_A) was 6.05, ranging from 4.71 (DCT) to 7.29 (KTJ). The mean allelic richness per locus (A_R) was 3.29, ranging from 2.97 (TY) to 3.44 (TKT). The mean private allelic richness (P_A) was 0.27, ranged from 0.10 (TY) to 0.50 (TKT). Mean observed (H_o) and expected heterozygosity (H_E) varied from 0.464 (TY) to 0.593 (PW) with 0.535 a mean value, from 0.525 (TY) to 0.634 (PW) with 0.586 a mean value respectively. The average inbreeding coefficient (F_{IS}) was 0.119, and H and E populations showed evidence of significant inbreeding (Table 6.3). Deviation from Hardy-Weiberg equilibrium was detected in most loci, and present in from one to six populations, but not in the FinsQ6 locus (Table 6.4).

With the chloroplast DNA, eight haplotypes and 12 alleles, reconstructed from five polymorphic CpSSR loci, were detected in nine *F. montana* populations (Table 6.5. and 6.6.; Fig 6.3.). The numbers of haplotypes (A) ranged from one (TY and TN) to four (KTJ), and the mean was 2.33 haplotypes. One and two private haplotypes (P) were found in the E and TKT populations respectively. The average effective haplotype number (N_e) was 1.76 across all populations, ranged from 1.00 (TY and TN) to 2.84 (TKT). The mean haplotypic richness (Rh) was 1.073, varying from 0.00 (TY and TN) to 1.976 (TKT). The mean haplotype diversity (H) was 0.339 and ranged from 0 (TY and TN) to 0.674 (TKT) (Table 6.7).

Table 6.3. Sampling locations and nuclear genetic diversities of nine populations of *F. montana* from riparian forest of western Thailand. N_A: mean number of alleles per locus, A_R: mean allelic richness per locus, P_A: private allelic richness, H_o: observed heterozygosity, H_E: expected heterozygosity, F_{is}: inbreeding coefficient.

Population	Abbr.	Location	Sample size	A	A_R	P_A	H_o	H_E	F_{IS}	Loci with null alleles
Takientong	TKT	N15°30'/ E98°45'	24	6.14	3.44	0.50	0.542	0.577	0.082	FinsM5
DaiChongTong	DCT	N14°98'/ E98°62'	24	4.71	3.18	0.23	0.565	0.561	0.013	
Kratengjeng	KTJ	N15°03'/ E98°60'	36	7.29	3.43	0.31	0.532	0.578	0.095	
Tapernkeeyai	TY	N14°98'/ E99°31'	12	4.86	2.97	0.10	0.464	0.525	0.159	FinsI12
Tapernkeenoi	TN	N14°96'/ E99°29'	20	6.00	3.32	0.19	0.514	0.569	0.124	FinsM5 and FinsQ5
Phasawan	PW	N14°68'/ E98°83'	39	7.14	3.42	0.27	0.593	0.634	0.076	FinsM5
Phatad	PT	N14°65'/ E98°77'	22	6.14	3.32	0.22	0.571	0.624	0.108	FinsM5 and FinsJ10
HueyMaeKamin	H	N14°63'/ E98°98'	45	6.29	3.17	0.24	0.505	0.599	0.168*	FinsI12, FinsM5 and FinsQ5
Erawan	E	N14°36'/ E99°14'	32	5.86	3.38	0.35	0.531	0.611	0.146*	FinsM5 and FinsJ10
		Mean	**28.22**	**6.05**	**3.29**	**0.27**	**0.535**	**0.586**	**0.119**	

Table 6.4. The significance values of Hardy-Weiberg equilibrium tests of different *F. montana* populations from riparian forest of western Thailand, *: P < 0.05, **: P < 0.01, ***: P < 0.001.

Populations	Locus						
	FinsI12	**FinsM5**	**FinsQ6**	**FinsJ10**	**Fs4-11**	**FinsQ5**	**FinsH5**
TKT	0.556	0.000***	0.917	0.393	0.025*	0.179	0.328
DCT	0.060	0.834	0.533	0.917	0.893	0.677	0.700
KTJ	0.000***	0.310	0.119	0.000***	0.038*	0.091	0.090
TY	0.144	0.621	0.386	-	0.175	0.843	0.774
TN	0.015*	0.000***	0.064	0.909	0.013*	0.156	0.423
PW	0.528	0.009**	0.189	0.746	0.000***	0.660	0.024*
PT	0.953	0.000***	0.804	0.494	0.898	0.730	0.019*
H	0.397	0.000***	0.278	0.534	0.685	0.002**	0.207
E	0.732	0.000***	0.162	0.000***	0.021*	0.208	0.130

Table 6.5. Composition of base pair length products used for reconstructing haplotypes of *F. montana*.

Haplotypes	**CpSSR Markers**				
	ccmp2	**FC13**	**NTCP9**	**FC29**	**FC34**
A	248	284	330	195	264
B	249	264	330	196	264
C	249	284	322	196	264
D	249	284	330	194	264
E	249	284	330	195	263
F	249	284	330	195	264
G	249	284	330	195	265
H	249	284	330	196	264

Table 6.6. Haplotype composition of nine populations *F. montana* along riparian forest of western Thailand. The numbers denoted are the number of recorded individuals in each population.

Populations	**Haplotypes**							
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
TKT	0	0	11	6	0	0	0	9
DCT	0	23	0	0	0	0	0	3
KTJ	0	1	0	0	0	13	20	1
TY	0	0	0	0	0	0	11	0
TN	0	0	0	0	0	0	21	0
PW	10	0	0	0	0	15	20	0
PT	25	0	0	0	0	0	3	0
H	6	0	0	0	0	28	18	0
E	0	0	0	0	30	3	0	0

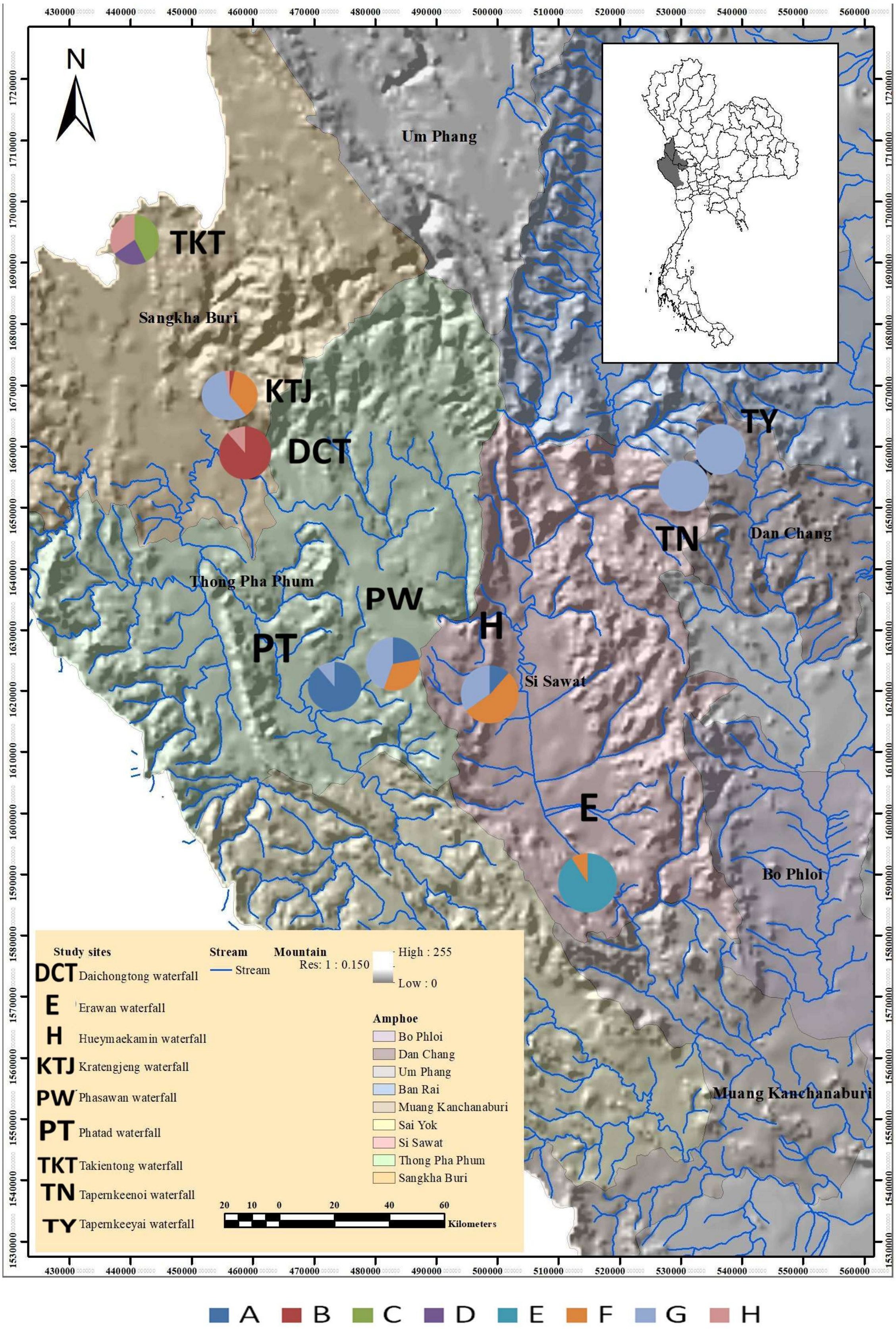

Fig. 6.3. Chloroplast DNA haplotype distributions in nine populations of *F. montana* in riparian forest of western Thailand.

Table 6.7. Sampling locations and chloroplast genetic diversities of *F. montana* from nine populations in riparian forest of western Thailand. A: haplotype number, P: number of private haplotypes, Ne: effective haplotype number, Rh: Haplotypic richness, H: Haplotype diversity.

Populations	Abbr.	Location	Sample size	A	P	Ne	Rh	H
Takientong	TKT	N15°30'/ E98°45'	26	3	2	2.84	1.976	0.674
DaiChongTong	DCT	N14°98'/ E98°62'	26	2	0	1.23	0.825	0.212
Kratengjeng	KTJ	N15°03'/ E98°60'	35	4	0	2.15	1.627	0.550
Tapernkeeyai	TY	N14°98'/ E99°31'	11	1	0	1.00	0	0
Tapernkeenoi	TN	N14°96'/ E99°29'	21	1	0	1.00	0	0
Phasawan	PW	N14°68'/ E98°83'	45	3	0	2.79	1.953	0.657
Phatad	PT	N14°65'/ E98°77'	28	2	0	1.24	0.792	0.198
HueyMaeKamin	H	N14°63'/ E98°98'	52	3	0	2.36	1.774	0.588
Erawan	E	N14°36'/ E99°14'	33	2	1	1.20	0.718	0.170
		Mean	**30.78**	**2.33**	**0.33**	**1.76**	**1.073**	**0.339**

6.4.2 Bottleneck effect detection

Historical bottleneck events were not detected in any *F. montana* populations. It is likely therefore that allele distributions in all *F. montana* populations were not affected by alteration of population size, based on the Wilcoxon and sign test under TPM estimation (P > 0.05, Table 6.8).

Table 6.8. Probability of historical bottleneck events in nine *F. montana* populations in western Thailand, based on the estimation of heterozygosity excess by sign and two-tailed Wilcoxon tests under the two-phase model of mutation (TPM).

Populations	Sign Test	Wilcoxon
TKT	0.358	0.375
DCT	0.089	0.109
KTJ	0.119	0.109
TY	0.252	0.562
TN	0.381	0.689
PW	0.356	0.813
PT	0.340	0.813
H	0.631	1.000
E	0.633	0.375

6.4.3 Genetic structure and gene flow estimation

Overall, moderate level of genetic differentiation was detected from nuclear DNA of nine population of *F. montana* ($F_{ST(nuclear)}$ = 0.050, 95% CI: 0.041 – 0.068, $P < 0.05$), ranged from 0.028 (H v. E) to 0.118 (TKT v. TY). All pairs of populations, except TY v. TN, showed significantly genetic differentiation (Table 6.9). The AMOVA test revealed that the major source of genetic variation occurred within populations (94.79% of total genetic variances), with only 5.21% of total variation from between populations. Although low genetic variances were found, significant genetic differentiation was detected among all populations ($P < 0.001$) (Table 6.10). In contrast, high levels of genetic differentiation were detected in Chloroplast DNA ($F_{ST(choloplast)}$ = 0.499, $P < 0.001$), suggesting that gene flow via seed dispersal was relatively low.

Total gene flow (N_m) for each pair of populations varied from 0.656 (TKT v. TY) to 3.247 (H v. E), and 88.89% of all population pairs showed values larger than 1.00, suggesting that historical gene flow occurred among most populations. However, gene flow between the TKT population, which is located up north, to some southern populations (TY, TN, H and E) had a low probability (Table 6.11). When separating maternally and paternally inherited markers, gene flow by pollination (Nm_p) of *F. montana* was 7.49 pollen grains transferred to other populations in each generation. However, the overall gene flow mediated by seed dispersal (Nm_s) was much lower than that of pollen flow, with only 1.00 seeds dispersed to other populations in each generation. Gene flow is clearly dominated by pollination rather than seed dispersal. The pollen-to-seed ratio (*r*) value was 8.59, estimated from fixation indexes of nuclear ($F_{ST(nuclear)}$) and chloroplast DNA ($F_{ST(chloroplast)}$).

Based on nuclear DNA, isolation by distance (IBD) was detected from nine *F. montana* populations at a regional scale ($F_{ST(nuclear)}$: r = 0.6469, P = 0.003; $F'_{ST(nuclear)}$: r = 0.6457, P = 0.002). When separating into two different river systems, IBD was not detected within the river systems, but showed a slightly positive relationship (Kwai Yai river, TY, TN, H and E populations, $F_{ST(nuclear)}$: r = 0.5047, P = 0.125; $F'_{ST(nuclear)}$: r = 0.5619, P = 0.125, Kwai Noi river, TKT, DCT, KTJ, PT and PW populations, $F_{ST(nuclear)}$: r = 0.3114, P = 0.242; $F'_{ST(nuclear)}$: r = 0.3599, P = 0.175; Fig. 6.4).

The STRUCTURE analysis divided *F. montana* populations into four highest likelihood groups (K = 4, ΔK = 10.77), and the second most likely genetic cluster was two groups (K = 2, ΔK = 7.93). However, distinct clusters were not found, suggesting that there is no clear subgroup divergence of *F. montana* in western Thailand (Fig 6.5).

Based on the Bayesian analysis of recent migration, it has mainly occurred within each population, but migration among populations was detected in some pairs of population in the same river system. Within the Kwai Noi river populations, some migrants from the source population (KTJ) are likely to migrate to the DCT (*m* = 0.0765), PT (*m* = 0.0916) and PW (*m* = 0.1005) populations respectively. Moreover, some migrants were likely to move from population PW to DCT (*m* = 0.0953), PT (*m* = 0.1121) and KTJ (*m* = 0.1182) populations, suggesting that reciprocal migration has occurred between the KTJ and PW populations. Within the Kwai Yai river populations, high migrant movements were only found from the TN to the TY population (*m* = 0.1598). They are located close together in the north and are separated by around 10 kilometers. Migration between river systems was low, suggesting that gene flow of *F. montana* has mainly occurred within river systems (Table 6.11) Some migrant movements could be comparable with wind directions (N, NW, S and SE) in Kanchanaburi which might relate to long distance pollinator movements (Table 6.12).

Table 6.9. Genetic differentiation estimated by the pairwise F_{st} (upper part) and total gene flow estimation (N_m : lower part) of each *F. montana* population in western Thailand. *: $P < 0.05$.

Populations	TKT	DCT	KTJ	TY	TN	PW	PT	H	E
TKT	0	0.069*	0.039*	0.118*	0.097*	0.062*	0.037*	0.106*	0.107*
DCT	1.277	0	0.035*	0.035*	0.040*	0.033*	0.029*	0.038*	0.042*
KTJ	2.421	2.710	0	0.077*	0.043*	0.029*	0.029*	0.052*	0.050*
TY	0.656	2.886	1.142	0	0.036	0.063*	0.075*	0.061*	0.064*
TN	0.813	2.373	2.175	2.746	0	0.069*	0.060*	0.029*	0.039*
PW	1.297	2.678	3.055	1.302	1.140	0	0.035*	0.050*	0.038*
PT	2.362	3.114	3.104	1.085	1.363	2.350	0	0.042*	0.053*
H	0.695	2.440	1.701	1.439	3.191	1.634	2.033	0	0.028*
E	0.668	2.146	1.728	1.337	2.249	2.160	1.480	3.247	0

Table 6.10. AMOVA tests of nine *F. montana* populations in western Thailand.

Source of variation	df	Sum of squares	Mean sum of squares	Estimate variances	Percentage variation (%)	*P* value
Among Populations	8	68.586	8.573	0.116	5.21	< 0.001
Within Populations	499	1055.784	2.116	2.116	94.79	< 0.001
Total	507	1124.370		2.232		

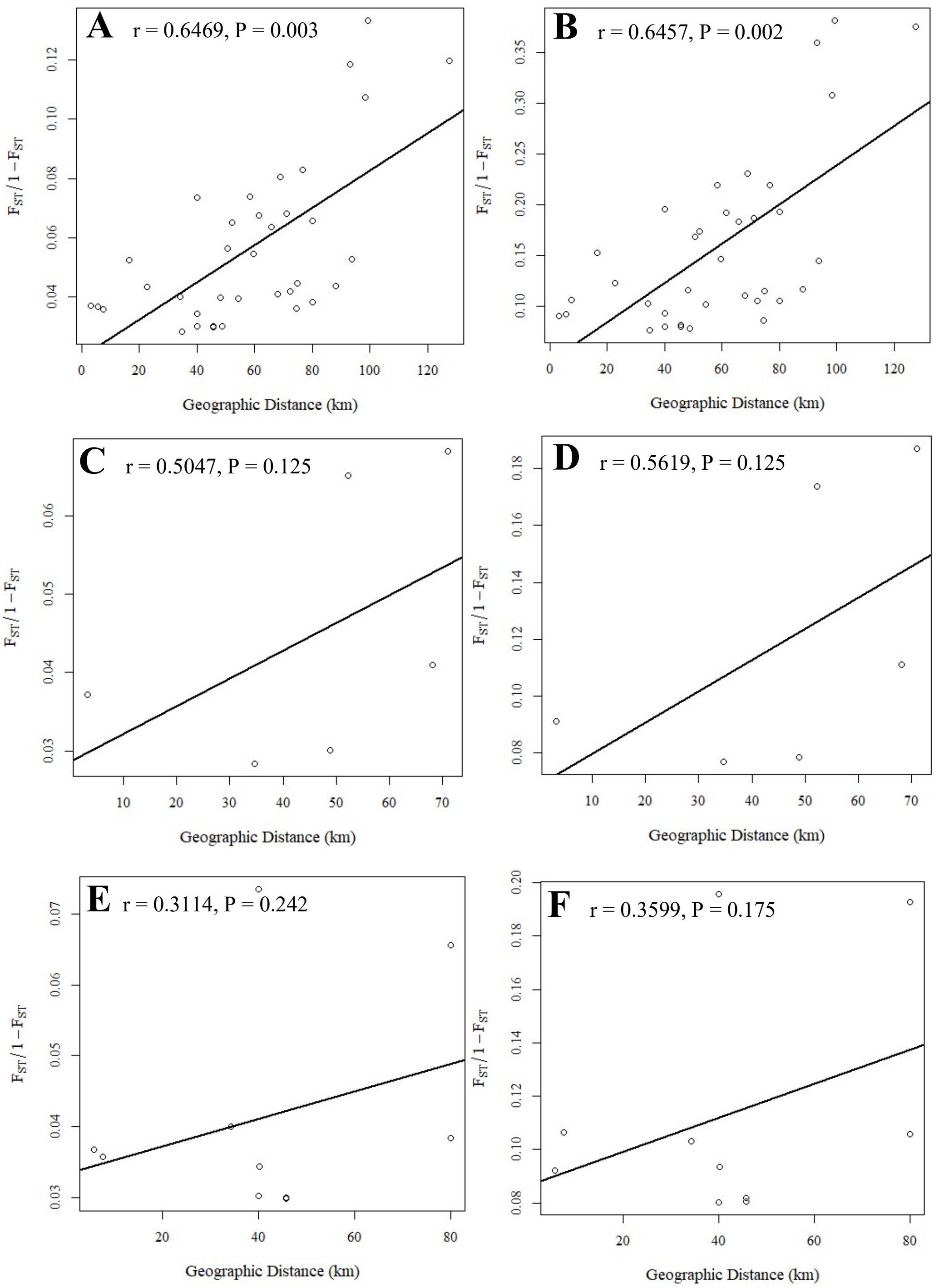

Fig. 6.4. Relationships between pairwise $F_{st(n)}$/(1-$F_{ST(nuclear)}$, $F'_{ST(nuclear)}$/(1-$F'_{ST(nuclear)}$ and geographic distances between nine *F. montana* populations for (A) estimated by $F_{ST(nuclear)}$, (B) $F'_{ST(nuclear)}$ of all populations, (C) $F_{ST(nuclear)}$, (D) $F'_{ST(nuclear)}$ of Kwai Yai populations, (E) $F_{ST(nuclear)}$, (D) $F'_{ST(nuclear)}$ of Kwai Noi populations.

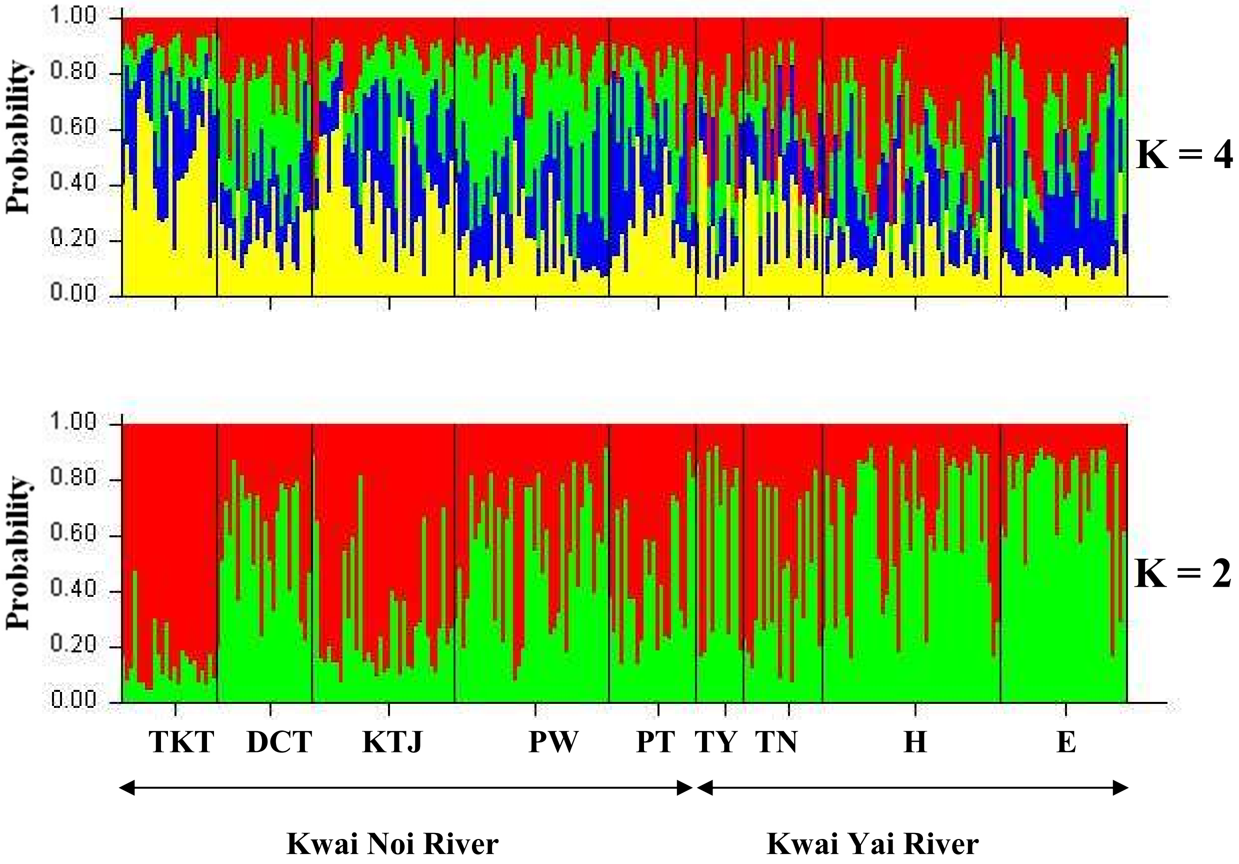

Fig. 6.5. Genetic clusters of nine *F. montana* populations in riparian forest of western Thailand with the highest likelihood cluster numbers, K = 4, and K = 2.

Table 6.11. Estimated migration probability (*m*) between *F. montana* populations inferred from nuclear DNA in western Thailand. Each value refers to the proportion of individuals that had migrated from the original population. Values larger than 0.05 are in bold.

		Migration from								
	Populations	TKT	DCT	KTJ	TY	TN	PW	PT	H	E
Migration to	TKT	**0.9745**	0.0022	0.0032	0.0025	0.0028	0.0076	0.0023	0.0026	0.0025
	DCT	0.0220	**0.6891**	**0.0765**	0.0151	0.0240	**0.0953**	0.0154	0.0422	0.0202
	KTJ	0.0105	0.0042	**0.8133**	0.0043	0.0201	**0.1182**	0.0044	0.0167	0.0080
	TY	0.0205	0.0161	0.0208	**0.6909**	**0.1598**	0.0298	0.0161	0.0227	0.0233
	TN	0.0082	0.0057	0.0153	0.0057	**0.9054**	0.0138	0.0058	0.0239	0.0162
	PW	0.0043	0.0034	**0.0916**	0.0034	0.0082	**0.8593**	0.0041	0.0134	0.0121
	PT	0.0151	0.0096	**0.1005**	0.0095	0.0182	**0.1121**	**0.6825**	0.0367	0.0157
	H	0.0014	0.0013	0.0017	0.0013	0.0118	0.0143	0.0013	**0.9651**	0.0017
	E	0.0025	0.0021	0.0032	0.0022	0.0115	0.0095	0.0022	0.0053	**0.9615**

Table 6.12. Monthly predominant wind directions and mean speeds (knots) in Kanchanaburi, western Thailand from 2011 – 2014. Based on data obtained from the Thai Meteorological Department, Thongphaphum station, Kanchanaburi, western Thailand.

	Month											
Year	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
2011	E (0.1)	NW (0.1)	SE,NW (0.2)	NW (0.2)	N,NW (0.1)	N (0.1)	N (0.1)	N (0.1)	Calm (0.1)	Calm (0.1)	SE,S (0.2)	SE (0.5)
2012	N (0.2)	N (0.3)	N (0.2)	N,NW (0.1)	Vary (0.2)	Calm (< 0.1)	NW (0.1)	Vary (0.2)	N (0.1)	SE (0.1)	S (0.2)	S (0.1)
2013	NW (0.2)	N (0.4)	Vary (0.6)	N (0.4)	NW (0.4)	NW (0.1)	N (0.1)	N (0.3)	NW (0.2)	SE (0.1)	SE,S (0.2)	S (0.3)
2014	SE (0.3)	NW (0.8)	N (0.7)	N (0.4)	NW (0.4)	N,NW (0.1)	NE,NW (0.2)	NW (0.2)	NW (0.3)	N (< 0.1)	Vary (0.1)	SE (0.2)

6.5 Discussion

Moderate genetic differentiation (F_{ST} = 0.050) between populations and a high level of genetic diversity within populations were detected in nine *F. montana* populations in riparian forests of western Thailand. These results are consistent with other studies of dioecious fig tree species such as *F. pumila* (F_{ST} = 0.094, Liu et al., 2013), *F. hirta* (F_{ST} = 0.037, Yu & Nason, 2013) and *F. sarmentosa* (F_{ST} = 0.055, Wang et al., 2018) that were carried out in China. It is suggested that this pattern results from long distance gene flow among fig trees populations (Ahmed et al., 2009; Yu et al., 2010).

Monoecious fig trees have been shown to be more likely to exhibit extensive gene flow due the long range movement of their pollinators, from 5.8 - 160 km (Nason et al., 1998; Ahmed et al., 2009). Most pollination of dioecious fig trees is believed to occur at shorter distances (Harrison, 2003; Compton et al., 2005). Unlike monoecious fig trees, most dioecious fig trees are small shrubs, growing mostly in the understorey level of forest, whereas monoecious figs are often tall trees (Harrison & Rasplus, 2006). Trees having a large canopy and height can gain the benefits of long range pollination because of high wind speeds blowing above the canopy level, although the dispersal direction of their pollinators is uncontrollable (Ware & Compton, 1994; Compton et al., 2000). Long distance movements of dioecious fig tree pollinators may also be inferred from the low genetic differentiation in the pollinators of *F. montana (Liporrhopalum=Kradibia tentacularis),* and *F. septica* (*Ceratosolen bisulcatus*), which suggested that the pollinators of these dioecious fig trees may be carried by the wind across the Sunda Straits and that sea was not a gene flow barrier (Zavodna et al., 2005a). However, more restricted gene flow of *F. montana* pollinator within mainland populations might be affected by geographical barriers (Zavodna et al., 2005a). Also, it has been suggested that *Wiebesia callida,* the pollinator of the dioecious *F. sarmentosa*, which mostly grows in open habitats, could be transported for long distances by air currents across open areas in the same way that pollinators can be transported by the wind across dense forest (Wang et al., 2018). In this study, all the *F. montana* individuals grew along stream banks, which are more open than in the adjacent forest, so wind currents can potentially move along the streams and promote long distance pollinator movement. Moreover, both sexes of *F. montana* individuals bore small number of fig throughout the year, ranging from less than 10 to nearly 100 figs (CHAPTER 2). Thus, the small number of immature figs present at one time may drive a longer movement range of pollinators because they need to find figs in other areas (Wang et al., 2018).

Although most of the genetic variation was within *F. montana* populations, with only 5% estimated to have been obtained by migration from other populations, gene flow could still be detected in most pairs of population ($N_m > 1$). Significant isolation by distance (IBD) was detected among all nine *F. montana* populations. However, within river systems IBD was not found, suggesting that gene flow has occurred more frequently between populations within the same river system. No populations showed evidence of having experienced historical bottlenecks.

In Kanchanaburi, from February to September, 2011 - 2014, all the sample sites were influenced by North and North Westerly winds. This is presumably typical and is likely to influence the direction of movement of the pollinators of *F. montana*. It is revealed that higher migrant movement has occurred from PW to the

North West populations (DCT and KTJ), which is consistent with the main wind direction. Predominantly South and South Easterly winds affected only three months, from November to January, and air currents at this time of year may have aided pollen flow from the Northern to the Southern populations. Higher migrant transportation was detected from population KTJ to the South and South East populations (DCT, PW and PT), and from PW to the southern population, PT. This is in the same direction of South East air current (Table 6.12). Lower migrant movement was detected from other populations, which may be blocked by geographical barriers. For example, population TKT is separated from population KTJ by a long ridge of mountains running from South to South East. Also, populations PW and H are separated by a mountain that might be a barrier to North West and South East air currents and any pollinators they contain.

F. montana individuals produce figs throughout the year, but flowering peaks from April to July (CHAPTER 2) at a time when the North and North West air currents affected the areas. During this time female fig wasps might have more chance to find receptive figs to lay their eggs if they are carried long distances. However, the phenological data were obtained from one study site (KTJ), and there are no data from the other eight populations to confirm this possibility. Nonetheless, all the populations are affected by a similar monsoon climate, and it is expected that the fig production peak might not be much different.

Gene flow via seed dispersal was relatively low between the populations of *F. montana*, as shown by the high levels of genetic differentiation of chloroplast DNA and low maternal inherited gene flow parameter (Nm_s). Several birds, especially bulbuls (Pycnonotidae), are the major eaters of *F. montana* figs in western

Thailand (CHAPTER 3). Bulbuls disperse the seeds of many oriental plants, and seeds are still viable after being defaecated by bulbuls (Corlett, 2017). However, bulbuls are territorial species and occupy a small area of core home range, covering 1-3 ha (Weir, 2004; Tanasarnpaiboon, 2008; Khamcha et al., 2012; Kerdkaew, 2014). They also have a short gut passage time of around 20-40 minutes, suggesting that they are short distance seed dispersers (< 100 m) and ingested seeds are mostly dispersed within a couple of meters from parent plants (Weir, 2004; Khamcha et al., 2014; Kerdkaew, 2014). However, some bulbul species, for example, the Black-and-white bulbul (*Pycnonotus melanoleucos*) can travel a long distance which extends its range size to 50 ha when it is tracking fruit production in Malaysian lowland rain forest (Lambert, 1989). Therefore, it is possible that bulbuls can be long distance seed dispersers; although it rarely happens.

Other possible long distance seed dispersal events could be due to the aquatic animals or water currents as *F. montana* grows close to the stream banks where some figs could fall down directly into the water (CHAPTER 2; CHAPTER 4). In western Thailand, one of the most common fish in the riparian forest is the Blue mahseer (*Neolissochilus stracheyi*: Cyprinidae) which is known to feed on fallen *F. montana* and other riparian figs that fall into the water. Although the Blue mahseer responded to fallen figs and fed on them immediately, most *F. montana* seeds were destroyed after passing its digestive tract, suggesting that the fish acts mainly as a seed predator rather than disperser (CHAPTER 4). The gut passage time of the Blue mahseer was six to ten hours approximately (CHAPTER 4), and some seed may be retained in the gut for longer than 24 hours. The movement ranges of the Blue mahseer are still unknown, but it is suggested that some species of the cyprinids migrate during the breeding season to spawn upstream (Liu & Yu, 1992). This suggests that *N. stracheyi* may extend their movements and any seed dispersal during their breeding season, but their mobility is limited by weirs and long distance movements may only be possible during the rainy season, when water levels are high.

Water currents could also affect gene flow in *F. montana* by moving floating figs from upstream to downstream populations, potentially generating long distance seed dispersal. In this study, high possibility of migration of *F. montana* genes was found from an upstream (PW) to a downstream site (PT), but low gene flow of chloroplast DNA was detected. Moreover, chloroplast haplotype richness in the downstream populations was lower than the upstream populations. Therefore, long distance seed dispersal by water seems to be seldom in *F. montana*. Man-made permanent weirs are common at all the study sites, including two big dams which were constructed between 1974 - 1979 located close to the KTJ, DCT, H and E populations. It is suggested that dams increase fragmentation in riparian ecosystems (Dynesius & Nilsson, 1994) because they can block the dispersal of riparian plant seeds (Nilsson et al., 1993). The strong genetic isolation between *Myricaria germanica* (Tamaricaceae) populations separated by a large dam in southern Germany, suggesting a block to gene flow, provides an example (Werth et al., 2014). However, the effect of dams on gene flow in *F. montana* requires more population sampling to describe the effect precisely. Seed dispersal by water currents can be inferred by a higher haplotype richness among downstream populations, for example in the riparian plant *Ainsliawa faurieana* (Asteraceae) (Mitsui et al., 2010). Together with transporting seeds, water currents could move whole individuals of riparian plants downstream during flash flooding, (Mitsui et al., 2010). Neither seems to be happening among the populations of *F. montana* along the streams in Kanchanaburi.

In summary, the extensive gene flow among populations of *F. montana*, reflected in weak genetic structure and differentiation, is likely to reflect long range pollination, aided by air currents that carry pollinator fig wasps. In contrast, long distance seed dispersal, which was potentially assisted by water currents in this riparian species, appears to be rare. Although there was evidence of gene flow among populations, genetic variation was primarily within populations, suggesting that most dispersal events occur at a local scale. Further studies should highlight the patterns of gene flow among fig wasps and seed dispersers, and why the movements of frugivores do not appear to provide extensive *Ficus* gene flow.

Chapter 7 A global review of fig-eating by vertebrate frugivores: 2018 update

7.1 Abstract

Fig trees (*Ficus* spp., Moraceae) provide food resources for wide variety of frugivores. In 2001, Shanahan et al. (2001) published a global summary of interactions between vertebrate frugivores and fig trees that confirmed the importance of fig trees for maintaining a huge range of frugivores and also shed light on the coevolution between animals and fruiting plants. They also highlighted gaps in our knowledge. Here, the global fig-eating vertebrate frugivore database is updated, based on 482 published papers from 2001 to 2017 and ad hoc communications. The taxonomy of both the fig trees and frugivores has also been updated based on recent scientific nomenclature. Combining the earlier and later data, figs of 322 fig tree species (38.8% of global fig tree species richness) are confirmed as eaten by vertebrate frugivores. The largest increase in records is from the Neotropics from where 69 species (52.3% of the regional species) have recorded frugivore interactions. *Ficus* subgenus *Urostigma* species, which comprise the strangler figs, have the highest number of frugivory records (at least 20 frugivore species per tree), which emphasises their role as keystone resources for frugivores. Other subgenera, especially those containing smaller dioecious fig trees, may not fit with a keystone status. The high number of frugivores associated with strangler fig trees has negative economic impacts when it facilitates the spread of invasive species such as *Ficus microcarpa*. This species readily recruits frugivores when outside its native range, including frugivores that have themselves been introduced. Most of the new frugivory records had been obtained from dietary studies, mainly of

terrestrial mammals, fruit bats and birds. In total, 1,432 bird species (from 99 families) and 435 mammal species (from 49 familes) are recorded as fig eaters, with a few records of fish and reptiles as fig eaters. Frequently-recorded bird families were Mynahs (Sturnidae), Parrots (Psittacidae), Bulbuls (Pycnonotidae) and Pigeons (Columbidae). The main groups of mammals were Old World fruit bats (Pteropodidae), Old World monkeys (Cercopithecidae) and New World fruit bats (Phyllostomidae). The weaknesses in the data set outlined by Shanahan et al. (2001) are still present, with most of the new studies recording only that figs of species X were eaten by frugivore species Y, and with a continued bias in records towards records from larger fig tree species. The dataset has increased mainly in breadth of coverage, rather than detailed studies of the quality and quantity of seed dispersal services and the geographical spread of studies is still concentrated in certain areas. Future studies should emphasise intensive studies of focal species, ideally carried out at multiple sites.

7.2 Introduction

Ficus (fig trees) is one of the most diverse plant genera in the world (Berg, 1989), characterised by its unique enclosed inflorescences (figs, also called syconia). It has a predominantly tropical and sub-tropical distribution, but with a few species extending into northern temperate areas. The most species rich continent is Asia, where more than half the total number of species are found (The Plant List, 2018). Asia is also the continent where a majority of species exhibit a functionally dioecious (anatomically gynodioecious) breeding system, with some trees producing figs that support the development of seeds and other trees having figs that support only the development of the fig wasps (Agaonidae) that are their only pollinators.

Outside of Asia, dioecious species are in a minority or entirely absent. Currently, 19 different sections of fig trees, belonging to six subgenera (*Ficus, Synoecia, Sycidium, Sycomorus, Pharmacosycea* and *Urostigma*), are described (van Noort & Rasplus, 2018), which differ in their growth form and details of their inflorescence structure.

Seed dispersal has several benefits for plants, such as reducing competition under parent trees and transporting seeds to new suitable sites for germination (Howe & Smallwood, 1982; Schupp et al., 2010). Seed dispersal can be characterised as either abiotic or biotic. Abiotic dispersal by water is likely to be significant for many species that live in riparian habitats (CHAPTER 3 ; CHAPTER 4) and a small number of species, such as *F. squamosa,* probably do not depend at all for animals to feed on their figs and disperse the seeds they contain (Pothasin et al., 2016). Two different types of biotic seed dispersal are recognised. Endozoochorous dispersal is where seeds are eaten by animals and dispersed after defaecation or spitting and exozoochorous dispersal involves seeds (and their surrounding diaspores) that stick to the outside of animals (Howe & Smallwood, 1982; Corlett, 1998). Exozoochory has not been recorded among *Ficus* species, and almost all the species depend on endozoochory. Endozoochory requires plants to produce rewards for dispersal agents, often in the form of fleshy fruits, and the fruits must offer cues such as bright colours that attract the frugivores (Shanahan, 2000). *Ficus* genus produces fleshly fruits that are rich in sugar (Vinson et al., 2005) and also have a wide variety of colours to target different frugivorous species (Shanahan et al., 2001).

Figs show great variation in physical characteristics, while at the same time maintaining a common basic structure. This variation in position, size, colour and smell, together with the all-year fruiting of some species, and their sometimes huge figcrops, has led to *Ficus* being thought of as keystone resources for frugivorous animals, especially in tropical forests (Shanahan et al., 2001). It is also becoming realised that fig trees are important sources of food for insectivorous species (see Sreekar et al., 2010).

Among the 830 currently described *Ficus* species (The Plant List, 2018), only 260 had any records of their associated frugivores when a global review was published based on records up to and including the year 2000 (Shanahan et al., 2001). The review of Shanahan et al. (2001) nonetheless highlighted the diversity and complexity of interactions between the 260 fig tree species and over 1200 species of associated vertebrate frugivores. The review highlighted the wide variety of frugivores that interact with figs, including birds, mammals, fish and reptiles. It also noted that some frugivorous groups appear to rely almost entirely on ripe figs (Shanahan et al., 2001**.** Furthermore, vertebrates are not the only frugivores that eat figs, and the small size of fig seeds means that they can also be dispersed by ants (Kaufmann et al., 1991) and crabs (Staddon et al., 2010).

This study updates the database of global vertebrate fig-eaters published by Shanahan et al. (2001) and brings records up until 2017. The aims of this update are (i) to explore trends in the study of interactions between fig trees and vertebrate fig-eaters; (ii) to recalibrate the scientific nomenclature of *Ficus* and its frugivores to incorporate the most recent taxonomic revisions, (iii) to collate records of interactions between fig trees and their dispersal agents and (iv) to determine whether the gaps in understanding of these relationships highlighted by Shanahan et al. (2001) have subsequently been addressed.

7.3 Methods

The original database of global figs and fig-eaters based on a total of 568 published records, unpublished data and personal communication, up to year 2000 (Shanahan et al., 2001) was updated by reviewing the published literature from 2001 to 2017, including referencing the world bird biological database– Handbook of the Birds of the World: Alive where the diet information of birds was explored species by species (total = 11,232 bird species) (del Hoyo et al., 2017). The published research was accessed through online databases using Google Scholar and the keywords '*Ficus*' and 'Frugivore', '*Ficus*' and 'Fish', '*Ficus*' and 'Reptile', '*Ficus*' and 'Bird' or '*Ficus*' and 'Mammal', resulting in more than 3,000 published sources, of which 482 provided usable data. Only published sources that confirmed feeding by frugivores were included for further analysis. The studies that did not clearly confirm frugivore consumption of figs were excluded from the dataset. The fig-eater database consists of the vertebrate fig-eaters' taxonomic data (Class, Order, Family, Genus and Species), the consumed fig species, the region of study, and how important figs are to their diet. The taxonomic nomenclature of frugivorous birds and mammals was updated by referring to the Handbook of the Birds of the World: Alive (del Hoyo et al., 2017) and the Global Mammals Checklist, last updated in September 2017 (Mammal Watching, 2017) respectively. The Reptile Database (Uetz et al., 2018) and the Fish Base (Froese & Pauly, 2017) were used to update the reptile and fish nomenclature, respectively. *Ficus* taxonomy and nomenclature was updated by referring to the World Checklist of Selected Plant Families (WCSP, 2017), The Plant List (2018) and Fig Web (van Noort & Rasplus, 2018), an online database that provided the recently updated data of around 830 global fig species. Ad hoc additions were made when additional records were detected. The updated fig and frugivore species lists were merged (with permission) with the original data of Shanahan et al. (2001) for further analysis (https://figfrugivory.wordpress.com/) (QR 7.1). The small numbers of European records were merged with Indo-Australian. The importance of each frugivore family in seed dispersal and their effectiveness was summarised from the articles published from 2001 to 2017.

QR 7.1

The annual published article numbers from 2001 to 2017 were tested among geographic distribution ranges using a generalised linear model (GLM) with a Poisson error distribution. The relationship between the number of published papers and years was tested using the GLM with a Poisson error distribution. Chi-squared tests were applied for detecting the deviation of frequency of genera and species of frugivores and fig trees. When the degrees of freedom were equal to one, the Yates' correction was applied to Chi-squared tests (Zar, 2010). As the number of frugivore species interacting with different subgenera of fig trees displayed overdispersion, a GLM with a Quasi-Poisson error distribution was applied. The F value was reported instead of the Chi-squared values because of the overdispersion of the data. All analyses were performed in R-version 3.4.3.

7.4 Results

7.4.1 Dataset exploration

There were 482 published records detected from 2001 to 2017 that were reviewed. The number of records detected peaked in 2015 and then declined slightly (Fig. 7.1). A positive relationship between the year of publication and the total number of published papers was detected (GLM: $\chi^2 = 27.78$, df = 1, $P < 0.001$), suggesting a general increase in interest in the topic. Three biogeographical regions were recognised. The frequency of published records in each region was not significantly different, suggesting that relevant activity in the three regions has been equal (Table 7.1) (GLM: $\chi^2 = 2.00$, df = 2, P = 0.37). The interaction between frequency of published records in different regions and year of study was not significance (GLM: $\chi^2 = 0.13$, df = 2, P = 0.94).

Table 7.1. The annual number of published records of *Ficus*-frugivore interactions from three biogeographical regions.

Years	Regions			Total
	Afrotropical	Indo-Australian	Neotropical	
2001	5	3	5	13
2002	4	5	8	17
2003	6	9	5	20
2004	6	6	11	23
2005	3	11	8	22
2006	9	8	10	27
2007	5	9	11	25
2008	7	6	8	21
2009	8	11	14	33
2010	9	9	8	26
2011	9	15	11	35
2012	14	14	14	42
2013	7	12	13	32
2014	13	19	11	43
2015	13	19	14	46
2016	12	12	9	33
2017	4	11	9	24
Mean	**7.88**	**10.53**	**9.94**	**28.35**
SE	**0.84**	**1.09**	**0.69**	**2.28**

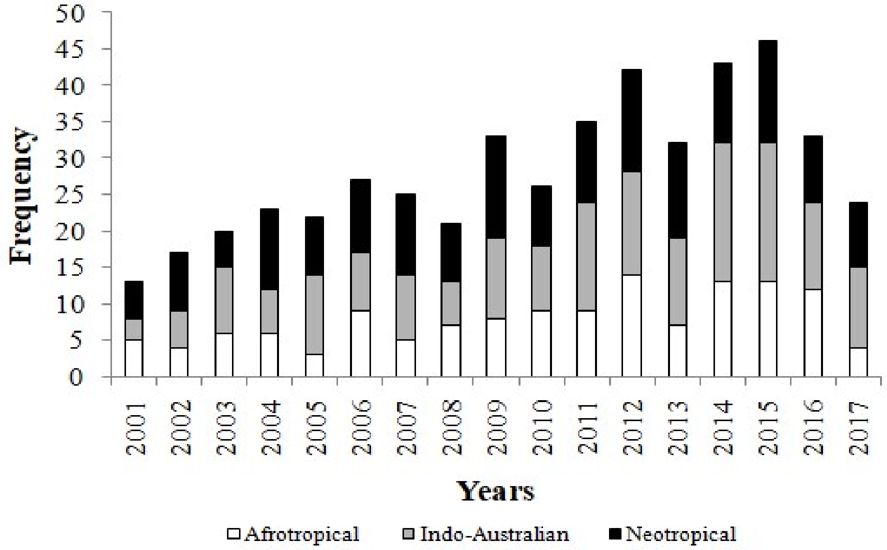

Fig. 7.1. Annual variation since 2001 in the frequency of published records in three different regions.

The majority of the 482 published sources were based on animal-centred research (432 records, 89% of records) that did not focus on particular plants. These included dietary studies inferred from faecal analysis, gut contents or stable isotopes and following the feeding of focal animals. Within these animal-centred studies, the research was primarily conducted on the diet or feeding behaviour of terrestrial mammals (259 records, 54% of records), fruit bats (81 records, 17% of records), and birds (72 records, 15% of records) (Table 7.2). Far fewer of the records were based on plant-centred studies. Some involved watching fig trees (44 records, 9.13% of records) and others were reviews (seven records, 1.45% of records). In plant-centred studies, almost all the observational results of fig trees reported combined bird and non-flying mammal records (24 records, 4.98% of records) or birds only (13 records, 2.70% of records of records) (Table 7.2).

Checking for current plant names in the recent and earlier Shanahan et al. (2001) datasets resulted in some synonymies being recognised. As a result, the list of *Ficus* species with associated frugivore data in the original dataset decreased from 260 to 245. The post 2000 data set added a further 77 species, giving a combined total of 322 *Ficus* species for which at least one associated frugivore has been recorded. This represents 42.6% of currently-recognised global *Ficus* species richness. Afro-tropical fig trees have the highest proportion of species with frugivore records (78 species, 69.0% of the Afrotropical flora). More than half of Neotropical fig trees also have frugivore records (69 species, 52.3% of the flora). In contrast, the more species-rich Indo-Australian fig tree flora provided only 175 recorded species, which is just 34.2% of the total.

In comparison with Shanahan et al.'s (2001) data, the known fig species that interacted with frugivores has slightly increased over the past 17 years (Afro-tropical *Ficus*: from 55.8% to 69.0%; Indo-Australian *Ficus*: from 28.2% to 34.2%). Moreover, there was a large increase in the proportion of Neotropical fig species found in this review (from 28.8% to 52.3%, Table 7.3).

The number of monoecious *Ficus* species with records of frugivores is over-represented in the database, relative to dioecious figs, and linked to the relative shortage of records from Asia, where dioecious species predominate (Table 7.4). This pattern is similar to what was described by Shanahan et al. (2001). Focusing on subgenera and sections, there is over-representation in section *Sycomorus*, subgenus *Sycomorus*; and in section *Urostigma*, subgenus *Urostigma*. These are trees that tend to have large, synchronised crops that can attract large assemblages of frugivores. Conversely, there is significant under-representation of research in section *Oreosycea* of subgenus *Pharmacosycea* (Table 7.4).

Table 7.2. The themes of published records from 2001-2017 used in the review.

Study types	Number of sources	% of total
Reviews	**7**	**1.45**
Animal-centred studies	**432**	**89.42**
Birds	72	14.94
Fruit bats	81	16.80
Terrestrial mammals	259	53.73
Reptiles	11	2.28
Fishes	8	1.66
Plant-centred studies	**44**	**9.13**
Birds only	13	2.70
Fruit bats only	2	0.41
Terrestrial mammals only	1	0.21
Birds and fruit bats	1	0.21
Birds and terrestrial mammals	24	4.98
Terrestrial mammals and fruit bats	0	0.00
Birds, terrestrial mammals and fruit bats	2	0.41
Terrestrial mammals, fruit bats and fishes	1	0.21
Total	**482**	

Table 7.3. The number of *Ficus* species with frugivore records based on Shanahan et al. (2001) and the current update.

Areas	*Ficus* species richness	Frugivore records			
		Shanahan et al. (2001)		Updated data	
		N	% of flora	N	% of flora
Afrotropical	113	63	55.8	78	69.0
Indo-Australian	511	144	28.2	175	34.2
Neotropical	132	38	28.8	69	52.3
Total	**756**	**245**	**32.4**	**322**	**42.6**

Table 7.4. Comparisons of global fig tree interactions with frugivores from the original Shanahan et al. (2001) dataset and the updated dataset (2001-2017). The deviation from global fig species of the updated dataset was examined by Chi-square test with Yates' correction (degrees of freedom equal one. < = under representation and > = over-representation). Taxonomy follows van Noort & Rasplus (2018). Some 'unknown' species could not be related to currently recognised plant names.

		Pre-2001 Shanahan et al. (2001)		**Pre-2018 (this study)**		**Global species richness**		**χ2**	***P*-Value**	
		Species	**%**	**Species**	**%**	**Species**	**%**			
(a) Sexual system										
Monoecious		163	66.5	206	64.0	420	55.1	9.625	< 0.001	>
Dioecious		82	33.5	108	33.5	342	44.9			<
Unknown		-	-	8	2.5	-	-			
(b) Fig taxonomy										
<u>Subgenus</u>	**<u>Section</u>**									
Ficus	*Eriosycea*	5	2.0	7	2.2	30	3.9	1.521	0.217	
Ficus	*Ficus*	5	2.0	9	2.8	31	4.1	0.645	0.421	
Synoecia	*Kissosycea*	5	2.0	5	1.6	28	3.7	2.611	0.106	
Synoecia	*Rhizocladus*	11	4.5	11	3.4	44	5.8	1.937	0.164	
Sycidium	*Palaeomorphe*	9	3.7	9	2.8	31	4.1	0.648	0.421	
Sycidium	*Sycidium*	24	9.8	29	9.0	85	11.2	0.712	0.399	
Sycomorus	*Adenosperma*	0	0.0	2	0.6	20	2.6	3.484	0.062	
Sycomorus	*Bosscheria*	2	0.8	2	0.6	2	0.3	0.114	0.735	
Sycomorus	*Dammaropsis*	1	0.4	2	0.6	5	0.7	0.122	0.727	
Sycomorus	*Hemicardia*	1	0.4	1	0.3	3	0.4	0.117	0.732	
Sycomorus	*Papuasyce*	1	0.4	1	0.3	3	0.4	0.117	0.732	
Sycomorus	*Sycocarpus*	13	5.3	16	5.0	37	4.9	0.006	0.937	
Sycomorus	*Sycomorus*	14	5.7	19	5.9	21	2.8	4.969	< 0.05	>
Pharmacosycea	*Oreosycea*	7	2.9	9	2.8	76	10.0	13.265	< 0.001	<
Pharmacosycea	*Pharmacosycea*	5	2.0	14	4.3	23	3.0	0.773	0.379	
Urostigma	*Americana*	33	13.5	51	15.8	111	14.6	0.136	0.712	
Urostigma	*Galoglychia*	46	18.8	52	16.1	97	12.7	1.436	0.231	
Urostigma	*Malvanthera*	11	4.5	12	3.7	23	3.0	0.156	0.693	
Urostigma	*Urostigma*	52	21.2	63	19.6	92	12.1	7.076	< 0.001	>
Unknown	*Unknown*	-	-	8	2.5	-	-			
Total		**245**		**322**		**762**				

Among the 322 species for which there are frugivory records, 15.74 ± 1.40 (Mean ± SE) species were recording as eating their figs. Most of the *Ficus* species (158 species, 49.06%) were recorded as interacting with between one and six frugivore species, suggesting that additional studies would add to their totals (Fig. 7.2). Conversely, 24 *Ficus* species are known to interact with more than 50 species of frugivores (Fig. 7.2 and Table 7.5). Fig trees in the subgenus *Urostigma* (20.47 ± 2.29) had recorded interactions with a significantly higher number of frugivore species than the other five subgenera (GLM: $F_{(5, 321)} = 3.305$, $P < 0.001$; Fig. 7.3). Figs of *F. microcarpa* and *F. benjamina* are recorded as being consumed by the most frugivore species, reflecting their wide distribution ranges and they have also been introduced to many areas around the world (Table 7.5). Most of the top 30 fig tree species (19 species) are native to the Indo-Australian region, despite the relative shortage of *Ficus* species that have any records in this region (Table 7.3).

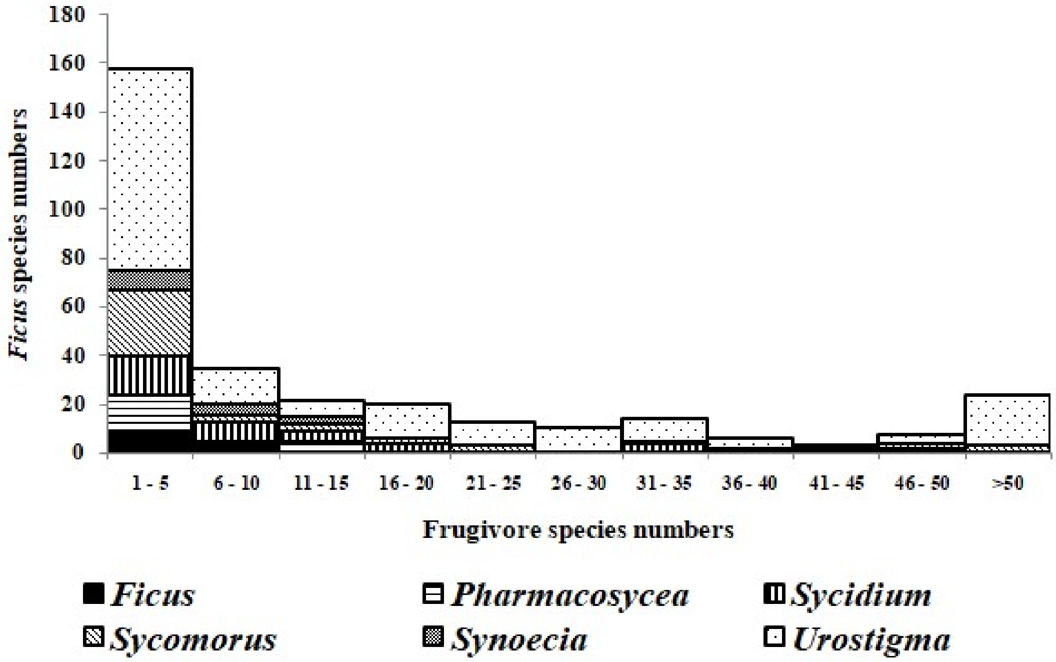

Fig. 7.2. Frequency distribution of frugivore species records from *Ficus* species from six different subgenera.

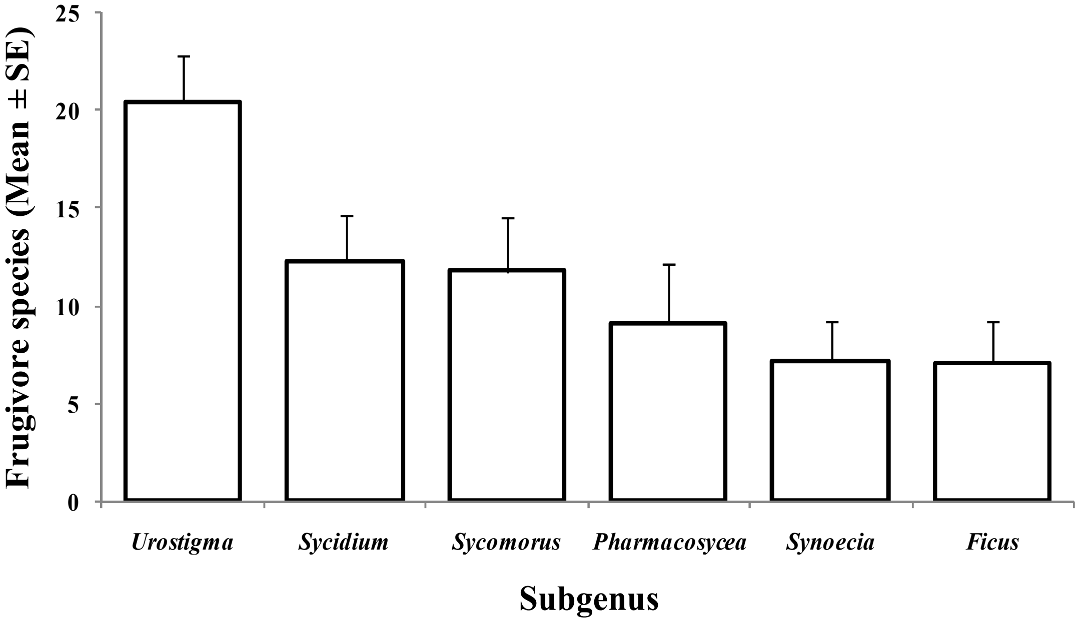

Fig. 7.3. Frugivore species recorded as interacting with different fig trees belonging to subgenera of *Ficus*.

Table 7.5. The thirty fig tree species with the greatest numbers of frugivore species recorded as feeding on their figs.

Ficus **species**	**Subgenus**	**Region**	**Frugivore species**
Ficus microcarpa	Urostigma	Indo-Australian, Neotropical (introduced)	240
Ficus benjamina	Urostigma	Indo-Australian, Neotropical (introduced)	158
Ficus thonningii	Urostigma	Afrotropical	112
Ficus lutea	Urostigma	Afrotropical	102
Ficus virens	Urostigma	Indo-Australian	99
Ficus pertusa	Urostigma	Neotropical	98
Ficus drupacea	Urostigma	Indo-Australian	92
Ficus cotinifolia	Urostigma	Neotropical	87
Ficus americana	Urostigma	Neotropical	75
Ficus sur	Sycomorus	Afrotropical	74
Ficus subcordata	Urostigma	Indo-Australian	74
Ficus caulocarpa	Urostigma	Indo-Australian	73
Ficus crassiramea	Urostigma	Indo-Australian	67
Ficus luschnathiana	Urostigma	Neotropical	67
Ficus altissima	Urostigma	Indo-Australian	66
Ficus insipida	Pharmacosycea	Neotropical	63
Ficus citrifolia	Urostigma	Neotropical	63
Ficus racemosa	Sycomorus	Indo-Australian	60
Ficus stupenda	Urostigma	Indo-Australian	60
Ficus sumatrana	Urostigma	Indo-Australian	58
Ficus superba	Urostigma	Indo-Australian	58
Ficus kerkhovenii	Urostigma	Indo-Australian	54
Ficus benghalensis	Urostigma	Indo-Australian	52
Ficus pisocarpa	Urostigma	Indo-Australian	51
Ficus exasperata	Sycidium	Afrotropical	50
Ficus religiosa	Urostigma	Indo-Australian	50
Ficus obliqua	Urostigma	Indo-Australian	49
Ficus tinctoria	Sycidium	Indo-Australian	48
Ficus variegata	Sycomorus	Indo-Australian	48
Ficus sycomorus	Sycomorus	Afrotropical	46

F. microcarpa has 190 recorded frugivores in its native range (Indo-Malayan to New Guinea and Northern Australia, see Fig. 7.4). Of the 190 native-range frugivores, 149 species are birds (78.42% of native-range frugivores), 28 are terrestrial mammals (14.74% of native-range frugivores) and 13 are bats (6.84% of native-range frugivores). There are 12 frugivore species (nine birds, 75% of wide-distribution range frugivores, and three terrestrial mammal species, 25% of wide-distribution range frugivores) that have a wide distribution range and may feed on *F. microcarpa* figs in both its native and introduced ranges (Table 7.6). The further 38 associated species in its introduced range include 35 bird species (34 Neotropical and one European species, 92.11% of frugivores in the introduced range of *F. microcarpa*) and three bat species (two Neotropical and one Afro-tropical, 7.89% of frugivores in the introduced range of *F. microcarpa*) that consumed *F. microcarpa* figs (Table 7.7). In the introduced range of *F. microcarpa*, figs were likely consumed by birds in higher percentage than that of its in native ranges (92.11% vs. 78.42%). However, the frequency of frugivores in two different groups (birds and mammals, including bats) was not significantly different among distribution ranges of *F. microcarpa* (introduced, native and both introduced, and native ranges) (Chi-square: $\chi^2 = 5.658$, df = 2, P = 0.06).

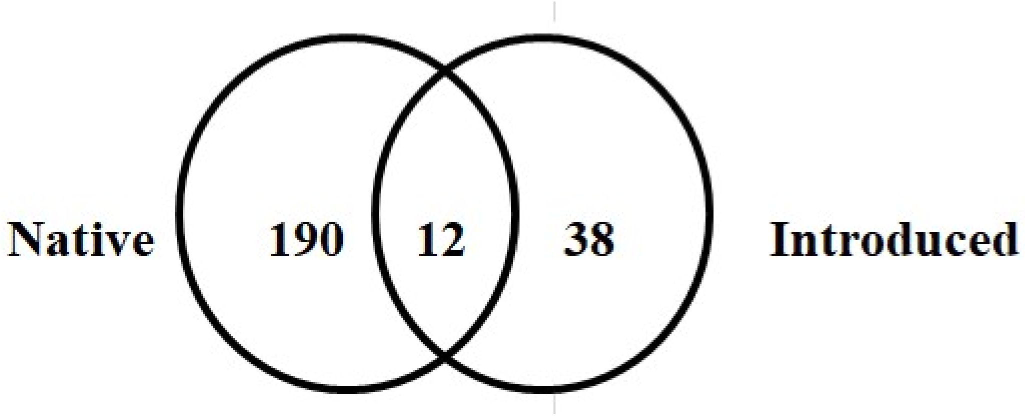

Fig. 7.4. The number of frugivore species recorded feeding on *F. microcarpa* figs in the native ranges of the plant and the frugivores (190), in the introduced or native ranges of both groups (12) and, where *F. microcarpa* has been introduced and its figs were eaten by native species (38).

Table 7.6. The 12 frugivore species known to feed on *F. microcarpa* figs that have ranges suggesting they can feed on the plant in both its native and introduced ranges.

Class	Order	Family	Common name	Scientific name	Range
Aves	Passeriformes	Turdidae	Eyebrowed thrush	*Turdus obscurus*	Eurasian
Aves	Columbiformes	Columbidae	Rock dove (Feral pigeon)	*Columba livia*	Worldwide
Aves	Columbiformes	Columbidae	Oriental turtle dove	*Streptopelia orientalis*	Eurasian
Aves	Passeriformes	Muscicapidae	Blue rock thrush	*Monticola solitarius*	Eurasian
Aves	Passeriformes	Paridae	Great tit	*Parus major*	Eurasian
Aves	Passeriformes	Passeridae	House sparrow	*Passer domesticus*	Eurasian
Aves	Passeriformes	Passeridae	Eurasian tree sparrow	*Passer montanus*	Eurasian
Aves	Passeriformes	Corvidae	Black-billed magpie	*Pica pica*	Eurasian
Aves	Psittaciformes	Psittacidae	Rose-ringed parakeet	*Psittacula krameri*	Indian-African
Mammalia	Rodentia	Muridae	House mouse	*Mus musculus*	Worldwide
Mammalia	Rodentia	Muridae	Brown rat	*Rattus norvegicus*	Worldwide
Mammalia	Rodentia	Muridae	Black rat	*Rattus rattus*	Worldwide

Table 7.7. The 38 frugivore species known to feed on *F. microcarpa* figs in the introduced range of this fig tree species.

Class	Order	Family	Common name	Scientific name	Range
Aves	Psittaciformes	Psittacidae	Canary-winged parakeet	*Brotogeris versicolurus*	Neotropics
Aves	Piciformes	Picidae	Blond-crested woodpecker	*Celeus flavescens*	Neotropics
Aves	Passeriformes	Thraupidae	Bananaquit	*Coereba flaveola*	Neotropics
Aves	Piciformes	Picidae	Green-barred woodpecker	*Colaptes melanochloros*	Neotropics
Aves	Columbiformes	Columbidae	Ruddy ground-dove	*Columbina talpacoti*	Neotropics
Aves	Cuculiformes	Cuculidae	Smooth-billed ani	*Crotophaga ani*	Neotropics
Aves	Passeriformes	Corvidae	Curl-crested jay	*Cyanocorax cristatellus*	Neotropics
Aves	Passeriformes	Thraupidae	Blue dacnis	*Dacnis cayana*	Neotropics
Aves	Piciformes	Picidae	Lineated woodpecker	*Dryocopos lineatus*	Neotropics
Aves	Passeriformes	Tyrannidae	Yellow-bellied elaenia	*Elaenia flavogaster*	Neotropics
Aves	Passeriformes	Tyrannidae	Variegated flycatcher	*Empidonomus varius*	Neotropics
Aves	Passeriformes	Fringillidae	Purple-throated euphonia	*Euphonia chlorotica*	Neotropics
Aves	Psittaciformes	Psittacidae	Blue-winged parrotlet	*Forpus xanthopterygius*	Neotropics
Aves	Passeriformes	Tyrannidae	Cattle tyrant	*Machetornis rixosus*	Neotropics
Aves	Passeriformes	Tyrannidae	Boat-billed flycatcher	*Megarhynchus pitangua*	Neotropics
Aves	Piciformes	Picidae	White woodpecker	*Melanerpes candidus*	Neotropics
Aves	Passeriformes	Mimidae	Chalk-browed mockingbird	*Mimus saturninus*	Neotropics
Aves	Passeriformes	Tyrannidae	Streaked flycatcher	*Myiodynastes maculatus*	Neotropics
Aves	Passeriformes	Thraupidae	Hooded tanager	*Nemosia pileata*	Neotropics
Aves	Columbiformes	Columbidae	Picazuro pigeon	*Patagioenas picazuro*	Neotropics
Aves	Passeriformes	Thraupidae	Fawn-breasted tanager	*Pipraeidea melanonota*	Neotropics
Aves	Passeriformes	Cardinalidae	Hepatic tanager	*Piranga flava*	Neotropics
Aves	Passeriformes	Tyrannidae	Great kiskadee	*Pitangus sulphuratus*	Neotropics
Aves	Passeriformes	Thraupidae	Burnished-buff tanager	*Tangara cayana*	Neotropics
Aves	Passeriformes	Thraupidae	Sayaca tanager	*Tangara sayaca*	Neotropics
Aves	Passeriformes	Thraupidae	Swallow tanager	*Tersina viridis*	Neotropics
Aves	Passeriformes	Turdidae	Creamy-bellied thrush	*Turdus amaurochalinus*	Neotropics
Aves	Passeriformes	Turdidae	Eurasian blackbird	*Turdus merula*	European
Aves	Passeriformes	Turdidae	Andean slaty-thrush	*Turdus nigriceps*	Neotropics
Aves	Passeriformes	Turdidae	Rufous-bellied thrush	*Turdus rufiventris*	Neotropics
Aves	Passeriformes	Tyrannidae	Tropical kingbird	*Tyrannus melancholicus*	Neotropics
Aves	Passeriformes	Tyrannidae	Fork-tailed flycatcher	*Tyrannus savana*	Neotropics
Aves	Passeriformes	Tyrannidae	Eastern kingbird	*Tyrannus tyrannus*	Neotropics
Aves	Passeriformes	Vireonidae	Red-eyed vireo	*Vireo olivaceus*	Neotropics
Aves	Passeriformes	Emberizidae	Rufous-collared sparrow	*Zonotrichia capensis*	Neotropics
Mammalia	Chiroptera	Phyllostomidae	Jamaican fruit bat	*Artibeus jamaicensis*	Neotropics
Mammalia	Chiroptera	Pteropodidae	Egyptian fruit bat	*Rousettus aegyptiacus*	Afrotropics
Mammalia	Chiroptera	Phyllostomidae	Tent-making bat	*Uroderma bilobatum*	Neotropics

7.4.2 Vertebrate animals feeding on figs

Shanahan et al. (2001) reported that 1,271 species of frugivores were known to eat figs. Merging this with the dataset obtained from 2001 to 2017, the number of fig-eating animal species increased to 1,909 species. The number of fig-eating birds increased from 979 to 1432 species, and the number of mammal species has increased from 280 to 435. The increase in fish (from 3 to 25) and reptile (from 9 to 17) species was also noted, but there was not as large an increase as birds and mammals because few species of these animals were recorded. The global vertebrate fig-eaters were categorised into families alphabetically and were separated into four different classes (fish, reptiles, birds and mammals, see Tables 7.8–7.11).

Table 7.8. Comparison of fig-eating fishes and their families between the original Shanahan et al. (2001) dataset and the updated dataset. Percentages reflect the proportion of genera and species in each family that are recorded as eating figs.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Fishes												
Auchenipteridae	22	0	0.0	119	0	0.0	22	2	9.1	119	2	1.7
Characidae	146	1	0.7	1116	1	0.1	146	1	0.7	1116	5	0.4
Clariidae	16	1	6.3	116	1	0.9	16	1	6.3	116	1	0.9
Cyprinidae	376	0	0.0	3112	0	0.0	376	4	1.1	3112	4	0.1
Doradidae	33	1	3.0	95	1	1.1	33	1	3.0	95	1	1.1
Pangasiidae	4	0	0.0	28	0	0.0	4	1	25.0	28	2	7.1
Pimelodidae	32	0	0.0	113	0	0.0	32	1	3.1	113	1	0.9
Serrasalmidae	16	0	0.0	98	0	0.0	16	3	18.8	98	6	6.1
Triporthidae	5	0	0.0	23	0	0.0	5	1	20.0	23	3	13.0
Total fresh water fishes	**604**	**3**	**0.5**	**15000**	**3**	**0.02**	**604**	**15**	**2.5**	**15000**	**25**	**0.2**

Table 7.9. Comparison of fig-eating reptiles and their families between the original Shanahan et al. (2001) dataset and the updated dataset.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Reptiles												
Crocodylidae	2	0	0.0	15	0	0.0	2	1	50.0	15	1	6.7
Cordylidae	10	1	10.0	80	2	2.5	10	1	10.0	80	2	2.5
Corytophanidae	3	1	33.3	9	1	11.1	3	1	33.3	9	1	11.1
Dactyloidae	1	1	100.0	391	1	0.3	1	1	100.0	391	1	0.3
Iguanidae	8	1	12.5	35	1	2.9	8	2	25.0	35	2	5.7
Lacertidae	39	0	0.0	300	0	0.0	39	1	2.6	300	1	0.3
Tropiduridae	9	0	0.0	280	0	0.0	9	1	11.1	280	1	0.4
Varanidae	2	1	50.0	60	1	1.7	2	1	50.0	60	2	3.3
Emydidae	10	0	0.0	50	0	0.0	10	1	10.0	50	1	2.0
Geoemydidae	19	1	5.3	70	1	1.4	19	1	5.3	70	1	1.4
Testudinidae	11	2	18.2	50	2	4.0	11	3	27.3	50	4	8.0
Global reptiles	**1199**	**8**	**0.7**	**10711**	**9**	**0.1**	**1199**	**14**	**1.2**	**10711**	**17**	**0.2**

There are 99 bird families recorded eating figs globally. The proportion of species and genera of fig-eaters varies significantly between familes with Aegithinidae, Bombycillidae, Hypocoliidae, and Nesospingidae under-represented (Table 7.10). Based on the updated dataset, the frequency of fig-eating genera and species of passerine and non-passerine birds also deviated slightly from the global bird genera and species totals (Genera: Chi-square: $\chi^2 = 5.761$, df = 1, $P < 0.05$; Species: Chi-square: $\chi^2 = 3.880$, df = 1, $P < 0.05$; Table 7.10). The records of bird genera feeding on figs tree species biased to the passerine birds (23.9% and 18.8% of global passerine and non-passerine bird genera), but the number of species biased to the non-passerine birds (12.2% and 13.6% of global passerine and non-passerine bird species; Table 7.10). An alternative comparison method was adopted by multiplying the frequency of each fig-eating genus with the percentage of fig-eaters in the family, and the species propensity values were calculated in the same way as the genera propensity values, giving two values (for genera and species). The genus propensity value of each bird family was plotted against the species propensity. If a bird family showed high-propensity indices in both genus and species, it meant that this bird family contributed a high proportion of fig-eaters within the family. Based on this criterion the bird families Sturnidae, Psittacidae, Pycnonotidae and Columbidae are particularly likely to contribute fig-eating species (Fig 7.5).

Table 7.10. Comparison of fig-eating birds between the original Shanahan et al. (2001) dataset and the updated dataset.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Acrocephalidae	6	2	33.3	54	3	5.6	6	3	50.0	54	6	11.1
Aegithinidae	1	1	100.0	4	2	50.0	1	1	100.0	4	2	50.0
Alcedinidae	19	1	5.3	119	1	0.8	19	1	5.3	119	1	0.8
Ardeidae	19	1	5.3	64	1	1.6	19	1	5.3	64	1	1.6
Artamidae	6	3	50.0	24	5	20.8	6	3	50.0	24	5	20.8
Bombycillidae	1	1	100.0	3	1	33.3	1	1	100.0	3	1	33.3
Bucerotidae	16	15	93.8	62	40	64.5	16	14	87.5	62	46	74.2
Cacatuidae	7	2	28.6	21	7	33.3	7	2	28.6	21	7	33.3
Calyptomenidae	2	1	50.0	6	2	33.3	2	1	50.0	6	2	33.3
Campephagidae	11	4	36.4	99	14	14.1	11	5	45.5	99	19	19.2
Capitonidae	2	0	0.0	18	0	0.0	2	2	100.0	18	4	22.2
Cardinalidae	11	6	54.5	52	12	23.1	11	8	72.7	52	15	28.8
Casuariidae	2	1	50.0	4	2	50.0	2	2	100.0	4	3	75.0
Chloropseidae	1	1	100.0	13	5	38.5	1	1	100.0	13	7	53.8
Cisticolidae	26	1	3.8	161	1	0.6	26	4	15.4	161	7	4.3
Cnemophilidae	2	2	100.0	4	2	50.0	2	2	100.0	4	2	50.0
Coliidae	2	1	50.0	6	2	33.3	2	2	100.0	6	5	83.3
Columbidae	49	31	63.3	351	123	35.0	49	31	63.3	351	153	43.6
Coraciidae	2	1	50.0	13	1	7.7	2	1	50.0	13	1	7.7
Corvidae	21	12	57.1	131	27	20.6	21	12	57.1	131	35	26.7
Cotingidae	24	6	25.0	67	8	11.9	24	12	50.0	67	18	26.9
Cracidae	11	6	54.5	56	8	14.3	11	8	72.7	56	24	42.9
Cuculidae	36	9	25.0	149	9	6.0	36	11	30.6	149	16	10.7

Table 7.10. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Dicaeidae	2	2	100.0	54	15	27.8	2	2	100.0	54	19	35.2
Dicruridae	1	1	100.0	26	3	11.5	1	1	100.0	26	3	11.5
Emberizidae	1	0	0.0	44	0	0.0	1	2	200.0	44	2	4.5
Estrildidae	34	3	8.8	141	8	5.7	34	3	8.8	141	12	8.5
Eurylaimidae	7	3	42.9	12	4	33.3	7	3	42.9	12	5	41.7
Fringillidae	46	7	15.2	213	15	7.0	46	9	19.6	213	35	16.4
Furnariidae	69	0	0.0	333	0	0.0	69	1	1.4	333	1	0.3
Hyliidae	2	0	0.0	2	0	0.0	2	1	50.0	2	1	50.0
Hyliotidae	1	1	100.0	4	1	25.0	1	1	100.0	4	1	25.0
Hypocoliidae	1	1	100.0	1	1	100.0	1	1	100.0	1	1	100.0
Icteridae	31	5	16.1	114	12	10.5	31	7	22.6	114	21	18.4
Indicatoridae	4	1	25.0	16	1	6.3	4	3	75.0	16	4	25.0
Irenidae	1	1	100.0	3	1	33.3	1	1	100.0	3	2	66.7
Laniidae	4	1	25.0	33	2	6.1	4	1	25.0	33	2	6.1
Laridae	21	1	4.8	101	1	1.0	21	1	4.8	101	1	1.0
Leiotrichidae	20	6	30.0	148	15	10.1	20	8	40.0	148	20	13.5
Lybiidae	10	9	90.0	52	34	65.4	10	10	100.0	52	39	75.0
Malaconotidae	9	1	11.1	48	1	2.1	9	1	11.1	48	2	4.2
Megalaimidae	2	2	100.0	35	20	57.1	2	2	100.0	35	34	97.1
Megapodiidae	7	1	14.3	21	1	4.8	7	1	14.3	21	1	4.8
Melanocharitidae	4	2	50.0	11	4	36.4	4	2	50.0	11	4	36.4
Meliphagidae	52	17	32.7	191	23	12.0	52	19	36.5	191	27	14.1
Mimidae	10	3	30.0	34	5	14.7	10	4	40.0	34	8	23.5

Table 7.10. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Momotidae	6	2	33.3	14	2	14.3	6	3	50.0	14	5	35.7
Monarchidae	16	1	6.3	105	1	1.0	16	1	6.3	105	1	1.0
Muscicapidae	56	11	19.6	335	14	4.2	56	15	26.8	335	19	5.7
Musophagidae	7	6	85.7	24	15	62.5	7	6	85.7	24	16	66.7
Nectariniidae	15	5	33.3	147	10	6.8	15	8	53.3	147	21	14.3
Nesospingidae	1	1	100.0	1	1	100.0	1	1	100.0	1	1	100.0
Nicatoridae	1	1	100.0	3	1	33.3	1	1	100.0	3	1	33.3
Numididae	4	1	25.0	8	1	12.5	4	1	25.0	8	1	12.5
Odontophoridae	10	1	10.0	35	1	2.9	10	1	10.0	35	1	2.9
Oriolidae	3	3	100.0	38	16	42.1	3	3	100.0	38	22	57.9
Pachycephalidae	5	2	40.0	52	2	3.8	5	2	40.0	52	2	3.8
Paradisaeidae	15	11	73.3	41	21	51.2	15	11	73.3	41	21	51.2
Paridae	14	4	28.6	60	4	6.7	14	6	42.9	60	7	11.7
Parulidae	18	1	5.6	122	6	4.9	18	2	11.1	122	9	7.4
Passerellidae	17	2	11.8	145	2	1.4	17	2	11.8	145	2	1.4
Passeridae	8	3	37.5	43	7	16.3	8	3	37.5	43	7	16.3
Pellorneidae	15	1	6.7	64	1	1.6	15	2	13.3	64	2	3.1
Petroicidae	20	1	5.0	53	1	1.9	20	1	5.0	53	1	1.9
Phasianidae	51	11	21.6	187	18	9.6	51	12	23.5	187	20	10.7
Philepittidae	2	1	50.0	4	1	25.0	2	1	50.0	4	1	25.0
Phoeniculidae	2	0	0.0	8	0	0.0	2	1	50.0	8	1	12.5
Phylloscopidae	4	1	25.0	78	1	1.3	4	1	25.0	78	4	5.1
Picidae	33	8	24.2	254	19	7.5	33	11	33.3	254	29	11.4
Pipridae	17	3	17.6	52	3	5.8	17	9	52.9	52	13	25.0
Pittidae	3	1	33.3	48	1	2.1	3	1	33.3	48	1	2.1

Table 7.10. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Platysteiridae	4	1	25.0	34	1	2.9	4	2	50.0	34	2	5.9
Ploceidae	15	1	6.7	124	1	0.8	15	2	13.3	124	14	11.3
Psittacidae	79	42	53.2	375	114	30.4	79	45	57.0	375	151	40.3
Psophiidae	1	0	0.0	6	0	0.0	1	1	100.0	6	1	16.7
Ptilonorhynchidae	8	6	75.0	20	11	55.0	8	6	75.0	20	13	65.0
Pycnonotidae	31	20	64.5	157	61	38.9	31	26	83.9	157	90	57.3
Rallidae	38	2	5.3	142	2	1.4	38	2	5.3	142	2	1.4
Ramphastidae	5	4	80.0	50	8	16.0	5	6	120.0	50	29	58.0
Remizidae	3	0	0.0	12	0	0.0	3	1	33.3	12	2	16.7
Semnornithidae	1	0	0.0	2	0	0.0	1	1	100.0	2	1	50.0
Sittidae	3	1	33.3	32	1	3.1	3	1	33.3	32	1	3.1
Spindalidae	1	0	0.0	4	0	0.0	1	1	100.0	4	2	50.0
Steatornithidae	1	1	100.0	1	1	100.0	1	1	100.0	1	1	100.0
Stenostiridae	4	0	0.0	9	0	0.0	4	1	25.0	9	1	11.1
Struthionidae	1	1	100.0	2	1	50.0	1	1	100.0	2	1	50.0
Sturnidae	33	27	81.8	123	60	48.8	33	31	93.9	123	78	63.4
Sylviidae	17	1	5.9	69	7	10.1	17	2	11.8	69	9	13.0
Thraupidae	105	17	16.2	408	42	10.3	105	27	25.7	408	75	18.4
Timaliidae	10	1	10.0	54	1	1.9	10	2	20.0	54	2	3.7
Tityridae	10	2	20.0	49	2	4.1	10	2	20.0	49	4	8.2
Todidae	1	0	0.0	5	0	0.0	1	1	100.0	5	1	20.0
Troglodytidae	19	0	0.0	94	0	0.0	19	1	5.3	94	1	1.1
Trogonidae	8	3	37.5	43	6	14.0	8	4	50.0	43	15	34.9
Turdidae	20	5	25.0	176	24	13.6	20	7	35.0	176	38	21.6
Tyrannidae	101	10	9.9	449	22	4.9	101	13	12.9	449	29	6.5

Table 7.10. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Vangidae	21	3	14.3	40	3	7.5	21	3	14.3	40	3	7.5
Vireonidae	8	1	12.5	64	4	6.3	8	2	25.0	64	6	9.4
Zosteropidae	12	3	25.0	136	15	11.0	12	4	33.3	136	27	19.9
Passerines	**1358**	**246**	**18.1**	**6713**	**540**	**8.0**	**1358**	**324**	**23.9**	**6713**	**817**	**12.2**
Non-passerines	**1008**	**164**	**16.3**	**4519**	**439**	**9.7**	**1008**	**189**	**18.8**	**4519**	**615**	**13.6**
Total	**2366**	**410**	**17.3**	**11232**	**979**	**8.7**	**2366**	**513**	**21.7**	**11232**	**1432**	**12.7**

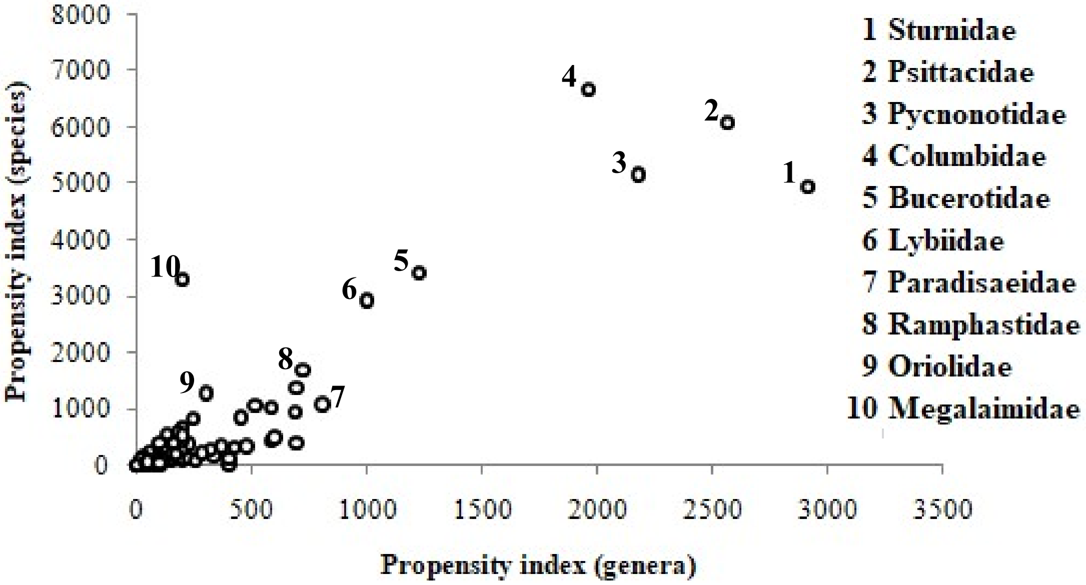

Fig. 7.5. The propensity indices of 99 fig-eating bird families.

In total, there are 49 mammalian families that are known to be fig-eaters. Families such as Dinomyidae, Elephantidae and Hypsiprymnodontidae showed a particularly high proportion of fig-eating genera and species, reflecting the small number of included species (Table 7.11). The propensity indices of each mammal family indicated that there are ten major mammal families of fig-eaters. Of these ten families, the Old World fruit bats (Pteropodidae), Old World monkeys (Cercopithecidae) and New World fruit bats (Phyllostomidae) showed the higher numbers of fig-eating species (Fig 7.6).

Table 7.11. Comparison of fig-eating mammals between the original Shanahan et al. (2001) dataset and the updated dataset.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Aotidae	1	0	0.0	11	0	0.0	1	1	100.0	11	3	27.3
Atelidae	5	3	60.0	26	9	34.6	5	5	100.0	26	19	73.1
Bovidae	52	6	11.5	147	6	4.1	52	8	15.4	147	10	6.8
Callithricidae	6	2	33.3	41	4	9.8	6	3	50.0	41	9	22.0
Canidae	13	2	15.4	40	4	10.0	13	4	30.8	40	9	22.5
Cebidae	3	3	100.0	22	4	18.2	3	3	100.0	22	9	40.9
Cercopithecidae	23	13	56.5	135	34	25.2	23	17	73.9	135	60	44.4
Cervidae	18	4	22.2	55	7	12.7	18	5	27.8	55	10	18.2
Cheirogaleidae	5	2	40.0	32	2	6.3	5	2	40.0	32	2	6.3
Cricetidae	141	0	0.0	701	0	0.0	141	1	0.7	701	1	0.1
Cuniculidae	1	1	100.0	2	1	50.0	1	1	100.0	2	1	50.0
Dasypodidae	9	0	0.0	20	0	0.0	9	1	11.1	20	1	5.0
Dasyproctidae	2	0	0.0	15	0	0.0	2	1	50.0	15	1	6.7
Didelphidae	18	5	27.8	97	5	5.2	18	6	33.3	97	10	10.3
Dinomyidae	1	0	0.0	1	0	0.0	1	1	100.0	1	1	100.0
Echimyidae	24	2	8.3	91	2	2.2	24	2	8.3	91	2	2.2
Elephantidae	2	2	100.0	3	2	66.7	2	2	100.0	3	3	100.0
Emballonuridae	14	0	0.0	53	0	0.0	14	1	7.1	53	1	1.9
Herpestidae	13	1	7.7	35	1	2.9	13	2	15.4	35	2	5.7
Hominidae	4	4	100.0	7	5	71.4	4	4	100.0	7	7	100.0
Hylobatidae	4	4	100.0	16	9	56.3	4	4	100.0	16	14	87.5
Hypsiprymnodontidae	1	1	100.0	1	1	100.0	1	1	100.0	1	1	100.0
Hystricidae	3	2	66.7	11	3	27.3	3	2	66.7	11	3	27.3

Table 7.11. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Indriidae	3	1	33.3	19	1	5.3	3	1	33.3	19	4	21.1
Lemuridae	5	4	80.0	21	7	33.3	5	4	80.0	21	14	66.7
Lepilemuridae	1	0	0.0	26	0	0.0	1	1	100.0	26	1	3.8
Lorisidae	4	1	25.0	12	1	8.3	4	1	25.0	12	1	8.3
Macropodidae	11	3	27.3	68	5	7.4	11	3	27.3	68	5	7.4
Muridae	151	6	4.0	728	6	0.8	151	10	6.6	728	13	1.8
Mustelidae	22	5	22.7	65	6	9.2	22	6	27.3	65	8	12.3
Nesomyidae	21	0	0.0	63	0	0.0	21	2	9.5	63	2	3.2
Noctilionidae	1	0	0.0	2	0	0.0	1	1	100.0	2	1	50.0
Peramelidae	6	2	33.3	21	4	19.0	6	2	33.3	21	4	19.0
Petauridae	4	2	50.0	11	3	27.3	4	2	50.0	11	3	27.3
Phalangeridae	6	3	50.0	27	5	18.5	6	3	50.0	27	5	18.5
Phyllostomidae	58	16	27.6	183	36	19.7	58	25	43.1	183	58	31.7
Pitheciidae	5	1	20.0	45	1	2.2	5	4	80.0	45	7	15.6
Procaviidae	3	1	33.3	5	1	20.0	3	1	33.3	5	1	20.0
Procyonidae	6	3	50.0	14	3	21.4	6	4	66.7	14	5	35.7
Pseudocheiridae	6	2	33.3	20	2	10.0	6	2	33.3	20	2	10.0
Pteropodidae	43	21	48.8	187	47	25.1	43	28	65.1	187	60	32.1
Sciuridae	60	12	20.0	280	28	10.0	60	13	21.7	280	32	11.4
Suidae	6	3	50.0	19	4	21.1	6	3	50.0	19	4	21.1
Tapiridae	1	1	100.0	4	2	50.0	1	1	100.0	4	2	50.0

Table 7.11. cont.

	Shanahan et al. (2001)						Updated data					
	Genera			Species			Genera			Species		
Family	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%	Total	Fig-eaters	%
Tayassuidae	3	1	33.3	3	1	33.3	3	2	66.7	3	2	66.7
Tragulidae	3	2	66.7	10	2	20.0	3	2	66.7	10	2	20.0
Tupaiidae	4	1	25.0	19	4	21.1	4	1	25.0	19	4	21.1
Ursidae	5	4	80.0	8	4	50.0	5	4	80.0	8	5	62.5
Viverridae	14	7	50.0	36	8	22.2	14	8	57.1	36	11	30.6
Total	**1270**	**159**	**12.5**	**5630**	**280**	**5.0**	**1270**	**211**	**16.6**	**5630**	**435**	**7.7**

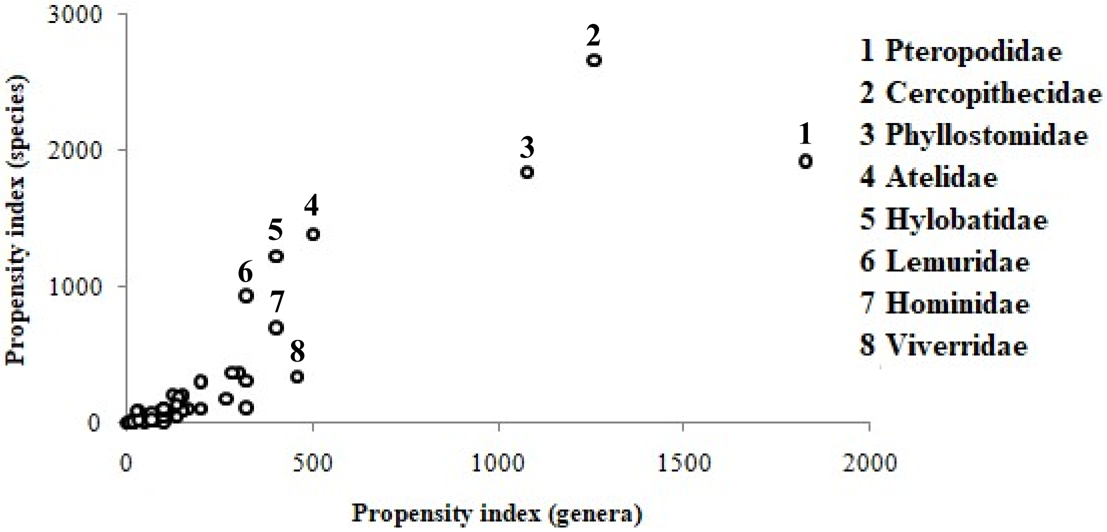

Fig. 7.6. The propensity indices of 49 fig-eating mammal families.

The overall degree of frugivores (of all taxa) and fig tree interactions was recalculated by following the standardised propensity indices of birds and mammals from Figs. 7.5 and 7.6, and by calibrating overall mean genera and species propensity indices to 1000 (converting the number of fig species interacted with such frugivore genus, in which the highest number was converted to 1000 and the rest of the values were calculated proportionately). The calibrated values for each frugivore family were separated into four quartiles depending on the interaction degrees to genus *Ficus*. It was found that most of the frugivore families (126 families, 85.14%) fall into the first quartile (up to 250 in both axes) (Fig 7.7). Among birds and mammals, only four families are in the top quartile (more than 750 in both indices). These include two bird families (Pigeons, Columbidae and African and Asian bulbuls, Pycnonotidae) and two mammal families (Old World monkeys, Cercopithecidae and Old World fruit bats, Pteropodidae), suggesting figs are particularly widely used by these families. The other 18 families were distributed in the second and third quartiles, reflecting the different frequencies of interactions with *Ficus* (Fig 7.7).

Almost all the frugivore species that fed on a large number of fig tree species were found in the Indo-Malayan ecozone (Table 7.12). The most widely-recorded fig-eating species is the Fairy blue bird (*Irena puella*), which feeds on at least 39 different fig species. Numerous studies from Africa have focused on the Chimpanzee (*Pan troglodytes*) and this has led to an increase in the numbers of fig species known to be eaten by this species of hominid (with 38 *Ficus* species consumed). The New World has about as many species of fig trees as Africa, but there are only two Neotropical fruit bat species found in the top 30 fig-eater species list (*Artibeus jamaicensis* and *A. lituratus*, with 25 fig species consumed). No other

New World frugivores were not found in the list. Lower numbers of fig tree species in the Neotropics, compared with Asia, and the greater difficulty in identifying fig trees to species than in Africa, may have reduced the apparent dietary breadth of fig consumers in the New World (Table 7.12).

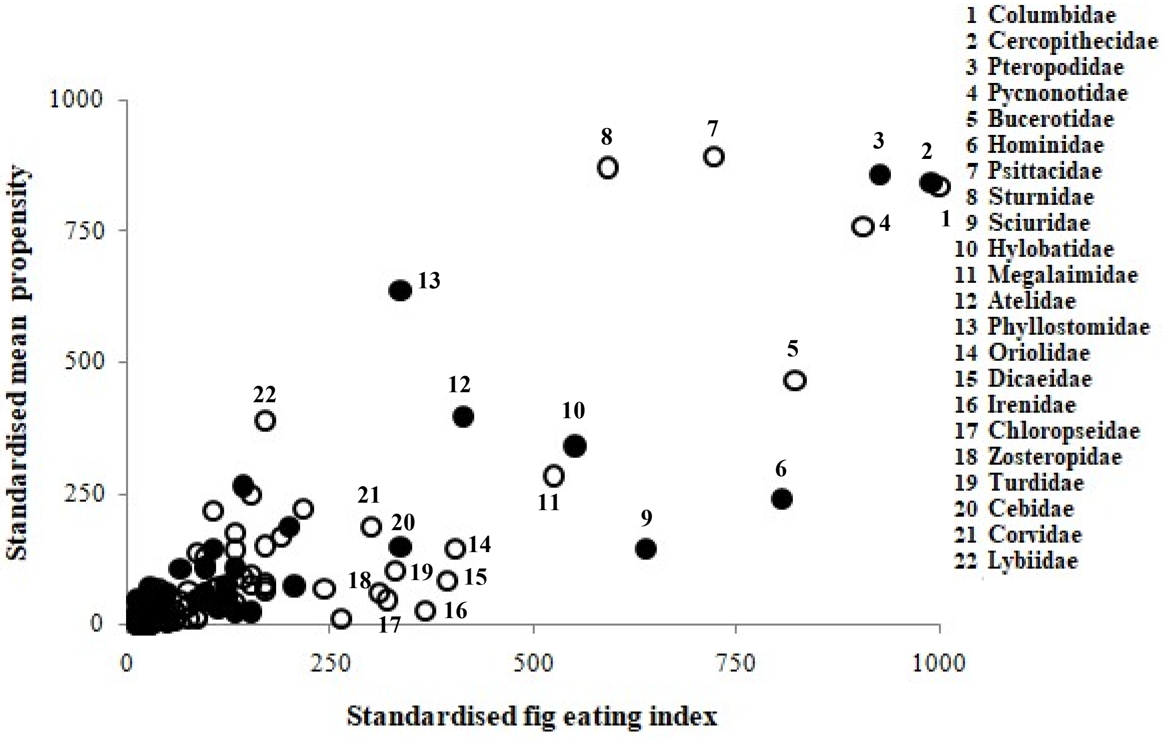

Fig. 7.7. The standardised mean propensity indices of 148 fig-eating bird and mammal families.

Table 7.12. The top thirty animal species in terms of the number of *Ficus* species that they are known to eat.

Frugivore species	Class	Order	Family	Distribution ranges	*Ficus* species consumed
Irena puella	Aves	Passeriformes	Irenidae	Indomalayan	39
Pan troglodytes	Mammalia	Primates	Hominidae	Afrotropical	38
Pongo pygmaeus	Mammalia	Primates	Hominidae	Indomalayan	37
Macaca fascicularis	Mammalia	Primates	Cercopithecidae	Indomalayan	34
Psilopogon australis	Aves	Piciformes	Megalaimidae	Indomalayan	33
Psilopogon mystacophanos	Aves	Piciformes	Megalaimidae	Indomalayan	29
Anthracoceros malayanus	Aves	Bucerotiformes	Bucerotidae	Indomalayan	28
Buceros rhinoceros	Aves	Bucerotiformes	Bucerotidae	Indomalayan	28
Callosciurus prevostii	Mammalia	Rodentia	Sciuridae	Indomalayan	28
Calorhamphus fuliginosus	Aves	Piciformes	Megalaimidae	Indomalayan	28
Calyptomena viridis	Aves	Passeriformes	Calyptomenidae	Indomalayan	28
Chloropsis sonnerati	Aves	Passeriformes	Chloropseidae	Indomalayan	28
Hylobates lar	Mammalia	Primates	Hylobatidae	Indomalayan	28
Pycnonotus brunneus	Aves	Passeriformes	Pycnonotidae	Indomalayan	27
Treron curvirostra	Aves	Columbiformes	Columbidae	Indomalayan	26
Artibeus jamaicensis	Mammalia	Chiroptera	Phyllostomidae	Neotropical	25
Artibeus lituratus	Mammalia	Chiroptera	Phyllostomidae	Neotropical	25
Buceros bicornis	Aves	Bucerotiformes	Bucerotidae	Indomalayan	25
Psilopogon chrysopogon	Aves	Piciformes	Megalaimidae	Indomalayan	25
Gracula religiosa	Aves	Passeriformes	Sturnidae	Indomalayan	24
Anorrhinus galeritus	Aves	Bucerotiformes	Bucerotidae	Indomalayan	23
Callosciurus notatus	Mammalia	Rodentia	Sciuridae	Indomalayan	23
Homo sapiens	Mammalia	Primates	Hominidae	All ecozones	23
Ratufa bicolor	Mammalia	Rodentia	Sciuridae	Indomalayan	23
Eudynamys scolopaceus	Aves	Cuculiformes	Cuculidae	Indomalayan	22
Pycnonotus eutilotus	Aves	Passeriformes	Pycnonotidae	Indomalayan	22
Chloropsis cochinchinensis	Aves	Passeriformes	Chloropseidae	Indomalayan	21
Pycnonotus flaviventris	Aves	Passeriformes	Pycnonotidae	Indomalayan	21
Rhyticeros undulatus	Aves	Bucerotiformes	Bucerotidae	Indomalayan	21
Chloropsis cyanopogon	Aves	Passeriformes	Chloropseidae	Indomalayan	20

Overlap in potential dispersal services provided to individual species of fig trees by the three major frugivorous groups (birds, bats and terrestrial mammals) is shown in Fig. 7.8. All three groups are recorded from 87 fig tree species (27.02%). Conversely, 80 fig tree species only have terrestrial mammals records (24.85%). There is more overlap with other groups when birds are recorded.

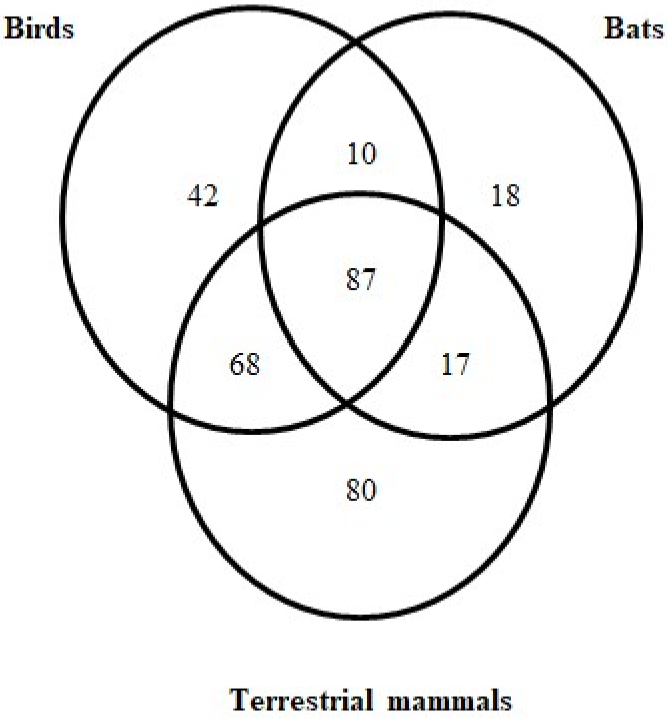

Fig. 7.8. The three main fig-eating groups (combined data). The numbers refer to the fig species.

7.4.3 Frugivores and fig tree seed dispersal

The concept of effectiveness of seed dispersal was proposed by Schupp (1993) and revised again by Schupp et al. (2010). To measure seed dispersal effectiveness, two compartments – quantity and quality – of the seed dispersal services provided by frugivores must be evaluated. The quantity of seed dispersal refers to how many seeds were carried by frugivore species after removal from the parent trees by endozoochorous or exozoochorous methods, which is directly related to the frequency that the frugivore visits the particular tree and how quickly it eats. Seed dispersal quality depends on the process of seed handling by frugivores, how far the seeds can be transported from the parent tree and also deposition site quality which influences seed germinability and survivorship.

In the following review section, new information on the roles of each frugivore family on seed dispersal of genus *Ficus* are described based on the published sources from 2001 to 2017. The content therefore complements the discussion given in Shanahan et al. (2001). The figures given for the number of fig-eaters in each group are based on the combined data sets.

7.4.3.1 Fish and Reptiles

Globally, figs are eaten by Old World and New World ray-finned fishes (Actinopterygii), including 14 species of piranhas and allies (Characiformes), seven species of catfish (Siluriformes) and four species of carp and allies (Cypriniformes). These fish feed on figs that fall down into the water (Baird, 2007). Figs are considered as one of the most important food sources for fish such as Brycon

(*Brycon hilarii*, Characidae, 10.7% of overall frequency occurrence in the diet of that species) in Brazil (Rey et al. 2009). Neotropical figs could be potentially dispersed by fishes, as fig seeds are still viable after being ingested by Tambaqui (*Colossoma macropomum*, Serrasalmidae) and Pirapitinga (*Piaractus brachypomus*, Serrasalmidae) (Lucas, 2008). Likewise, Rey et al. (2009) suggested that *B. hilarii* is a seed disperser of several Neotropical fig trees, such as *Ficus pertusa* and *F. calyptroceras,* in Brazil as it egests intact seeds. *F. insipida* seeds retrieved from several Neotropical freshwater fishes (Characidae: *Brycon amazonicus*; Serrasalmidae: *C. macropomum*, *P. brachypomus*; Triporthidae: *Triportheus albus, T. algulatus, T. auritus*; Auchenipteridae: *Auchenipterus nuchalis, Trachelyopterus galeatus*; Doradidae: *Pterodoras granulosus*; Pimelodidae: *Pimelodus blochii*) showed a high germination rate of more than 85% when results from the different species were pooled (Weiss et al., 2016). Moreover, the intact seed retrieval rate showed a positive correlation with the Pacu's (*P. mesopotamicus*, Serrasalmidae) body size in Brazil, suggesting that bigger fish may be more effective seed dispersers of riparian plants (Galetti et al., 2008). Although Neotropical fish seem to be effective seed dispersers, the Old World cyprinid fishes are seed eaters. Less than 15% of *F. montana* seeds ingested by Red-tailed tinfoil (*Barbonymus altus*, Cyprinidae) and Blue mahseer (*Neolissochilus stracheyi*, Cyprinidae) were retrieved, and all egested seeds showed lower germination rates than unpassed seeds (CHAPTER 4).

There are only 17 reptile species confirmed as fig-eaters, including one species of Crocodile (*Crocodylus palustris*, Crocodilia), ten species of squamatae reptiles (Squamata) and six species of land turtles (Testudines). It is suggested that *F. carica* is present in the highest frequency of diet, 19.3%, of Gallot's lizard

(*Gallotia galloti*, Lacertidae) scats in Bajama in Tenerife, so therefore figs are considered as an important food source for this particular lizard species (Valido & Nogales, 2003). On average, ten *F. luschnathiana* seeds (range 2–40) were found in each scat sample of Amazon lava lizards (*Tropidurus torquatus*, Tropiduridae) in Brazil, and seeds could be dispersed from 0 to 46 metres from the parent trees (Pietczak et al., 2013). Fig seeds were found in scats of Green iguana (*Iguana iguana*, Iguanidae) in Puerto Rico, and seeds extracted from the scat were still viable (with a 40–50% germination rate) and germinated faster than unpassed seeds. Scats were found up to 100 metres of the *Ficus* spp. trees, suggesting that the Green iguana can be a potential seed disperser of many Puerto Rican fig trees (Burgos-Rodriguez 2014). *Ficus* spp. seeds collected from Yellow-footed tortoises (*Chelonoidis denticulata*, Testudinidae) in Peru showed higher germination rates than uningested seeds (Guzman & Stevenson, 2008). Tortoises (*Chelonoidis* spp.) have a long gut passage time, ranging from 10 to 28 days, and they were able to defaecate viable seeds, suggesting their potential roles as seed dispersers (Strong, 2005).

7.4.3.2 Birds

Struthioniformes

Cassowaries (*Casuarius* spp., Casuariidae) are found in Australian and New Guinean habitats (del Hoyo et al. 2017). There are few published records of them being fig-eaters. Figs were found in only 0.7–1.4% of the overall diet composition of the Dwarf cassowary (*C. bennetti*) in Papua New Guinea (Wright, 2005). Southern cassowaries (*C. casuarius*) in Australia retained *Ficus crassipes* seeds for 379 minutes on average before depositing them, and it was estimated that the mean seed dispersal distance provided by this bird was 337 metres (Wescott et al., 2005). *F. crassipes* seeds ingested by *C. casuarius* also increased seed germination rates (Bradford & Wescott, 2010). Figs were not likely to be a major dietary constituent of *C. casuarius*. They constituted less than 3.47% of overall diet volume (Bradford et al., 2008). Australian Emu (*Dromaius novaehollandiae*, Casuariidae) is another fig-eater, but it was suggested that the Emu defecated fig seeds with low viability, which ranged from 11.1–13.3% of all the seeds eaten by the bird (Calvino-Cancela et al., 2006).

Galliformes

Cracidae

Guans, Chachalacas and Curassows are members of the family Cracidae which are distributed throughout the Neotropical zone (del Hoyo et al., 2017). Guans, in the genera *Aburria*, *Chamaepetes*, *Penelope* and *Pipile*; Chachalacas, in the genus *Ortalis*; and Curassows in the genera *Crax*, *Mitu* and *Pauxi* are all fig-eaters (Tello, 2003; Zaca et al,. 2006; Munoz et al., 2007; Diaz-Martin et al., 2014; Ragusa-Netto, 2015; Stevenson et al., 2015; Palacio et al., 2016; Bello et al., 2017; del Hoyo et al., 2017). It was reported that the Trinidad piping guan (*Pipile pipile*) visits and perches on the branches of fig trees and swallows figs whole when feeding (Tello, 2003). Figs were not the major food source of the Rusty-margined guan (*Penelope superciliaris*) that lives in fragmented forested areas of Brazil, as they only made up 1.79–2.69% of their overall diet (Zaca et al., 2006). Likewise, figs were also a minor dietary constituent (9% of overall diet composition) of the Cauca guan (*P. perspicax*) in Andean forest (Munoz et al., 2007). Flocks of Chaco chachalaca (*Ortalis canicollis*) feed on figs of large trees (*Ficus luschnathiana*) during their fruiting peaks, consisting of 5.9% of annual feeding records in Brazilian gallery forest (Ragusa-Netto, 2015). The estimated home range of the Trinidad pipingguan (*P. pipile*) is approximately 19 hectares (Hayes et al., 2009), suggesting that it could be a relatively long-distance seed disperser. However, the roles of cracid birds in seed dispersal are still largely unknown.

Phasianidae

This family includes species of Pheasants, Partridges, Turkeys and Grouses. Fig consumers in the genera *Afropavo* and *Pternistis* were recorded in the Afro-tropic region and records from tropical East Asia include the genera *Caloperdix, Francolinus, Galloperdix, Gallus, Lophura, Pavo, Polyplectron* and *Rollulus* (del Hoyo et al., 2017). Feeding behaviours and seed dispersal services of these birds for figs are still not well understood, but it is suggested that most of the members in this genus are ground-feeders, which feed on fallen figs (del Hoyo et al., 2017). Many are likely to be mainly seed predators.

Other galliform families

The Melanesian scrub fowl (*Megapodius eremite*, Megapodiidae), the Vulturine guineafowl (*Acryllium vulturinum,* Numididae) and the Gorgeted wood-quail (*Odontophorus strophium*, Odontophoridae) are all known to eat figs (del Hoyo et al., 2017). However, there is insufficient information to determine how these birds promote seed dispersal of the fig trees.

Columbiformes

Pigeons and Doves (Columbidae) have a wide global distribution including the Indo-Australian, Afro-tropical and Neotropical regions (del Hoyo et al., 2017). 153 species from 31 genera have been found to be fig-eaters. The birds of family Columbidae feed primarily on figs (59.1%) in the lowland rainforests of Sulawesi, Indonesia, suggesting that figs are one of the most important constituents of the diets of this bird family (Walker, 2007). The Mountain imperial pigeon (*Ducula badia*) feeds primarily on *Ficus nervosa,* which accounted for 23% of the total visits to trees in the tropical forests of North-East Thailand (Sankamethawee et al., 2011). The African green pigeon (*Treron calvus*) was the major visitor of *Ficus lutea* in the severely degraded habitat of Kakameka forest, Kenya (Menke et al., 2012). However, figs might not be the major diet of pigeons and doves in some areas. For example, *Ficus drupacea* seeds were found in the diet of only 8.42% of the Nilgiri wood pigeons (*Columba elphinstonii*) in the wet montane temperate forest of India (Somasundaram & Vijayan, 2010). Also, in the rainforest of French Polynesia, *Ficus prolixa* was a minor diet constituent of the Grey-green fruit dove (*Ptilinopus purpuratus*) which was found to be only 2.54% of the overall diet (Spotswood, 2011). Columbidae species can be both biters (Peh & Chong, 2003) and swallowers (Kitamura et al., 2005), depending on the size of the fig they are feeding on. The rate of fig consumption by the African green pigeon was 1.04 figs/minute while visiting *Ficus thonningii* trees, which could be typical of other similar-sized birds (Kirika et al., 2008). It was found that the Mountain imperial pigeon (*D. badia*) fed on at least nine fig species in South-East Asian mixed deciduous forest, but the role of this bird as a seed disperser or a seed eater remains unclear (Kitamura et al., 2002). Many studies reported that pigeons and doves are seed eaters. The Pink-necked pigeon (*T.*

vernans) was the most common fruit eater of *Ficus fistulosa* and *Ficus grossularioides*, but it was suggested that this bird is a seed predator of fig trees in the degraded habitats of Singapore (Peh & Chong, 2003). Tello (2003) also suggested that the Neotropical plumbeous pigeon (*Patagioenas plumbea*) acts as a seed predator rather than a potential disperser. The White-tipped dove (*Leptotila verreauxi*) spends relatively short times, 180 seconds, similar to other small birds feeding in *Ficus colubrinae* trees, and it was reported to be a seed eater in the tropical rainforest of Costa Rica (Grade & Stoddard, 2006). Pigeons can nonetheless also be seed dispersal agents. The Pacific pigeon (*D. pacifica*) for example dispersed 99% of defaecated seeds, including fig seeds, within 50 metres of the parent trees. Although it is likely to be a short-distance seed disperser, some seeds carried by this bird could possibly be dispersed over a longer distance (> 100 km) (McConkey et al., 2004). Moreover, the Madagascan blue pigeon (*Alectroenas madagascariensis*) and the Madagascan green pigeon (*T. australis*) were considered to be seed dispersers, as they swallowed whole fruits and defaecated viable seeds (Bollen, 2007). In addition, *F. drupacea* seeds passing through Nilgiri wood pigeons (*C. elphinstonii*) were still viable (Somasundaram & Vijayan, 2010).

Cuculiformes

Most members of the Cuckoo family (Cuculidae) are known to be insectivorous (del Hoyo et al., 2017). However, several studies have suggested that some cuckoos include fruits in their diet. The Asian koel (*Eudynamys scolopaceus*) is a prolific fig-eater which feeds on at least 22 fig tree species throughout the East. The Asian koel also fed specifically on fig trees when they were available in the area, and it abandoned the area when fig numbers were low (Kamruzzaman &

Asmat, 2008). The other two species in the genus *Eudynamys,* the Eastern koel (*E. orientalis*) and the Black-billed koel (*E. melanorhynchus*) are also known as fig-eaters (Walker, 2007; del Hoyo et al., 2017). Other Asian cuckoos in the genera *Phaenicophaeus*, *Hierococcyx* and *Surniculus*; Australian cuckoos in the genus *Microdynamis*; African cuckoos in the genus *Centropus*; and New World cuckoos in the genus *Piaya* are all reported to be fig-eaters (Velho et al., 2012; Daru et al., 2015; Stevenson et al., 2015; del Hoyo et al., 2017). However, the roles of cuckoos in seed handling and dispersal of fig trees are almost unknown.

Gruiformes

The Pale-winged trumpeter (*Psophia leucoptera*, Psophiidae) is the only species known to feeding on Neotropical figs (Tello, 2003; Diaz-Martin et al., 2014). It is a ground feeder that mostly feeds on fallen figs (Tello, 2003). Another bird in this order, the White-breasted waterhen (*Amaurornis phoenicurus*, Rallidae), was observed to feed on *Ficus ischnopoda* figs in riparian forests of South-East Asia, where it is likely to be an opportunistic feeder (CHAPTER 3). As there are very limited records describing birds in this order interacting with fig trees, the potential role of these birds as seed dispersers is likely to be small.

Musophagiformes

A total of 17 species from six genera of turacos (*Corythaeola*, *Corythaixoides, Crinifer, Gallirex, Musophaga* and *Tauraco*, Musophagidae) are known to be fig-eaters in the Afrotropics. Turacos feed primarily on fruits (Bleher et al., 2003). The feeding rates of these birds are similar to those of other small-bodied frugivorous birds in the African region, ranging from 1.31–1.35 fruits/minute (Kirika et al., 2008; Flörchinger et al., 2010). The Knysna turaco (*T. corythaix*) defaecates fig seeds after ingestion within 12–28 minutes, suggesting that turacos have a short gut passage time (Wilson & Downs, 2012). Schalow's turaco (*T. schalowi*) was one of the top three visitors to *Ficus natalensis* in African tropical woodland, and it might therefore play an important role as a seed disperser (Fujita, 2014).

Coliiformes

Five mousebird species from two genera (*Colius* spp. and *Urocolius* spp., Coliidae) are fig-eaters. The Speckled mousebird (*C. striatus)* visits at least seven fig tree species and made the highest number of avian visits to *Ficus lutea* crops in the tropical forests of Nigeria, suggesting that it is likely to be an obligate frugivore (Daru et al., 2015). However, the role of mouse birds in the seed dispersal of fig trees is still largely unknown.

Trogoniformes

In total, there are 15 trogon species (genera *Apalharpactes*, *Harpactes*, *Pharomachrus* and *Trogon*, Trogonidae) that are known to eat figs. However, most published studies have focused on the Neotropical trogons. Trogons are found in both the Paleotropical and Neotropical regions. In the Neotropics, trogons removed 1.3–2.7 figs per visit to fig trees and accounted for 0.1–3.3% of overall visits, suggesting that this trogon species is a potentially significant seed disperser (Ragusa-Netto, 2002; Tello, 2003). The White-tailed trogon (*T. viridis*) moves between adjacent forest gaps, (Lees & Peres, 2009), suggesting that this bird is likely to be a short-distance seed disperser. However, the information of how trogons interact with fig trees in Paleotropical regions is very limited. Other aspects and roles of trogons in seed dispersal of fig trees are not known, and there is still a lack of information.

Bucerotiformes

Bucerotidae

Globally, there are 62 species from 16 genera of hornbills distributed widely in the rainforests of Africa and tropical East Asia. Of the 62 species, 46 are reported to be fig-eaters. Although hornbills forage almost exclusively in fig tree canopies, rather than lower down, they will sometimes feed on figs that have fallen onto the forest floor (Kitamura et al., 2009). Asian hornbills can have a large home range size (*Ptilolaemus tickelli*: 4.3 km^2; *Rhyticeros undulatus*: 10-28 km^2, *Buceros bicornis:* 14.7 km^2) in their natural habitat (Kitamura et al., 2004), but the home range size could be smaller when foraging in human-dominated landscapes or in fragmented forest. For example, the Oriental pied hornbill (*Anthracoceros albirostris*) has a relatively low mean home range size (0.13 km^2, range: 0.02–0.26 km^2) in the Khao Kheow open zoo, Thailand (Chaiyarat et al., 2012). The home ranges of African hornbills (*Ceratogymna atrata* and *C. cylindricus*) range from 925–4,474 hectares in tropical forest in Cameroon, which is comparable with Asian hornbills (Holbrook & Smith, 2000). The availability of *Ficus* in natural habitats can be an indicator to judge habitat quality for hornbills (Hata et al., 2015). Many hornbills feed primarily on figs (Walker, 2007; Naniwadekar et al., 2015; Wagh et al., 2015), and they also make the largest numbers of avian visits to several fig tree species in both the Paleotropics and Afrotropics (Kitamura et al., 2005; Daru et al., 2015). For example, figs consisted of 60% of the overall diet of the Malabar pied hornbill (*A. coronatus*) in the non-breeding season, and figs delivered to nest cavities in the breeding season were 75.6% of all food items in mixed deciduous forest in the western Ghats, India (Balasubramanian et al., 2004). Hadiprakarsa & Kinnaird (2004) reported that figs consisted almost the entire diet (98.6%) of the Helmeted hornbill (*Rhinoplax vigil*), and 76.9% for the Rhinoceros hornbill (*Buceros rhinoceros*) in the lowland rainforest of Sumatra, Indonesia, showing that figs are the most important part of the diet of these hornbill species in South-East Asia. Figs were also the main items in the diet of three sympatric hornbill species, the Great hornbill (*Buceros bicornis*), the Wreathed hornbill (*R. undulatus*) and the Oriental pied hornbill (*A. albirostris*) in seasonal evergreen forest of North-Eastern Thailand (Kanwatanakid-Savini et al., 2009). The fig-removal rate of the Black-and-white-casqued hornbill (*Bycanistes subcylindricus*) on African *Ficus thonningii* was 2.25 figs/minute, and it was one of the five main frugivores on this species (Kirika et al., 2008). Due to a large body and gape size, hornbills can swallow figs whole, even if they are large. For example, the Great hornbill (*B. bicornis*) and the Oriental pied hornbill (*A. albirostris*) swallow whole *Ficus racemosa* figs (diameter: 3–4 cm.). They removed 6–11 figs (mean = 7.8 figs) and spent 192–327 seconds (mean = 253.2 seconds) per visit on *F. recemosa* in riparian forest in Kanchanaburi, western Thailand (CHAPTER 3). The Indian grey hornbill (*Ocyceros birostris*) defaecated all its consumed seeds in a viable condition, including the seeds of seven fig tree species in dry deciduous forest of the Eastern Ghats, India, suggesting that hornbills promote seed dispersal for many forest trees, including fig trees (Santhoshkumar & Balasubramanian, 2011). The gut passage times of African hornbills (*Ceratogymna atrata* and *C. cylindricus*) ranged from 51–765 minutes in tropical forest in Cameroon. They are likely to be long-distance seed dispersers, as most seeds (> 80%) are transported 500 metres from their source trees, with the maximum seed dispersal range being nearly seven kilometres (Holbrook & Smith, 2000).

Phoeniculidae

The Green woodhoopoe (*Phoeniculus purpureus*) is native to Africa, and it is the only species that is recorded to be a fig-eater in this family (Bleher et al., 2003; Chama et al., 2013). As the woodhoopoes are mainly insectivorous birds and only occasionally feed on plant materials (Bleher et al., 2003), figs are unlikely to be an important constituent of the diet of these birds.

Coraciiformes

Only eight species in this order are fig-eaters. Five species belong to the Motmots (Momotidae) (Grade & Stoddard 2006; Bianchini et al., 2015; Stevenson et al., 2015; Palacio et al., 2016; del Hoyo et al., 2017). Members of this order are mainly insectivorous or carnivorous birds. Therefore, figs are unlikely to be an important food source for these birds.

Piciformes

Ramphastidae

Toucans occur in Neotropical forests, and 31 species from six genera (*Andigena*, *Aulacorhynchus*, *Baillonius*, *Pteroglossus*, *Ramphastos* and *Selenidera*) are known to be fig-eaters. Figs are reported to be one of the most important food items for the Toco toucan (*Ramphastos toco*) in the dry season in the Southern Pantanal forest of Brazil, accounting for 13% of their overall food (Ragusa-Netto, 2006). However, figs are less important in the diet of the Toco toucan in urban areas in central Brazil, where figs contributed only 4% of from feeding events (Santos & Ragusa-Netto, 2013). Toucans show large home range sizes (86 hectares in *Ramphastos* toucans and 191 hectares in *Pteroglossus pluricinctus*: the Many-banded Araçari), and they can move approximately three kilometres within 30 minutes (Holbrook, 2011). However, the estimated seed dispersal distance of toucans is approximately 100 metres in Panama (Kays et al., 2011), and from 269 to 449 metres in Equador (Holbrook, 2011). While feeding on *Virola* seeds (Myristicaceae), the average seed passage time of toucans is 25 minutes but ranging from 4–98 minutes (Kays et al., 2011). As there are limited studies focusing on the interactions of fig trees and toucans, the potential role of toucans in seed dispersal services of *Ficus* plants may be underestimated.

Capitonidae

There are limited records of figs being eaten by New World barbets, of which only four species (from genera: *Capito* and *Eubucco*) are known. Although the New World barbets feed primarily on fruits and are therefore considered to be frugivores (> 60% of their diet is fruit) (del Hoyo et al., 2017), it remains unclear whether figs are the main diet of these birds or not. The information of how these birds affect seed dispersal of *Ficus* plants has still not been investigated.

Megalaimidae

In total, 34 species of Asian barbets (genera *Caloramphus* and *Psilopogon*) are known to be fig-eaters. Barbets are often reported to be the dominant group feeding on fig trees in Paleotropic regions (Kitamura et al., 2005; Kamruzzaman & Asmat, 2008; Sanitjan & Chen, 2009; Velho et al., 2012). Moreover, figs are the most important part of the diet of Asian barbets: for example, the Coppersmith barbet (*P. haemacephala*) in tropical forests of India (David et al., 2011) and the Red-vented barbet (*P. lagrandieri*) in Southern Vietnam (Trounov & Vasilieva, 2014). Asian barbets are recognised as high-quality seed dispersers of fig trees. Because of their appropriate feeding behaviour and moderate gape width (27 mm), whole figs are easily swallowed (Peh & Chong, 2003; Sanitjan & Chen, 2009). The seed retention time of the Taiwan barbet (*P. nuchalis*) is short, ranging from 12 to 57 minutes, and ingested fig seeds by this bird show increased germinability, suggesting that barbets are high-quality fig seed dispersers (Chang et al., 2012).

Lybiidae

Similar to Asian barbets, numerous species of African barbets are known to feed on figs (40 species from ten genera: *Buccanodon, Cryptolybia, Gymnobucco, Lybius, Pogoniulus, Pogonornis, Stactolaema, Trachylaemus, Trachyphonus* and

Tricholaema). Several species of African barbets visit fig trees more frequently than other fruiting plants, and they are regarded as one of the major seed dispersers of African fig trees. They have a fig-removal rate ranging from 0.74 to 1.46 figs/minute (Flörchinger et al., 2010). The Yellow-spotted barbet (*B. duchaillui*) is the major visitor to *Ficus thonningii* and is likely to be one of the main seed dispersers of this fig tree (Kirika et al., 2008).

Indicatoridae

Only three species in this small family (Cassin's honeybird: *Prodotiscus insignis*, Lesser Honeyguide: *Indicator minor* and Lyre-tailed Honeyguide: *Melichneutes robustus*) are recorded as fig-eaters, all in Africa (Flörchinger et al. 2010; Schleuning et al. 2011; del Hoyo et al. 2017). There is also no information about fig seed dispersal effectiveness of these birds.

Picidae

A total of 29 species from 11 genera of woodpeckers are reported to be fig-eaters. Woodpeckers are mainly insectivorous and consume fruit as a minor food resource (del Hoyo et al., 2017). Woodpeckers are considered to be opportunistic feeders on fig trees (Daru et al., 2015). In Neotropical forests, woodpeckers spent between 3 and 11.5 minutes/visit foraging on fig trees (Grade & Stoddard, 2006). Woodpeckers are likely to be long-distance seed dispersers if they feed on fruits because their home range sizes are large, ranging from 31 to more than 700 hectares (Wiktander et al., 2001; Dudley & Saab, 2007). However, the roles of woodpeckers in the seed dispersal of fig trees are largely unknown.

Psittaciformes

Cacatuidae

In total, seven species of Australasian cockatoos (*Cacatua* and *Calyptorhynchus*) are fig-eaters. Although the records do not provide any information on seed dispersal by these birds, it is suggested that they can be similar to other parrots and largely act as seed predators.

Psitacidae

Parrots occur throughout the Palaeotropics, Afrotropics and Neotropics and have been introduced into North America and Europe (del Hoyo et al., 2017). Parrots are one of the largest groups that feed on figs (151 recorded species from 45 genera in total). Ragusa-Netto (2002) reported that the Green-cheeked parakeet (*Pyrrhura molinae*) feeds mainly on *Ficus calyptroceras* trees in neotropical dry forest, and that they removed up to 40% of the figs, with a fig-removal rate of approximately 2.8 figs/minute. It was suggested that figs are a major part of the diet of this bird. The visit length on fig trees by parrots can vary between approximately 15 minutes for the Green-cheeked parakeet (*Pyrrhura molinae*) to more than 40 minutes for the Yellow-chevroned parakeet (*Brotogeris chiriri*) (Ragusa-Netto, 2002). In Amazonian forests, the Pacific parrotlet (*Forpus coelestis*) feeds mainly on figs (Blanco et al., 2016). In the Afrotropics (Botswana), *Ficus sycomorus* is one of the top three items in the diet of the Meyer's parrot (*Poicephalus meyeri*) (Boyes & Perrin, 2009). Although figs are likely to be one of the most important food resources for some parrots, they were found to be less important in some studies

(Vaughan et al., 2006; Walker, 2007). The daily movement distance of the Maroon-fronted parrot (*Rhynchopsitta terrisi*) can be up to 27 kilometres in Mexico (Ortiz-Maciel et al., 2010). Amazonian macaws (*Ara* spp.) are also known as long-distance flyers (up to 1.2 kilometres), suggesting that they can be long-distance seed dispersers if they do not destroy all the seeds they eat (Tello et al., 2015). It is suggested that parrots mainly act as seed eaters rather than seed dispersers of fig trees (Tello, 2003), but species such as the Seychelles black parrot (*Coracopsis barklyi*) are considered to be a potential seed dispersal agent of *Ficus lutea* (Reuleaux et al., 2014).

Passeriformes

Comprising 819 currently-recognised species from 67 families, passerines are the largest group of fig-eaters. The bulbuls (Pycnonotidae) alone have 90 species known to interact with fig trees. The other main groups that are known as fig-eaters are shown in Table 7.10 and Fig. 7.5. In this review, only frugivores from those 18 major families are considered in detail.

Pycnonotidae

Bulbuls are distributed widely in Africa and Eurasia (del Hoyo et al., 2017). In total, 90 species from 26 genera are recorded fig-eaters. More broadly, bulbuls are considered to be the most important seed dispersers of small-sized fruiting plants in tropical Asia (Corlett, 2017). Focusing on the interaction between fig trees and bulbuls, at least 97 species of fig trees are dispersed by bulbuls, suggesting that they are the single most important seed vectors of fig trees. Figs are known as one of the most important food constituents of bulbul diets (Sreekar et al., 2010; Okosodo et al., 2016). Bulbuls are major visitors to fig trees in South-West China (Sanitjan & Chen, 2009). Figs represent 16.1% of the diet of the Red-vented bulbul (*Pycnonotus cafer*) in suburban habitats in India (Bhatt & Kumar, 2001). In Africa, the Common bulbul (*P. barbatus*) is the second most frequent visitor to *Ficus thonningii* crops (Kirika et al., 2008), and bulbuls have a similar fig-removal rate on this tree (approximately one fig/minute), as other small birds (Flörchinger et al., 2010). Weir (2004) found that Hong Kong endemic bulbuls have a short gut passage time. Examples include the Red-whiskered bulbul (*P. jocosus*: mean = 23.51 minutes, ranging from 6.43–35.13 minutes) and the Chinese bulbul (*P. sinensis*: mean = 19.11 minutes, ranging from 5.83–59 minutes). Similar gut passage times have been reported in two species of Southern Thailand bulbuls: the Red-eyed bulbul (*P. brunneus*: mean = 22.9 minutes, ranging from 4.9–45.9 minutes) and the Yellow-vented bulbul (*P. goiavier*: mean = 23.2 minutes, ranging from 3.8–56.3 minutes) (Kerdkaew, 2014). However, when consuming larger seeds, bulbuls tend to increase seed passage time (Khamcha et al., 2014). Seeds dispersed by bulbuls are mostly deposited within 20–40 metres of the parent trees, suggesting that they are mainly short-distance seed dispersers (Kerdkaew, 2014; Khamcha et al., 2014). The mean visit time by the Brown-eared bulbul (*Hypsypetes amaurotis*) to a *Ficus superba* crop was 95 seconds in Yakushima, Japan (Hamada & Hanya, 2016), which is comparable with other bulbuls in western Thailand (CHAPTER 3), where bulbul visit times were lower than bulbul gut passage times, so some dispersal was taking place.

Sturnidae

Starlings have a wide distribution across Africa, Eurasia and Australasia, and 79 species from 31 genera have been confirmed as fig-eaters. The Stuhlmanns starling (*Poeoptera stuhlmanni*) removes 0.84 figs/minute when feeding on *Ficus thonningii* in the tropical forests of Kenya (Kirika et al., 2008), and the violet-backed starling (*Cinnyricinclus leucogaster*) removes 0.56 figs/minute of this fig tree species (Flörchinger et al., 2010). *Ficus benghalensis* is the most important food source for the Jungle mynah (66.6%) during winter in urban Bangladesh (Kamruzzaman & Asmat, 2008). Moreover, the Common mynah (*Acridotheres tristis*) is often the most common species interacting with fig trees in urban habitats (Mahanta et al., 2014). The Common starling (*Sturnus vulgaris*) makes the highest number of visits by any birds to *Ficus crassiramea* and *Ficus forstenii* in the forest reserve area of Mindanao in the Philippines (Aribal et al., 2016).

Thraupidae

In total, 75 species from 27 genera of Tanagers are confirmed as fig-eaters in the Neotropics. The Puerto Rican spindalis (*Spindalis portoricensis*) is known as one of the main avian frugivores visiting *Ficus trigonata* in Puerto Rico (Saracco, 2002). The Grayish saltator (*Saltator coerulescens*) feeds primarily on *Ficus pertusa* (11.2% of their overall diet) in Venezuela (Rodriguez-Ferraro et al., 2007). In Suriname, the fig consumption rate of the Bay-headed tanager (*Tangara gyrola*) when they are foraging on strangler fig trees is approximately 1.67 figs/minute (Vanderhoff & Grafton, 2009). Likewise, the Sayaca tanager (*Tangara sayaca*) visits *Ficus calyptroceras* crops frequently and is responsible for 16–27% of overall fruit removal, visiting the crop for 6.1–8.6 minutes at a time (Ragusa-Netto, 2002). In contrast, tanagers in Costa Rica visited fig crops for a short space of time, mostly less than two minutes (Grade & Stoddard, 2006). Ingested fig seeds are passed within seven minutes after swallowing by the Diademed tanager (*Stephanophorus diadematus*), so these tanagers have a short gut passage time (Gasperin & Pizo, 2012) and are likely to disperse the figs intact. Tanagers are considered to be short-distance seed dispersers as their home range size is quite small. For example, Scarlet tanagers (*Piranga olivacea*) have a home range size of approximately 2.6-5.6 hectares, with the core area being less than one hectare (Vega-Rivera et al., 2003).

Turdidae

Thrushes are ubiquitous in many natural habitats and many are frugivorous (del Hoyo et al. 2017). There are 38 species from seven genera (*Catharus*, *Chlamydochaera*, *Geokichla*, *Hylocichla*, *Myadestes*, *Sialia* and *Turdus*) known to feed on figs throughout the tropics. The Creamy-bellied thrush (*Turdus amaurochalinus*) contributed more than 10 % of overall *Ficus calyptroceras* fig removal, with a moderate fig-removal rate (2 figs/minutes) and visit length (three minutes) in the dry forest habitat of western Brazil (Ragusa-Netto, 2002). Figs were found in the faeces of two species of thrush (*Turdus albicolis* and *Turdus rufriventris*) in suburban areas of Southern Brazil (Gasperin & Pizo, 2009). However, three species of thrush (*Turdus hauxwelli, Turdus ignobilis* and *T. albicollis*) in Southern Peru were not the main frugivores of *Ficus pertusa* figs (Tello, 2003). Fig trees provide important food resources for several thrush species in restored habitats in Brazil (Silva et al., 2015). *Ficus thonningii* figs are one of the main food resources for the Olive thrush (*Turdus olivaceus*) in South African coastal forest (Bleher et al., 2003) and the African thrush (*Turdus pelios*) in fragmented habitats and tropical forests of Kenya (Kirika et al., 2008; Schleuning et al., 2011). The Olive thrush (*T. olivaceus*) and African thrush (*T. pelios*) consume figs of *Ficus sur* and *Ficus lutea* in Kenya (Schleuning et al., 2011) and the African thrush (*T. pelios*) consumes several *Ficus* species in Nigeria (Daru et al., 2015). *Turdus libonyana* was the major visitor to *Ficus natalensis* crops in the montane forest of Malawi (Fujita, 2014). In degraded tropical forest in Singapore, the Eyebrowed thrush (*Turdus obscurus*) feeds on *Ficus grossularoides* figs. Although the thrush was not a major fig consumer, its habit of swallowing figs whole suggests they could be high-quality seed dispersers of fig trees (Peh & Chong, 2003). In tropical East Asia, three species of *Turdus* (*T. chrysolaus, T. obscurus* and *T. pallidus*) are known to be fig-eaters in the karst forest of Southern Taiwan (Sung, 2005). *Ficus retusa* is one of the major food sources for the Blackbird (*Turdus merula*) in suburban areas of Algeria (Salima & Salaheddine, 2014). The movement of post-fledgling *Turdus assimilis* was only between ten and several hundred metres (Cohen & Lindell, 2004), suggesting that this thrush is likely to be a short-distance seed disperser.

Corvidae

Globally, 35 species of corvids from 12 genera (*Calocitta, Cissa, Corvus, Cyanocorax, Cyanopica, Dendrocitta, Garrulus, Pica, Platysmurus, Pteridophora, Pyrrhocorax* and *Urocissa*) are recorded fig-eaters, distributed throughout the tropics. Most of the fig-eaters are in the genera *Corvus* (11 species) and *Cyanocorax* (ten species). The Purplish jay (*Cyanocorax cyanomelas*) was responsible for approximately 5% of the visits to *Ficus calyptroceras* crops in West Brazil. Although it spent a short period of time during visits to fig trees (4–8 minutes), it showed a high fruit removal rate (three figs/minute) (Ragusa-Netto, 2002). The House crow (*Corvus splendens*) visited *Ficus grossularoides* crops in Singapore, but it was not the major visitor to these fig trees (Peh & Chong, 2003). The Grey treepie (*Dendrocitta formosae*) was shown to eat the figs of *Ficus caulocarpa, Ficus ampelas* and *Ficus irisana* in the karst forests of Taiwan (Sung, 2005). In urban areas of Bangladesh, the House crow (*C. splendens*), the Large-billed crow (*Corvus macrorhynchos*) and the Rufous treepie (*Dendrocitta vagabunda*) were the major visitors (> 60% of overall visits) to several species of fig trees (Kamruzzaman & Asmat, 2008; Mahanta et al., 2014). The Large-billed crow (*C. macrorhynchos*) visited *Ficus amplissima* crops but did so infrequently (two times/hour) in India (David et al., 2011). Crows are likely to be potential seed dispersers of fig trees as they swallow figs whole (Peh & Chong, 2003). Crows have long movement ranges and large home range sizes (*Corvus mellori*: up to 9.9 km/hour; Whisson et al., 2015, *Corvus branchyrhynchos*: 6.4–9.6 km^2; Yaremych et al., 2004), suggesting that crows can be long-distance seed dispersal agents for fig trees.

Fringillidae

A total of 35 species from nine genera (*Carpodacus, Chlorophonia, Crithagra, Euphonia, Haemorhous, Linurgus, Serinus, Spindalis* and *Spinus*) of fringilid birds are recognised as fig-eaters, with 16 of them are in the genus *Euphonia.* In the forests of Southern Peru, *Euphonia* spp. was one of the major birds removing *F. pertusa* figs, but the visit length (4–5 minutes), figs removed per visit (1-3 figs) and fig-removal rate (0.5–1.3 figs/minute) were low in comparison to some other frugivorous birds (Tello, 2003). The small-bodied Olive-backed euphonia (*Euphonia gouldi*) made the highest number of visits and spent around four minutes at *Ficus colubrinae* trees in the tropical rainforests of Costa Rica (Grade & Stoddard, 2006). In primary and secondary rain forest of Suriname, the Golden-sided euphonia (*Euphonia cayennensis*) was the main visitor to an unidentified strangler fig tree (*Ficus* sp.). 81% of the figs removed were ripe and presumably contained viable seeds (Vanderhoff & Grafton, 2009). Citrils and canaries (*Crithagra* spp.) contribute to fig removal in the Afrotropics, but not in high proportions (Flörchinger et al., 2010; Schleuning et al., 2011; Menke et al., 2012; Chama et al., 2013). As the fringillids are small-bodied birds and closely related to tanagers (Thraupidae), the seed dispersal services provided by fringillids may be similar to tanagers. However, true finches may act mainly as seed predators.

Tyrannidae

Recorded Neotropical tyrannids reported to be fig-eaters include 29 species from 13 genera: *Elaenia, Empidonomus, Machetornis, Megarynchus, Mionectes, Myiarchus, Myiodynastes, Myiozetetes, Phylloscartes, Pitangus, Sayornis, Todirostrum* and *Tyrannus*. The great kiskadee (*Pitangus sulfuratus*) contributed 6.5–12% to overall *Ficus calyptroceras* fig removal, and the feeding activity (visit times = 1.1-1.5 minutes and fruit removal per visit = 1 fig) were relatively low compared to other other small birds in Brazil (Ragusa-Netto, 2002). Several tyrannid species visited a *Ficus colubrinae* crop in the tropical rainforests of Costa Rica, but they were not frequently found there (Grade & Stoddard, 2006). The potential roles of tyrannids in fig seed dispersal are still largely unknown. However, seeds of some other shrub species in Chile were still viable and germinated faster after passing through tyrannid bird guts, suggesting their possible role as seed dispersers (Reid & Armesto, 2011).

Meliphagidae

Although 27 species of Indo-Australian honeyeaters are known fig-eaters, they are primarily nectarivorous birds that probably consume figs as a minor food source. It has been reported that mistletoe seeds ingested by the Spiny-cheeked honeyeater *(Acanthagenys rufogularis*) were egested, mostly 30–40 minutes after ingestion, and that movements within the seed passage time were within 100 metres (Rawsthorne et al., 2011), suggesting that the honeyeaters are short-range seed dispersers. However, the roles of honeyeaters in *Ficus* seed dispersal have not yet been investigated.

Zosteropidae

The small-bodied White-eyes and Yuhinas are distributed widely throughout the African and Indo-Australian regions (del Hoyo et al., 2017). In total, 27 species from four genera are known as fig-eaters (*Cleptornis*, *Rukia*, *Yuhana* and *Zosterops*), of which 22 are species of *Zosterops*. Fig trees (*Ficus thonningii* and *Ficus sur*) comprised 10% of the overall visits to trees by the Kulal white-eye (*Zosterops kulalensis*) in the dry season at Mt. Kulal, Kenya, but 80% of feeding involved insects rather than fruits (Borghesio & Laiolo, 2004). The Yellow white-eye (*Zosterops senegalensis*) removed only 0.41 figs/minute of *F. thonningii*, which was low when compared with other frugivorous birds (Kirika et al., 2008). Faecal analysis of Japanese Bonin white-eye (*Zosterops japonicus*) in Bonin Island revealed a diet shift to incorporate the introduced *F. microcarpa* into their diet (Kawakami et al., 2009). White-eyes have been reported as fig-eaters in China (Sanitjan & Chen, 2009) and Kenya (Flörchinger et al., 2010; Schleuning et al., 2011; Menke et al., 2012), but they do not seem to be the major frugivores. As white-eyes are small birds, it is likely that they are short-distance seed dispersers.

Oriolidae

Orioles are common in the Afrotropics and the Indo-Australian tropics. There are a total of 21 species from three genera (*Oriolus*, *Pitohui* and *Sphecotheres*), with 17 belonging to the genus *Oriolus*, that are reported as fig eaters. Orioles are omnivorous birds that consume fruits and invertebrates in similar proportions (Walker, 2007) and they are not frequent visitors to fig trees (Bleher et al., 2003; Peh & Chong, 2003; Kirika et al., 2008; Sanitjan & Chen, 2009; Flörchinger et al,. 2010; Schleuning et al., 2011; Velho et al., 2012; Chama et al., 2013; Mahanta et al., 2014). The Black-naped oriole (*Oriolus chinensis*) removed 3.5–6 figs/visit when feeding on *Ficus fistulosa* and *Ficus grossularoides* in Singapore (Peh & Chong, 2003), and spent between 1 and 16 minutes during visits to fig trees in the tropical deciduous forests of Thailand (Kitamura et al., 2005). The western black-headed oriole (*Oriolus brachyrhynchus*) had a low fig-removal rate (0.49 fig/minute) when feeding on *Ficus thonningii* trees in Kenya (Kirika et al., 2008). Based on the swallowing behaviours when feeding on smaller figs (Peh & Chong, 2003), together with their short visits to the trees, it is likely that orioles can disperse fig seeds far away from the parent trees.

Icteridae

Although there are 21 species of icterids from seven genera (*Cacicus, Dives, Hypopyrrhus, Icterus, Molothrus, Psarocolius* and *Quiscalus*) that are known to consume Neotropical figs, information on how icterid birds interact with fig trees is limited. The Montezuma oropendora (*Psarocolius montezuma*) fed on *Ficus colubrinae* figs and spent a short time foraging (approximately two minutes) in tropical rainforest in La Selva, Costa Rica (Grade & Stoddard, 2006).

Nectariniidae

A total of 21 sunbird and spiderhunter species from eight genera (*Aethopyga, Anthreptes, Arachnothera, Chalcomitra, Cinnyris, Cyanomitra, Hedydipna* and *Nectarinia*) are recorded as feeding on African and Indo-Australian fig trees. However, sunbirds are mainly nectarivores (del Hoyo et al., 2017) and not likely to play significant roles in *Ficus* seed dispersal. All the updated records refer explicitly to fig consumers, but no feeding behaviours were studied (Sanitjan & Chen, 2009; Sreekar et al., 2010; Schleuning et al., 2011; Chama et al., 2013; Daru et al., 2015).

Paradisaeidae

Birds-of-paradise are found throughout Melanesia, New Guinea and Australia, and 21 species from 11 genera (*Astrapia, Cicinnurus, Drepanornis, Epimachus, Lophorina, Manucodia, Paradisaea, Paradisornis, Parotia, Phonygammus* and *Seleucidis*) are known to be fig-eaters. Since Shanahan et al. (2001) published the global fig-eater records, there are still no new updates about these birds' roles in *Ficus* seed dispersal. Shanahan et al. (2001) suggested that some species of birds-of-paradise are fig specialists and are likely to be important dispersers of fig seeds.

Leiotrichidae

The Laughingthrushes and allies occur throughout Eurasia and Africa (del Hoyo et al., 2017). Although 20 species from eight genera (*Acanthoptila, Actinodura, Alcippe, Garrulax, Heterophasia, Leiothrix, Trochalopteron* and *Turdoides*) are confirmed as fig-eaters, the roles of these birds in *Ficus* seed dispersal are still unknown.

Campephagidae

Cuckooshrikes are found throughout tropical and subtropical Asia, Australia and Africa (del Hoyo et al. 2017), and 19 species from five genera (*Campochaera, Coracina, Edolisoma, Lalage* and *Pericrocotus*) are fig-eaters. However, cuckooshrikes are mainly insectivores, so they may not play a significant role in *Ficus* seed dispersal.

Dicaeidae

Nineteen species of flowerpeckers from two genera (*Dicaeum* and *Prionochilus*) are known to eat figs in the Indo-Australian region. Flowerpeckers are small birds, having a small gape width, and all of them bite figs when they are feeding (Peh & Chong, 2003). As fig seeds are small, it is suggested that some of the fig seeds may be ingested by the flowerpeckers, even though the whole fig is not swallowed. The flowerpeckers are likely to be short-distance seed dispersers because of their small home ranges (core area = 1 ha.), and it was predicted that the mistletoe bird (*Dicaeum hirundinaceum)* disperses most mistletoe (Loranthraceae) seeds within 100 metres from the parent trees in Australia (Ward & Paton, 2007).

Muscicapidae

Old World flycatchers are found in Eurasia and Africa, and 19 species from 15 genera (*Chaimarrornis, Copsychus, Dessonornis, Ficedula, Fraseria, Geokichla, Melaenormis, Monticola, Muscicapa, Myophonus, Myrmecocichla, Oenanthe, Phoenicurus, Pogonocichla* and *Thamnolaea*) are known to eat figs. Although it is suggested that these birds mainly fed on invertebrates, and that fruits seem to be a minor food source for them, the Blue-whistling thrush (*Myophonus caeruleus*), a riparian specialist bird fed on two species of riparian fig trees (*Ficus ischnopoda* and *Ficus montana*) in western Thailand. The Blue-whistling thrush swallowed whole figs and they primarily foraged along stream banks where the riparian figs were growing. It is possible that this bird may tend to disperse fig seeds along stream banks, the most suitable microsite for riparian fig trees (CHAPTER 3).

Cotingidae

Cotingas occur in Neotropical South America, and 18 species from 12 genera (*Ampelioides, Carpodectes, Carpornis, Conioptilon, Cotinga, Gymnoderus, Lipaugus, Phoenicircus, Pipreola, Procnias, Querula* and *Xipholena*) are recorded to eat figs. Tello (2003) showed that the Screaming piha (*Lipaugus vociferans*) and the Purple-throated fruitcrow (*Querula purpurata*) fed on *Ficus pertusa* trees in Peru. The Screaming piha contributed 5% of overall fig removal, had a high fig-removal rate (4.6 figs/minute), and ashort visit time (two minutes), while the Purple-throated fruit crow visited less frequently (0.3% of total visits) with a low fig-removal rate (1.4 figs/minutes) and a short visit time (4.7 minutes). The Purple-throated fruitcrow (*Q. purpurata*) visited *Ficus insipida* crops briefly (approximately 2 minutes) and had a high fig-removal rate (3.1 figs/minute) in Colombia, and it is suggested that this species can transport seeds over long distances, between habitats (Parrado-Rosselli & Amaya-Espinel, 2006).

Other families

Two species of *Calyptromena* broadbills (Calyptromenidae), *Eurylaimus* broadbills (Eurylaimidae), the Asian fairy bluebird (*Irena puela*, Irenidae) and leafbirds (Chloropseidae) are known to feed on at least 20 species of Indo-Australian fig trees and are likely to be important dispersers of many fig species in the region. Species belonging to other families, such as the acrocephalid warblers (Acrocephalidae), cardinals (Cardinalidae), cisticolid warblers (Cisticolidae), drongos (Dicruridae), buntings (Emberizidae), estrildid finches (Estrildidae), ovenbirds (Furnariidae), hylias (Hyliidae), bushshrikes (Malaconotidae), berrypeckers (Melanocharitidae), mocking birds (Mimidae), Puerto Rican tanagers (Nesospingidae), tits (Paridae), New World warblers (Parulidae), sparrows (Passeridae), ground babblers (Pellorneidae), Old World leaf-warblers (Phylloscopidae), manakins (Pipridae), wattle-eyes (Platysteiridae), weavers (Ploceidae), catbirds (Ptilonorhynchidae), penduline tits (Remizidae), spindalis (Spindalidae), fairy flycatchers (Stenostiridae), typical warblers and allies (Sylviidae), Old World babblers (Timaliidae), tityras (Tityridae), wrens (Troglodytidae) and vireo (Vireonidae) are also known fig-eaters. However, the feeding records and intensive studies of most of these birds are still lacking and their roles in the seed dispersal of fig trees are still unknown.

7.4.3.3 Mammals

Marsupialia

Didelphimorphia

Ten species of nocturnal opossums (Didelphidae, including the genera *Didelphis, Marmosa, Micoureus*, and *Philander*, Caluromyidae, including *Caluromys*) are recorded to eat Neotropical fig trees. *Ficus luschnatiana* contributed 20% of the Brown-eared woolly opossum's (*Caluromys lanatus*) diet in Brazil (Casella & Caceres, 2006). Similarly, figs were one of the major dietary constituents (frequency of occurrence 29%) of the Big-eared opossum (*Didelphis aurita*) in Brazil (Caceres et al., 2009). Among other fruits, figs were the third most important constituent in the diet (11%) of the White-eared opossum (*Didelphis albiventris*) in Brazil (Silva et al., 2014), and *Ficus cestrifolia* was found in up to 66% of dietary examples (Junges et al., 2018). However, fig remains were only found in 0.02% of the faeces of the Woolly mouse opossum (*Micoureus demerarae*) in Brazil, showing that figs were a less important part of its diet (Pinheiro et al., 2002). The fate of the fig seeds after consumption by these opossums has not been investigated.

Diprotodontia

According to the previous review of fig-eaters (Shanahan et al., 2001), there are 16 species from five families that are known fig-eaters (Hypsiprymnodontidae, Macropodidae, Petauridae, Phalangeridae and Pseudocheiridae). However, very few reports have described how these marsupials are involved in *Ficus* seed dispersal (Shanahan et al., 2001). The Musky rat-kangaroo (*Hypsiprymnodon moschatus*, Hypsiprymnodontidae) found in Australian rainforests feeds on *F. crassipes* and *F. pleurocarpa* figs, which was recognised by the teeth markings on the figs (Dennis, 2002). What happens to the seeds after dispersal is still unknown.

Peramelemorphia

Four species of bandicoots from two families (Peramelidae, *Echymipera*; Peroryctidae, *Peroryctes*) are recorded fig-eaters, but nothing is known about their roles in the seed dispersal of fig trees.

Placentalia

Primates

In total, 14 lemur species (Lemuridae, *Eulemur, Lemur, Prolemur* and *Varecia*), two mouse lemur species (Cheirogaleidae, *Cheirogaleus* and *Microcebus*) and four sifaka species (Indriidae, *Propithecus*) are known to feed on Madagascan fig tree species. It is suggested that *Ficus reflexa* figs contributed very little (1.6%) to the diet of young Brown lemurs (*Eulemur fulvus*) (Tarnaud, 2004), and also the

Black lemur (*E. macaco*: 3.5% of overall diet) (Simmen et al., 2007). In contrast, ripe figs were one of the most important food sources for the Red ruffed lemur (*Varecia rubra*), accounting for approximately 13% of their foraging time (Martinez, 2010). *Ficus rubra* (37%) and *Ficus tiliifolia* (10%) figs were important food sources for the Grey-headed lemur (*Eulemur cinereiceps*) (Andriamaharoa et al., 2010). The Ring-tailed lemur (*Lemur catta*) consumed more figs during the dry season, suggesting the importance of figs increases when other foods are scarce (Gould & Gabriel, 2014). Lemurs mostly dispersed seeds more than 100 metres from the parent trees, and some seeds could occasionally be dispersed more than 500 metres (Razafindratsima et al., 2013), suggesting their potential as long distance seed dispersers.

There are three species of New World night monkeys (Aotidae, *Aotus*) known to eat figs in the tropical forests of South America, but little is known about their roles in *Ficus* seed dispersal.

A total of nine species of New World cebid monkeys are confirmed fig-eaters (Cebidae, *Cebus, Saimiri* and *Sapajus*). Three species of cebid monkeys (*Cebus albifrons, Saimiri sciureus* and *Sapajus apella*) contributed 41.5% of overall *Ficus pertusa* fig removal, and they also showed a long visit time at fig trees (12–17 minutes), and a high fig-removal rate per visit (17–49 figs), suggesting that they are large volume seed dispersers (Tello, 2003). It is suggested that White-headed capuchin (*Cebus capucinus*) dispersed most seeds from the parent trees (Wehncke et al., 2004). In addition, this capuchin species spent much of its time (31%) foraging on fig trees in Costa Rica (Melin et al., 2009), and figs are an important food source for them (Parr et al., 2011).

The New World atelids (Atelidae), includes 19 species from five genera (*Alouatta, Ateles, Brachyteles, Lagothrix* and *Oreonax*), that are recorded as fig-eaters. Mexican howler monkeys (*Alouatta palliata mexicana*) spent 64.2% of their feeding time on six *Ficus* species, and fig trees were clearly an important food source for them (Serio-Silva et al., 2002). In Peru the Red-faced spider monkey (*Ateles paniscus*) was the major *Ficus pertusa* fig-eater (12.5% of overall fig removed by frugivores), spent a long time feeding during visits (approximately 30 minutes) and removed the highest number of figs per visit (55 figs/visit) (Tello, 2003). *Ficus* plants were also important food sources for Brown woolly monkeys (*Lagothrix lagotricha*) in Ecuador (Fiore, 2004) and Colombia (Stevenson, 2004), the Peruvian spider monkey (*Ateles chamek*) in Bolivia (Felton et al., 2008) and the Silvery woolly monkey (*Lagothrix poeppigii*) in Ecuador (Fiore, 2004). However, *Ficus* was rare in the diet of Spix's red-handed howler (*Alouatta discolor*) (4.2% of its overall food) in Brazil (Pinto & Setz, 2004), 0.9% in the White-bellied spider monkey (*Ateles belzebuth*) and 2.7% in the Brown woolly monkey (*Lagothrix lagotricha*) in Ecuador (Dew, 2005). Differences in the proportion of *Ficus* in the diet of howler monkeys seem to vary between sites. The howlers were reported as potential seed dispersers for many plants, including fig trees. They fed primarily on figs and also swallowed them whole, suggesting that they are ideal seed-dispersal agents (Chaves et al., 2010). The seed passage time of the White-bellied spider monkey (*A. belzebuth*) was approximately 4.5 hours, and the average seed dispersal distance was 443 metres with >1250 metres the maximum range (Link & Fiore, 2006). When passing through the gut of either the Mexican howler (*A. palliata mexicana*), the Guatemalan black howler (*Alouatta pigra*) (Righini et al., 2004) or the Black howler (*Alouatta caraya*) (Sugai et al., 2009), fig seeds germinated faster than unpassed seeds (Righini et al., 2004) and also had an increased germination rate

(Sugai et al., 2009). However, howlers can be low-quality seed dispersers in some cases. For example, the distribution of the faeces of the Mantled howler (*Alouatta palliata*) in their home range were aggregated (0.5–5 metres apart) and are likely to be prone to seed predation and intense competition among seedlings (Wehncke et al., 2004). The Mantled howler monkey (*A. palliata*) was also likely to be a low-quality seed disperser of *Ficus insipida* in Costa Rica, as most of the consumed figs were still unripe, meaning that the seeds would not be fully developed (Banack et al., 2002).

Fig-eating by nine species of tamarins and marmosets (Callitrichidae, *Callithrix, Leontopithecus* and *Saguinus*) was confirmed in the Neotropics. In Suriname, the Golden-handed tamarin (*Saguinus* sp.) had a high visitation rate at strangler fig trees (3.5 visits/day) and spent short times on the trees during each visit (about six minutes), suggesting that it may be an important seed disperser if its faeces are deposited in appropriate sites (Vanderhoff & Grafton, 2009). The germination success of *Ficus americana* and *Ficus insipida* seeds after ingestion by Brown-mantled tamarins (*Saguinus fuscicollis*) and Moustachioed tamarins (*Saguinus mystax*) was found to be 5 to 12 times greater than in unpassed seeds. However, *Ficus pertusa* seeds passing through the same two dispersers showed a lower germination success than unpassed seeds, suggesting that the quality of dispersal provided can vary between fig tree species (Knogge et al., 2003). *F. gomelleira* seeds extracted from the faeces of the Golden-headed lion tamarin (*Leontopithecus chrysomelas*) had higher seed germination than the seeds obtained directly from ripe figs, but had a longer germination delay (Catenacci et al., 2009).

New World fig-eating is reported in seven species of sakis and allies (Pitheciidae, *Cacajao, Callicebus, Chiropotes* and *Pithecia*). Figs contributed only 1.4% of the diet of the Bald uakari (*Cacajao calvus ucayalii*) in Peru (Bowler & Bodmer, 2011), 0.05% of the diet of the White-nosed saki (*Chiropotes albinasus*) in Brazil (Barnett et al., 2012) and a very low percentage of the diet of Red-backed bearded saki (*Chiropotes chiropotes*) (Boyle et al., 2012) and Black-fronted titi (*Callicebus nigrifrons*) in Brazil (dos Santos et al., 2012) reflecting the minor role that figs play in their respective diets. The roles of pithecids in seed dispersal in fig trees have not yet been intensively researched.

With at least 60 species from 17 genera (*Cercocebus, Cercopithecus, Chlorocebus, Colobus, Erythrocebus, Lophocebus, Macaca, Mandrillus, Miopithecus, Nasalis, Papio, Presbytis, Procolobus, Pygathrix, Rungwecebus, Semnopithecus* and *Trachypithecus*), the Old World monkeys (Cercopithecidae) are one of the largest groups of fig-eaters. Among the 17 genera, the macaques (*Macaca* spp.) showed the highest representation, with 14 species known to eat figs. Figs are reported as the most frequently consumed food item among Old World monkeys, by always being present in the top five constituents of their diet (Sushma & Singh, 2006; Riley, 2007; Tolo et al., 2008; Tsujino & Yumoto, 2010; David et al., 2011; Hu, 2011; Wieczkowski, 2013; Pengfei et al., 2014; Hambali et al., 2014; Erinjery et al., 2015). In Japan, the Yakushima macaque (*Macaca fuscata yakui*) was the major remover of *Ficus superb* figs (Otani, 2001). Also, *Ficus* spp. accounted for a high frequency of occurrence (up to 80%) in the diet of the Formosan rock macaque (*Macaca cyclopis*) in Taiwan (Su & Lee, 2001). The Rhesus macaque (*Macaca mulatta*) dispersed fig seeds approximately 70–140 metres from parent trees in India, suggesting it provides relatively short-distance seed dispersal services

(Sengupta et al., 2014). Similarly, the Javan lutung (*Trachypithecus auratus*) mostly dispersed seeds within 50–100 metres (range = 1 – 299 metres.). Its gut passage times ranged from 24 to 96 hrs (Tsuji et al., 2017). Fig seeds ingested by the Vervet monkey (*Chlorocebus pygerythrus*) and the Hamadryas baboon (*Papio hamadryas*) showed higher germination rates than unpassed seeds (Righini et al., 2004). Unpassed seeds could also be dispersed after being 'processed' in the mouth. It is suggested that the Southern pig-tailed macaque (*Macaca nemestrina*) in Thailand usually dispersed seeds by spitting them from their cheek pouch (Kitamura et al., 2002). Fig leaves are another preferred food for some Old World monkeys. In China, White-headed langurs (*Trachypithecus poliocephalus*) fed primarily on leaves (approximately 15% of their total diet compared with 0.5% ripe *Ficus microcarpa* figs), reflecting its highly folivorous behaviour (Li & Rogers, 2003). In Uganda, the Red-tail monkey (*Cercopithecus ascanius schmidti*) and the Blue monkey (*Cercopithecus mitis stuhlmanii*) were mainly frugivorous (79–85% of feeding time), but sometimes they also fed on fig leaves (15–21% of feeding time). Both ripe and immature figs were consumed by these monkeys (Tweheyo & Obua, 2001). It was reported in Tanzania that young figs were consumed by the Red colobus monkey (*Procolobus badius*) (Chapman et al., 2002), the Eastern black-and-white colobus (*Colobus guereza*), the Ugandan red colobus (*Procolobus tephrosceles*) (Rode et al., 2003) and the Kipunji (*Rungwecebus kipunji*) (Davenport et al,. 2010). Similarly, un-ripe figs were eaten by the Proboscis monkey (*Nasalis larvatus*) in Malaysia (Boonratana, 2003), the Assam macaque (*Macaca assamensis*) and the Rhesus macaque (*Macaca mulatta*) in China (Zhou et al. 2014), suggesting that the Old World monkeys can also act as seed predators.

Asian figs are known to be consumed by 14 species of gibbons (Hylobatidae, *Hoolock, Hylobates, Nomascus* and *Symphalangus*). Hasan et al. (2005) suggested that figs were the main food of the western hoolock gibbon (*Hoolock hoolock*) in Bangladesh. Although the Black-crested gibbon (*Nomascus concolor*) was mainly folivorous, figs were also an important constituent of its diet in China (Fan et al., 2009). Figs were a major part of the diet of the endangered Eastern black-crested gibbon (*N. nasutus*) in China (Fan et al., 2011), and the White-handed gibbon (*Hylobates lar*) in Thailand (Kanwatanakid-Savini et al., 2009). Based on a high selective index (27.59) of *Ficus*, it is believed that the Javan gibbon (*Hylobates moloch*) relies heavily on figs in Indonesia (Kim et al., 2012). It is reported that Müller's Bornean gibbon (*Hylobates muelleri*) spent around 20 minutes/visit feeding on *Ficus benjamina* (Nakabayashi et al., 2016). The Bornean white-bearded gibbon (*Hylobates albibarbis*) moved approximately 500 metres a day (Vogel et al., 2009), and the Eastern hoolock gibbon (*Hoolock leuconedys*) moved approximately 1,100 m/day (range = 340–2600 m, Zhang et al. 2013) so they can potentially transport fig seeds well away from the parent trees.

Figs are known to be eaten by seven species of hominids (Hominidae, *Gorilla*, *Pan* and *Pongo*), including humans (*Homo sapiens*). Although the western lowland gorilla (*Gorilla gorilla*) is mainly a folivore, fruits including figs were other important dietary constituents (Remis et al. 2001). Figs are reported as being an important part of its diet (Ganas et al., 2004; Yamagiwa et al., 2005; Yamagiwa & Babose, 2006), as well as that of the Chimpanzee (*Pan troglodytes*) (Basabose, 2002; Tweheyo et al., 2004; Yamagiwa & Babose, 2006; Gross-Camp et al., 2009; Potts et al., 2011; Chancellor et al., 2012; Chemurot et al., 2012; Watts et al., 2012a; Bortolamiol et al., 2014; Dutton & Chapman, 2015) and of the Bornean orangutan

(*Pongo pygmaeus*) in Indonesia (Russon et al., 2015), based on faecal and observational studies. Chimpanzees are one of the most important seed dispersers of tropical forest fig trees in Africa, with at least 38 species of *Ficus* in their diet and fig seeds the most frequently found seeds in their faeces (Basabose, 2002). Immature figs and leaves were also eaten, along with ripe figs (Tweheyo & Obua, 2001; Tweheyo et al., 2004), suggesting that not all feeding will disperse viable seeds. The Bornean orangutan (*P. pygmaeus*) (Kanamori et al., 2010) and the Orangutan (*P. abelii*) (Kelle et al., 2014) feed primarily on figs in addition to the leaves and bark of figs trees. Bonobo (*Pan paniscus*) was reported as a potential seed disperser for many species of African figs, as they swallowed figs whole and defaecated intact seeds (Beaune et al. 2013). Bornean orangutan spent more than 100 minutes/visit feeding on *Ficus benjamina* trees (Nakabayashi et al., 2016). Passage through gorilla guts increased *Ficus* seed germination by 78% (Petre et al., 2015). In captivity, seeds of *Urostigma* fig tree species passing through the digestive tract of the Chimpanzee and Bornean orangutan had significantly higher germination rates and shorter germination times than seeds obtained directly from figs (Righini et al., 2004). These findings suggest they offer good quality seed dispersal services.

Carnivora

Although civets and their allies (Viverridae) are kown as nocturnal carnivores, fruits are also found in their diets. In total, 11 species from eight genera of civets (*Arctictis, Arctogalidea, Genetta, Nandinia, Paguma, Paradoxurus, Viverra* and *Viverricula*) are known to be fig-eaters globally. Civets are found mostly in Asia, but also in Africa and Europe, and they are recognised as seed dispersers of fig trees (Kitamura et al., 2002; Madappa et al., 2010). Figs accounted for 1.6–9% of the diet of the Brown palm civet (*Paradoxurus jerdoni*) in India, and it was noted that fig seeds that passed through its gut were still viable (Madappa et al., 2010). At least five fig tree species are consumed by the Binturong (*Arctictis binturong*) in India, suggesting that they are also likely to disperse fig seeds (Naniwadekar et al., 2013) and figs are reported to be the most important food source for this species in Borneo, Malaysia (Nakabayashi et al., 2017). Three species of civets had visits of approximately 100 minutes on fig trees in Malaysia (Nakabayashi et al., 2016). The Common genet (*Genetta genetta*) fed on *F. carica* figs in Europe and North Africa (Rosalino & Santos-Reis, 2009; Rosalino et al., 2010; Amroun et al., 2014). Based on a small sample it was noted that more than 200 *F. carica* seeds were found in one scat, and those seeds showed high germination rates, confirming the role of genets as fig seed dispersers (Rosalino et al., 2010).

Globally, although mostly in Asia, five species of bears (Ursidae, *Helarctos, Melursus, Tremarctos*, and *Ursus*) are known to include figs in their diet. Figs were the major part of the diet of the sun bear (*Helarctos malayanus*) in Indonesia (Fredriksson et al., 2006), whereas they contributed only a tiny part (0.05) of the diet of the Asian black bear (*Ursus thibetanus*) in India (Dasgupta et al., 2015). Likewise, the Apennine brown bear in Italy (*Ursus arctos marsicanus*) did not consume much in the way of figs (up to 3% found of the contents of faeces) (Ciucci et al., 2014). The quality of seed dispersal by bears is still largely unknown.

Fig seeds have been found in the faeces of nine species of canids (Canidae, *Canis, Cerdocyon, Chrysocyon* and *Vulpes*), two species of mongooses (Herpestidae, *Galerella* and *Herpestes*) and eight species of martens (Mustelidae, *Arctonyx, Eira, Martes, Meles, Melogale* and *Mustela*). However, these animals are primarily carnivores, and their roles in dispersing fig seeds are unknown.

Fig-eating by five species of New World procyonids (Procyonidae, *Bassariscus, Nasua, Potos* and *Procyon*) has also been confirmed. The kinkajou (*Potos flavus*) fed on *Ficus insipida* in Costa Rica but was recognised as only a moderate contributor to seed disperser due to its low visit rate (Banack et al., 2002). Fig seeds that passed through the South American coati (*Nasua nasua*) were still intact and germinateable, with a seed germination rate similar to the unpassed seeds, and slightly faster germination (Alves-Costa & Eterovick, 2007). The South American coati (*N. nasua*) has a high feeding rate (5.59 figs/minute), and so may germinate lots of seeds, if they pass intact into its faeces (Hirsch, 2009).

Scandentia

Since Shanahan et al. (2001) published the global review of fig-eater records, only two publications have mentioned this Order of mammals. Common tree shrews (*Tupaia glis*) (Peh & Chong 2003), and the Northern treeshrew (*T. belangeri*) (Suzuki et al., 2007), are both fig-eaters in South-East Asia. Shanahan et al. (2001) mentioned that they defaecate viable fig seeds, but there is no new updated information about their roles in *Ficus* seed dispersal.

Chiroptera

Comprising of 61 species of known fig-eaters from 29 genera, the Old World fruit bats (Pteropodidae, and one species of Emballonuridae) are one of the largest groups of fig-eating animals. It was found that figs are the dominant food source of the Giant golden-crowned flying fox (*Acerodon jubatus*, found in 79% of its faeces) and the Large flying fox (*Pteropus vampyrus*, found in 50% of all faeces) in the Luzon islands, Philippines (Stier & Mildenstien, 2005). Figs are similarly important in the diets of the Spectacled flying fox (*Pteropus conspicillatus*, forming approximately 60% of seeds found in faeces) (Parsons et al., 2006), the Grey-headed flying fox (*Pteropus poliocephalus*, forming nearly half of their diet) in Australia (Schmelitschek et al., 2009), the Indian flying fox (*Pteropus giganteus*, more than 50% of their diet) in Pakistan (Mahmood-Ul-Hassan et al., 2010), the Straw-coloured fruit bat (*Eidolon helvum*) in Kenya (Webala et al., 2014), Lyle's flying fox (*Pteropus lylei*, as 20.6% of total food items) in Thailand (Weber et al., 2015), and the Insular flying fox (*Pteropus dasymallus,* 94.6% of their diet) in Taiwan (Chen et al., 2017).

Not all bats are as reliant on figs. Fig seeds were only present in low numbers (approximately 4–8% of overall plant items) in the faeces of the Lesser short-nosed fruit bat (*Cynopterus brachyotis*) and the Greater short-nosed fruit bat (*Cynopterus sphinx*) in Thailand (Bumrungsri et al., 2007). Fig seed dispersal by bats could be generated by spitting and defaecation, depending on bat behaviours. *Ficus microcarpa* seeds that were spat out or defaecated by Orii's flying fox (*Pteropus dasymallus*) had higher germination rates than unprocessed seeds in Okinawain Japan (Nakamoto et al., 2007). In the Philippines, fig seeds ingested by the Greater musky fruit bat (*Ptenochirus Jagori*) showed higher viability than the spat-out seeds, suggesting that bats modify germination rates (Reiter, 2002). In contrast, passage through the gut of four Malaysian bat species (*Balionycteris maculata, Chironax melanocephalus, Cynopterus brachyotis* and *Dyacopterus* *spadiceus*) had no effect on fig seed germination (Hodgkison & Balding, 2003). Three species of New Guinean fruit bats (*Nyctimene albiventer, Paranyctimene raptor* and *Syconycteris australis*) fed only on ripe female figs, and they completely rejected the male figs of *Ficus pungens* (Dumont et al., 2004). The cues and rewards provided only by female figs (with higher sugar concentrations and a brighter colour) are clearly effective attractants for frugivorous bats. The gut passage time of the Straw-coloured fruit bat (*Eidolon helvum*) was 116 minutes (range = 4-1143 minutes), and most seeds were dispersed within 100 metres of their source. However, the maximum seed dispersal range could be larger than 50 kilometres (Abedi-Lartey et al., 2016). The Mauritian flying fox (*Pteropus niger*) could transport undamaged *Ficus reflexa* seeds in ejecta between 2 and 40 metres, and 5–20 ingested seeds were found in its faeces, which were deposited approximately 250 metres from the adjacent fig trees (Nyhagen et al., 2005). Likewise, fig seeds were dispersed by Orii's flying fox (*Pteropus dasymallus*) within 100 metres of the source trees in Japan (Nakamoto et al., 2009). Also, Peters' epauletted fruit bat (*Epomophorus crypturus*) and Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) dispersed *Ficus sycomorus* seeds primarily within 200 metres of parent trees in South Africa, but the foraging range could be larger than one kilometre, suggesting their potential to also be long-distance seed dispersers (Bonaccorso et al., 2014). Lyle's flying fox (*Pteropus lylei*) can move up to 22 kilometres a day, which means it may also be a long-distance seed disperser of fig trees (Weber et al., 2015).

The New World fruit bats, with 58 species of recorded fig-eaters from 25 genera (Phyllostomidae, and one species of Noctilionidae) are another major group of fig-eaters. Similar to the Old World fruit bats, figs are often the main fruits they eat. The Jamaican fruit bat (*Artibeus jamaicensis*) had figs in up to 100% of its faeces, and figs were found in their diet all year round (Herrera et al., 2001). Bat species from the genera *Artibeus*, *Carollia, Centurio, Chiroderma, Glossophaga, Lampronycteris, Phyllostomus, Platyrrhinus* and *Vampyressa* are fig specialists,with figs forming a large proportion of their overall diet (Herrera et al., 2001; Giannini & Kalko, 2004; Lopez & Vaughan, 2007; Tavares et al., 2007; Goncalves da Silva et al., 2008; Garcıa-Estrada et al., 2012; Munin et al., 2012; Prone et al., 2012; Andrade et al., 2013; Horsley et al., 2015; Porfilio & Bordignon, 2015; Batista et al., 2016).

It is suggested that *Artibeus* spp. fruit bats are highly effective seed dispersers of *Ficus insipida* in Costa Rica, as these bats ingested a high number of seeds, transporting seeds away from the parent trees and defecating viable seeds (Banack et al., 2002). Moreover, *F. insipida* (Lopez & Vaughan, 2004) and *F. pertusa* seeds (Teixeira et al. 2009) ingested by Jamaican fruit bats (*A. jamaicensis*) showed higher germination success than uningested seeds. However, *Ficus organensis* seeds consumed by the Little yellow-shouldered bat (*Sturnira lilium*) were egested within 40 minutes after feeding and passing through the digestive tract did not affect seed germination (Maccarini et al., 2017). The foraging ranges of the Honduran white bat (*Ectophylla alba*) were within 400–600 metres, but some movements were more than one kilometre, suggesting that it can be a long-distance seed disperser (Villalobos-Chaves et al., 2017).

Proboscidea

Both Asian (*Elephas maximus*) and African (*Loxodonta cyclotis*) elephants are fig-eaters and fig seeds are commonly found in their dung (Morgan and Lee, 2007; Jothish, 2013). Jothish (2013) suggested however that there was no *Ficus* seedling emergence and survival in Asian elephant dung. Asian elephants move from less than one to more than five kilometres a day in Borneo (Alfred et al., 2012), which means that, depending on gut passage times and survivorship, they could act as long-distance seed dispersers. Information about the role of elephants on fig seed dispersal is still limited.

Perissodactyla

Fig seeds have been found in the dung of two species of Neotropical tapirs (*Tapirus terrestris* and *Tapirus bairdii*) (Galetti et al., 2001; Talamoni & Assis, 2009; Tobler et al., 2010; Barcelos et al., 2013; Capece et al., 2013; Diaz-Martin et al., 2014). Seeds of several of the fig species could survive and germinate after passing through the lowland tapir's (*T. terrestris*) gut (Barcelos et al., 2013). However, other aspects of seed dispersal of fig trees by these animals have not yet been investigated.

Artiodactyla

Cattle (Bovidae, eight genera and ten species), deer (Cervidae, five genera and ten species), pigs (Suidae, five genera and ten species), peccaries (Tayassuidae, two genera and two species) and mouse-deer (Tragulidae, two genera and two species) are all confirmed as fig-eaters. No post 2001 records of antelope (Antilopinae) feeding on figs were detected. It is still unclear whether figs are a generally important food source for these mammals or not. However, Altrichter et al. (2001) suggested that figs are one of the more important food sources for the

White-lipped peccary (*Tayassu pecari*) in Costa Rica during periods of food scarcity. In Japan, fig seeds extracted from Kerama deer (*Cervus nippon keramae*) dung could be germinated with a more than 60% success rate (Yamashiro & Yamashiro, 2006). The interactions between even-toed mammals and *Ficus* plants are still largely unknown, however.

Cingulata

In Bolivia, fig seeds have been found in the gut contents of the vulnerable Giant armadillo (*Priodontes maximus*, Chlamyphoridae). However, it is suggested that this species rarely feeds on figs (Wallace & Painter, 2013).

Rodentia

With 32 species from 13 genera, squirrels (Sciuridae) contribute the largest group of rodents known to feed on figs. Squirrels are widely-distributed frugivorous arboreal mammals that forage on fig trees or the forest floor (Suzuki et al., 2007; CHAPTER 3). *Ficus* is reported as one of the most important food sources for squirrels. Examples include the Indian giant flying squirrel (*Petaurista philippensis*) in Taiwan (Kuo & Lee, 2003) and India (Nandini & Parthasarathy, 2008), the Three-striped palm squirrel (*Funambulus palmarum*) in India (David et al., 2011) and Finlayson's squirrel (*Callosciurus finlaysonii*) in Thailand (Tamaru et al., 2015). Squirrels feed on figs by breaking them down to smaller parts and chewing on them (Peh & Chong, 2003; CHAPTER 3), which could destroy some or all the seeds when they are crushed by the teeth. The Grey-bellied squirrel spent 8–10 minutes feeding on *Ficus racemosa* trees in Thailand, which may be shorter than their gut passage time, suggesting that intact seeds were likely to be dispersed away from source trees. However, some seeds can be deposited under the parent tree when the squirrel is chewing on a fig (CHAPTER 3). *Callosciurus* squirrels occupy a small home range size (1–2 hectares) in Malaysian dipterocarp forest (Saiful et al., 2001), suggesting that they are likely to be short-range seed dispersers.

Nocturnal rats (Muridae), with 13 species of known fig-eaters from ten genera, are another rodent group that are often recorded to feed on figs. Rats (*Rattus* spp.) are considered as mainly seed predators in the Cook Islands, where *Ficus prolixa* seeds passed through their digestive tracts (1–20 hours of passage time) and had low germination rates (Staddon et al., 2010). However, the black rat (*Rattus rattus*) is considered to be a seed dispersal vector for small-seeded species like the introduced *Ficus microcarpa* in the Hawaiian islands because seeds that passed through its gut showed high survival rates (Shiels, 2011).

Other rodents, such as true hamsters and allies (Cricetidae), paca (Cuniculidae), agoutis (Dasyproctidae), pacaranas (Dinomyidae), New World spiny rats (Echimyidae), Old World porcupines (Hystricidae) and African rats and allies (Nesomyidae) are all known to include species that are fig-eaters. However, their roles in seed dispersal of *Ficus* are still not yet known.

7.4.4 Summary of fig seed dispersed by frugivores

Since 2001, few new studies have described intensively the roles of frugivores in seed dispersal or seed predation of fig trees. The effect of gut passage on seed viability and survival in fig-eating fishes and reptiles are still poorly understood, although there is better representation of Cyprinidae fishes and land turtoises (Testudinidae). Although birds are the largest fig consumer group, knowledge about how fig seeds are affected by bird ingestion has hardly increased. There is updated knowledge of feeding by some small familes, such as Cassowaries (Casuariidae), and increased records of major frugivorous families such as Pigeons (Columbidae), Barbets (Megalaimidae) and Starlings (Sturdidae). Higher numbers of papers have covered fig-eating mammals than other animal groups, but most representation is found in already well documented families such as Old World monkeys (Cercopithecidae), Old World fruit bats (Pteropodidae) and New World fruit bats (Phyllostomidae). Across all fig-eating animals, most knowledge gaps listed by Shanahan et al. (2001) about how fig-eating animals affect seed dispersal of fig trees have not been filled (Table 7.13).

Table 7.13. Summary of fig seed dispersal data published since 2001 (including this thesis).

Family	Species (n)	Gut passage time	Seed viability? (%)	Impact on germination speed (+) and percentage (*)			Number of sources
				Elevated	Depressed	No effect	
Fishes							
Auchenipteridae	2	n/a	> 85%	n/a	n/a	n/a	1
Characidae	1	n/a	> 85%	n/a	n/a	n/a	1
Cyprinidae	2	6 - 10 hrs.	0 - 35%	+	*		1
Doradidae	1	n/a	> 85%	n/a	n/a	n/a	1
Pimelodidae	1	n/a	> 85%	n/a	n/a	n/a	1
Serrasalmidae	2	n/a	> 85%	n/a	n/a	n/a	1
Triporthidae	3	n/a	> 85%	n/a	n/a	n/a	1
Reptiles							
Iguanidae	1	n/a	45 - 49%	+	*		1
Testudinidae	2	10 - 28 days	50%	*			3
Tropiduridae	1	n/a	71.50%		*		1
Birds							
Casuariidae	2	105 - 1680 mins	11 - 13%	+,*			3
Columbidae	2	n/a	0.2 - 0.4%		*	*?	1
Megalaimidae	1	10.6 - 57 mins	5 - 90%	+,*	*	+	1
Musophagidae	1	12.4 - 22.6 mins	n/a	n/a	n/a	n/a	1
Phasianidae	1	15 mins - 1h15	5.80%			*	1
Pycnonotidae	1	6.43 - 35.13 mins	n/a	n/a	n/a	n/a	1
Sturdidae	1	9 hrs	3.50%		*		1
Turdidae	1	7 mins	n/a	n/a	n/a	n/a	1
Mammals							
Atelidae	2	20.4 - 23 hrs	73 - 83%	*			2
Callitrichidae	3	n/a	5 - 100%	+,*	+,*	+,*	2
Canidae	2	n/a	4.4%	*			2
Cebidae	1	n/a	85%	*			1
Cercopithecidae	5	14 - 96 hrs	64 - 68%	*	*	*	3
Cervidae	1	n/a	64 - 69%	n/a	n/a	n/a	1
Didelphidae	1	n/a	39%	+,*			1
Herpestidae	1	n/a	Y	n/a	n/a	n/a	1
Hominidae	3	18 - 30 hrs	45 - 100%	*		*	2
Muridae	2	1 - 19h45	3.3 - 100%		*		2
Mustellidae	2	n/a	Y	n/a	n/a	n/a	1
Phyllostomidae	5	11 - 67 mins	20 - 100%	+,*		+,*	8
Pteropodidae	7	4 mins - 24h30	10 - 100%	+,*	+	+,*	6
Tapridae	1	n/a	Y	n/a	n/a	n/a	1
Viverridae	2	n/a	Y	n/a	n/a	n/a	1

7.5 Discussion

This study updated records of frugivores feeding on a total of 322 *Ficus* species. This is an increase of 62 species since the review of Shanahan et al. (2001) and accounts for 38.8% of global fig tree diversity. As in the data set of Shanahan et al. (2001), African fig trees retained the highest proportion of recorded interactions with frugivores, with approximately 69% of all African *Ficus* species having at least one of their frugivores recorded. There was nonetheless a large increase of records for Neotropical fig trees, growing from 28.8% to 52.3% of the fig tree species in this region. The Indo-Australian fig trees continue to be under-represented in the frugivore records, with just 34.2% of the species having frugivore records. As this region is the largest in area and the most diverse there is scope for some sub-regions to be better represented than others and the fruivores associated with fig tree species from East Asia are more thoroughly covered than those from Oceania and New Guinea, where most species are still lacking information. The frugivory records continue to be heavily biased towards large monoecious fig trees, especially *Urostigma* and some of the *Sycomorus* figs that have large frugivore assemblages (approximately 20 frugivore species per fig tree species in subgenus *Urostigma*). It was suggested that the large crop sizes and canopy location of *Urostigma* figs enabled them to interact with a wide variety of frugivores that could be attracted long distances to the trees (Shanahan et al., 2001). These features contrast with the small crops and understory locations of fig trees belonging to subgenus *Sycidium* and these small dioecious fig tree species continue to be depauperate in frugivore records.

In the 17 years since the first fig-eater review was conducted by Shanahan et al. (2001), the known number of bird species feeding on figs has increased to 12.7% of global avian species richness, from 979 to 1,432 species. Among mammals, the known fig-eating mammal species number has increased from 280 to 435 species, which is equal to 7.7% of the world's mammals. The updated data set was mostly developed from animal diet and feeding behaviour studies. The high representation of some fig-eating mammalian and bird families is likely to reflect a strong relationship and corresponding evolutionary interactions with the genus *Ficus.* Interactions with fig trees were prevalent in birds such as pigeons (Columbidae), bulbuls (Pycnonotidae), hornbills (Bucerotidae), parrots (Psittacidae), starlings (Sturnidae), Asian barbets (Megalaimidae) and African barbets (Lybiidae), and mammal families such as Old World monkeys (Cercopithecidae), Old World fruit bats (Pteropodidae), apes (Hominidae), squirrels (Sciuridae), gibbons (Hylobatidae), New World monkeys (Atelidae) and New World fruit bats (Phyllostomidae). In the past 17 years there has been a large increase in the numbers the studies of certain frugivores, especially bulbuls, Old World monkeys, Old World fruit bats, gibbons, apes, New World monkeys and New World fruit bats. The under-representation of some families that contain frugivorous species may reflect their conservation status. Data on endangered species is difficult to obtain because, by definition, these animals are rarely found and hard to study in nature. In addition, animal groups living in areas that are difficult to access, for example, high elevation habitats, heavily forest areas, or nocturnal animals such as murid rodents (Muridae) are harder to observe.

As discussed earlier, the genus *Ficus* is one of the most important plants supplying food for wildlife. This strongly supports the statement of Janzen (1979) that ‘Everybody eats figs’. *Ficus* trees are often considered as a keystone plant resource, providing food for many animals in abundance and when other fruiting tree species have low availability (Terborgh, 1986). There are several reasons that fig trees are a reliable food source for frugivores. Firstly, many fig species, especially monoecious species, are known to produce fruits all year round (Corlett, 1984; Compton, 1993; Patel, 1997; Harrison et al., 2000; Yu et al., 2006; Zhang et al., 2006; Jia et al., 2008; Kuaraksa et al., 2012; Pothasin et al., 2016), but some fig trees, especially dioecious species, show single or double seasonal peaks in annual fig production, and these peaks are often when other trees are also fruiting (Patel, 1997; Kuaraksa et al., 2012; Pothasin et al., 2016; CHAPTER 2). At the population level, monoecious fig trees often produce fruits asynchronously, with some trees in fruit throughout the year (Compton, 1996; Patel, 1997; CHAPTER 2). Individual trees have synchronised crops, which forces pollinators to move between trees and avoids self-pollination, but adult pollinators have a short life span, so trees suitable for oviposition need to be available (Harrison, 2005). The numerous figs produced at one time by monoecious fig trees, with crops between 1,000 and 100,000 figs or more, aids in long distance attraction of pollinators, but at a later stage also attracts a great number of frugivores to forage on these fig trees, because they provide plentiful amounts of easily-eaten food, (Korine et al., 2000; Shanahan et al., 2001; Lomáscolo et al., 2010). The diversity of colour, size and vertical stratification of figs, together with their soft structure and small seeds, also enables fig trees as a group to interact with a wide range of frugivore species, though individual species vary in the frugivores they are likely to attract (Shanahan, 2000).

The features outlined above explain the broad ecological importance of fig trees for fruit-eating animals, but not all of these features apply to all fig tree species. They are features that characterise monoecious, hemi-epiphytic, or free-standing tall fig trees (such as *Urostigma* species). This is in contrast to the majority of dioecious fig trees, which are shrubby species, producing small crops that may be asynchronous on individual trees. As a consequence, they interact with a smaller number of frugivores than big monoecious fig trees (Fig 7.3; CHAPTER 3). Therefore, the term ‘keystone plant resource’ may not fit with many dioecious fig species.

Fig trees experience different seed dispersal services from different frugivores. However, generalising how effective these frugivores are as seed dispersers is complicated. The seed dispersal effectiveness framework consists of a combination of quantitative and qualitative seed dispersal methods (Schupp et al., 2010). The quantity itself relates directly with how many fig seeds are eaten by each frugivore, the frequency of their visits and their abundance of frugivores, all of which influence fig-removal rates. It is suggested that larger frugivores disperse relatively higher numbers of seeds than smaller frugivores. For example, hornbills (Bucerotidae) consume higher numbers of figs when visiting a fig crop, than smaller birds such as bulbuls (Pycnonotidae) (CHAPTER 3). Fruit bats, monkeys (both Old and New World), gibbons, and primates can also ingest large numbers of fig seeds when feeding (e.g. Herrera et al., 2001; Kanwatanakid-Savini et al., 2009; Hu, 2011; Potts et al., 2011; Wieczkowski, 2013; Petre et al., 2015).

The quality of seed dispersal depends on how frugivores process seeds, how far these seeds are dispersed from their parent tree, and whether these seeds are deposited in a suitable site, where they will be able to germinate and establish. Frugivore feeding behaviours such as pecking and especially biting are considered to often destroy seeds, as the seeds are crushed or otherwise damaged. These behaviours are exhibited by the beaks of birds when they are feeding on figs that are larger than their gape width or routinely by the teeth of mammals such murid rodents (Muridae) (Staddon et al., 2010) and squirrels (Sciuridae) (CHAPTER 3). Some frugivores also have morphological characteristics that make damage to fig seeds more likely. For example, cyprinid fishes (Cyprinidae) having pharyngeal teeth that crush their food, including ingested fig seeds (CHAPTER 4). Groups that gain nutrients mainly from seeds, rather than any surrounding fruit pulp, such as pigeons (Columbidae) (Lambert, 1989) and parrots (Psittacidae) (Janzen, 1981; Jordano, 1983) have gizzards that can grind fig seeds after ingestion.

Processing by frugivores that result in increased rates or speed of seed germination is considered to be a characteristic of high-quality seed dispersal (Schupp et al., 2010). Fig seeds consumed and defaecated by numerous birds and mammals exhibit this response. Larger frugivores are more likely to swallow figs and also tend to wider home ranges and longer movements between feeding sites, so they are expected to disperse seeds over a wider area than smaller frugivores, which is considered a positive attribute. Groups such as hornbills, fruit bats, monkeys, primates and elephants, are therefore potentially high-quality seed dispersers, although many other factors come into play. For example, elephant dung may not be a good medium for germination and establishment, and elephants that feed on fallen figs produced by stranglers will be of no value because the plant needs its seeds to be deposited above the ground, onto branches of host trees.

Fleshy, colourful, high in sugar and easy to access, ripe figs probably attract and interact with more frugivorous species than any other plants in the tropics and sub-tropics (Shanahan, 2000; Peh & Chong, 2003; Sreekar et al., 2010; CHAPTER 3). This has stimulated studies that assess the use of native fig trees to re-green degraded landscapes (Slocum, 2001; Guevara et al., 2004; Kuaraksa & Elliott, 2013; Cottee-Jones et al., 2016). Some fig trees also have other suitable characteristics for restoring degraded habitats. Some are recognised as pioneer species, especially the small dioecious figs, because they have the ability to colonise wide open areas with hot conditions and a high light intensity (Kuaraksa & Elliott, 2013). The rapid seed germination and high survival rates of *Ficus* seedlings in nursery plantings also facilitates their use, and many take easily from large woody cuttings ('truncheons') (Kuaraksa & Elliott, 2013), though establishment from seeds sown in degraded areas is rarely successful (Laman, 1995; Kuaraksa & Elliott, 2013). Once established they can then provide a microclimate under their canopy that is suitable for seedling germination and fig trees can facilitate the establishment of other species. It was found that a higher density and diversity of plants are found under isolated fig trees than under non-fig species in a tropical mosaic landscape of India, where their shade helped maintain soil moisture, and soil nutrients accumulated due to the decay of fig leaves (Cottee-Jones et al., 2016). High plant diversity below fig trees is also likely to result from high seed deposition rates from the faeces of frugivores visiting the trees to eat their figs (Cottee-Jones et al., 2016). A high seed rain (more than 1000 seeds/m^2) and high sapling densities were recorded under five *Ficus* species in Mexico (Guevara et al., 2004). However, it has also been shown in another Neotropical study system that seedling growth was slowed by low light intensities under the canopy (Slocum, 2001).

Although providing food rewards for frugivores is beneficial for both the fig trees and the animals, fig trees can become invasive when introduced with their pollinators outside their native range, and their spread is aided by the large number of frugivores they attract. The presence of an invasive fruiting plant can change the original ecosystem by shifting the diet of the native frugivores (Kerdkaew et al., 2014), altering the community of native animals (Aravind et al., 2010), and outcompeting the native plants (Oduor, 2013). Some fig trees, such as *Ficus microcarpa,* have been introduced to North and South America, the Mediterranean region and elsewhere (Ramírez, 1988; Nadel et al., 1992; Starr et al., 2003; Asner et al., 2008; Caughlin et al., 2012), where they are cultivated as ornamental plants (Ramírez, 1988). *F. microcarpa* is now considerd a harmful invasive in Hawaii, Bermuda and Florida, and has become established on some Mediterranean islands and Brazil (Starr et al., 2003; Wang et al., 2015). In South Florida USA, interactions between *F. microcarpa* trees and as many as 14 native frugivorous birds in urban areas has increased the abundance of seedlings, where they cause damage to property (Caughlin et al., 2012). Such new associations do not necessararily benefit the plant. In Malaga, Spain, the introduced South American Monk Parakeet (*Myiopsitta monachus*) feeds on figs of *F. microcarpa* introduced from East Asia, and probably acts as seed predator (Compton, S. G., pers. comm.).

As with Shanahan et al.’s (2001) dataset, the more recently generated information on frugivores feeding on figs was mainly obtained from dietary studies, and intensive research on how these frugivores played a role in seed dispersal of fig trees was rarely presented. The datasets generally only provided basic information on trophic links between fig trees and their associated frugivores. This dataset nonetheless further emphasises the central part played by fig trees in tropical ecosystems and provides valuable information on the global network of fig plants and frugivores for conservation biologists who are monitoring and restoring degraded habitats. It provides information on which fig subgenus or species can provide food for different groups of frugivore species and thereby can aid conservation planning. However, there are still large gaps in the literature, especially concerning dispersers of small dioecious *Ficus* species, and the effectiveness of fish, reptiles, some ground bird groups and rodents as dispersal agents.

Shanahan et al. (2001) noted that "although the data on figs and their associated frugivores was exceptional in breadth, it was lacking in depth". They highlighted gaps in our knowledge at that time. Specifically they stated:

1. "It is of interest to know not only which animals eat figs of a given species but also how reliable these animals are as potential seed dispersers and how important the figs are in their diets."
2. "Studies of any widespread *Ficus* species throughout its range are lacking, so we have no idea of the extent to which species attract markedly different frugivore assemblages in different parts of their range".
3. "Nor do we know the form of the relationship between the size of regional frugivore assemblages, the size of assemblages present at individual crops and its consequences for fig dispersal rates."

Since 2001 the volume and breadth of available data has increased greatly, but the gaps in their knowledge are largely still there. Firstly, figs contributed to different extents in frugivore diet, and quantitative and qualitative seed dispersal of figs assisted by fig-eaters was different among taxonomic groups. Most of the published records provide only the identities of frugivores that consumed figs without any assessment of their potential role as seed dispersers or predators, or network studies. There is an improvement of knowledge about how important figs are in the diets of several frugivore groups. For example, there are several records that figs are a major part of diets, for example, more than 50% of the overall diet of some hornbills (Bucerotidae) (Hadiprakarsa & Kinnaird, 2004; Kanwatanakid-Savini et al., 2009). However, most of the records are from Asian hornbills, and records of African hornbills are still limited. Barbets (Megalaimidae) are also reported as major fig-eaters in the Old World, and figs were reported as their most important food items (David et al., 2011; Trounov & Vasilieva, 2014). Furthermore, fig seeds they ingested had high germinability (Chang et al., 2012).

Among mammals, the greatest improvement of knowledge about their role as seed dispersers of fig trees is found among Primates. Lemurs (Lemuridae) consume figs as a minor part of their diet (less than 10% of the total) (Tarnaud, 2004; Simmen et al., 2007; Martinez, 2010; Andriamaharoa et al., 2010), but other primates such as Old World monleys (Cercopithecidae, Hu, 2011; Wieczkowski, 2013; Pengfei et al., 2014), Hominids (Hominadae, Yamagiwa & Babose, 2006; Potts et al., 2011) and gibbons (Hylobatidae, Kanwatanakid-Savini et al., 2009; Kim et al., 2012) have figs as a major part of their diet. Most fig seeds consumed by these primates show high germination rates and given that they are likely to deposit seeds on tree branches they are likely to have major roles in fig seed dispersal, especially for stranglers (Righini et al., 2004; Petre et al., 2015). Figs form a major part of the diet of both Old World (Pteropodidae) and New World fruit bats (Phyllostomidae) (Herrera et al., 2001; Stier & Mildenstien, 2005; Parsons et al., 2006; Lopez & Vaughan, 2007; Webala et al., 2014; Batista et al., 2016; Chen et al., 2017). Fig seeds ingested by Old and New World fruit bats germinate faster than unpassed seeds (Nakamoto et al., 2007; Teixeira et al., 2009 respectively), or at the same speed (Hodgkison & Balding, 2003; Maccarini et al., 2017 respectively), showing that their impacts are not consistent.

Studies of interactions between frugivores and fig trees that have wide distributions are still limited. For example, frugivore interactions with *Ficus racemosa*, which is distributed widely in Oriental East Asia and Northern Australia, have been intensively studied in India (Roy et al., 2011; Singh et al., 2011) and Thailand (Kitamura et al., 2002; CHAPTER 3; CHAPTER 4). This is similar to the situation with the pre 2000 records collated by Shanahan et al. (2001). Moreover, frugivory records involving *F. racemosa* had a bias towards fig-eating mammals, especially Old World fruit bats (Pteropodidae) and Old World monkeys (Cercopithecidae) in the pre 2000 records (see Shanahan et al. 2001), and also in the updated dataset. Similarly, most of the frugivore assemblage information for *Ficus microcarpa*, which has a roughly similar wide distribution as *F. racemosa*, are clumped in India (David et al., 2011), Taiwan (Walther et al., 2017) and South East Asia (del Hoyo et al., 2017), but not in other regions such as New Guinea and Northern Australia. As in Shanahan et al. (2001), the recent records of frugivores feeding on *F. microcarpa* trees were mainly available from bird field guides and unpublished records from India, China and South-East Asia (Indonesia and Malaysia). Consequently the full range of interactions between even the most-studied fig trees and frugivores is still largely unknown. Overall, the three major gaps in knowledge suggested by Shanahan et al. (2001) still remain.

In conclusion, there is no doubt that *Ficus* interacts with many frugivore species globally, and that these frugivores have differing levels of effectiveness as fig seed dispersal agents. Fig trees are not all the same and the term ‘Keystone

Resource' should be used to describe only members of some of *Ficus* species or subgenera, and the ecological role of each species has to be considered case by case. Some of the same features that make figs so valuable in their native habitats also make them potentially harmful when they are introduced elsewhere and become invasive.

Chapter 8 General Discussion

To understand the population dynamics of plants, knowledge is required of their vegetative and reproductive phenology patterns, how they disperse their diaspores, how fruiting plants and frugivores interact, how seed dispersal affects the fate of seeds and the new plant generation, and the form of their gene flow patterns. Chapter two of this thesis described the leaf and fruiting phenological patterns of four riparian fig tree species in relation to annual changes in climatic conditions. Chapter three described the quantities of fruits produced by the four riparian *Ficus* species, how many were fed on by terrestrial frugivores, and their feeding behaviours. Whether or not water plays a role in their seed dispersal was also considered. Chapter four examined the roles of two locally common cyprinid fish species in Kanchanaburi river systems, the Blue mahseer (*Neolissochilus stracheyi*) and the Red-tailed tinfoil (*Babonymus altus*) in seed dispersal of *Ficus montana*. Experiments examined survival and germination of its seeds after ingestion by the fish. Chapter five examined the functions of a mucilaginous jelly that surrounds *F. oligodon* seeds in relation to seed dispersal and germination. Chapter six examined the genetic diversity, structure and gene flow of populations of a riparian fig tree (*F. montana*) in western Thailand, as inferred from nuclear and chloroplast markers. The last results chapter of this thesis updated the database of global interactions between fig trees and vertebrate fig-eaters produced by Shanahan et al. (2001), considered whether knowledge of the effectiveness of different *Ficus* seed dispersal agents has improved and explored trends in fig and frugivore studies from different regions.

The vegetative and reproductive phenologies of *Ficus racemosa* (Subgenus: *Sycomorus*, monoecious), *F. oligodon* (Subgenus: *Sycomorus*, dioecious), *F. ischnopoda* (Subgenus: *Ficus*, dioecious) and *F. montana* (Subgenus: *sycidium*, dioecious) were monitored in riparian forests of Kanchanaburi, western Thailand for one year. Although leaf production occurred all year round, seasonality was detected in all four species. Leaf production was related to temperature and rainfall, but there was variation between the species. Fig production was seasonal in all three of the dioecious fig trees, but again with variation among species and sexes. Fig production by the monoecious *F. racemosa* trees was more stable and occurred all year round. Large crops of its large figs are produced on the trunk and branches, often higher than five metres from the ground, where they are likely to be easy to find and provide abundant resources for frugivores. Due to these aspects of its fig production, *F. racemosa* may be a keystone resource for wildlife, in the same way as some *Urostigma* strangler fig trees (Harrison et al., 2003). In contrast, the three dioecious species produced smaller crops located closer to ground level, where they are likely to be harder to locate and do not provide the same concentration of resources for frugivores as *F. racemosa*. They are unlikely to be a keystone resource for frugivores.

Asynchronous fig production on different trees but synchrony within trees is common in populations of monoecious *Ficus* species because it encourages cross pollination and allows the trees to conserve populations of their agaonid pollinator, which only survive for one or two days as adults (Bronstein, 1992; Compton et al., 1994). Female trees of monoecious species have no role in maintaining pollinator populations, which allows them to be more typical of plants in general and concentrate seed production at times of year when they are most likely to survive and become established. Asynchronous fig production within trees is more common in male dioecious fig tree species, where fig wasps are produced in small numbers and cycling of wasp populations within the same tree is sometimes possible (Suleman et al., 2011; Kuaraksa et al., 2012). Thus, these fig trees may be able to maintain populations of pollinating fig wasps even if they have small populations. The different fruiting patterns of monoecious and dioecious fig tree species have also resulted in different dispersal patterns in their pollinators, with pollinators of monoecious species often dispersing over long distances, while pollinators of dioecious species travel more locally (Ahmed et al., 2009). Patterns of pollen flow are therefore different.

Most studies of the frugivores that visit fig trees have been centred on monoecious fig trees because their large conspicuous and synchronised crops attract large, diverse groups of frugivores that are easily recorded. The work described in this thesis concentrated on frugivore interactions the little-studied small dioecious fig trees that have only a few ripe figs present at any one time. This inevitably meant that rates of data collection were slow and sometimes whole days produced no relevant observations because visits by frugivores to the figs were infrequent.

Direct observations and camera traps are both useful for monitoring frugivory, but both have disadvantages. Direct observations are time consuming and a team is required to produce continuous night and day time observations. As the female fig trees produced ripe figs for only a short time in a year, few trees were available for monitoring frugivores with camera traps. Some of the study sites, for example Huey Maekhamin waterfall, are affected heavily by a large number of tourists, so safe setting of camera traps was difficult and may not be successful when frugivores are sensitive to human activities in the area. Although camera traps were suitable for monitoring the small dioecious fig trees for 24 hours, the larger monoecious tree, *F. racemosa*, was not suitable for camera trap monitoring, because many of the figs are high above the ground. Direct observations were therefore required, but low visibility prevented recording of nocturnal frugivores without specialist equipment.

Although interactions between frugivores and females of the dioecious fig trees *F. oligodon*, *F. ischnopoda* and *F. montana* were intensively monitored, few visits to their fig crops were recorded. Because of their streamside locations, many uneaten ripe figs were likely to fall into the water, which can provide abiotic seed dispersal for these riparian fig trees. Other figs fell to the ground or became rotten while still on the branches of the trees. These are unlikely to be dispersed from their parent trees, though dispersal by ground foraging animals cannot be ruled out. This contrasts with the larger *F. racemosa* crops where fig removal rates (number of fig removed per hour, the proportion of fig removal by frugivores) were high and all the crops were visited by wide variety of diurnal frugivores. Additional frugivores, especially bats, are likely to have been visiting the trees at night, but they were not included in the study. In contrast to the dioecious species, the monoecious fruiting style and large growth form of *F. racemosa* clearly results in interactions between far more species and larger numbers of frugivores and makes them likely to be keystone resources (e.g. Sreekar et al., 2010).

Different frugivore species were associated with different fig tree species. The two smallest species, *F. ischnopoda* and *F. montana,* attracted mostly frugivorous birds, and the larger *F. oligodon* and *F. racemosa* were more likely to interact with small mammals (rodents). It is suggested that brighter fruit colours, for example, red, orange and black (reflecting ultraviolet) are attractive to frugivorous birds (Kitamura et al., 2002). Mammals are often colour blind and use olfactory organs to detect fruit ripeness by its smell (Nakabayashi et al., 2016). The figs of the two smaller species have no obvious smell, but *F. racemosa* and *F. oligodon* figs have a distinct smell when ripe (Kerdkaew T., pers. obs.). *F. ischnopoda*, and *F. montana* also produce small figs, which attracted small-bodied frugivorous birds, especially, bulbuls (Pycnonotidae).

F. racemosa and *F. oligodon* produce much larger figs, and in the past it is likely that large mammals (such as elephants, rhino, pigs, deer and tapirs) may have played a major role in their seed dispersal. These large species are rare or absent at the study sites, despite being in National Parks. The only larger mammal seen near the trees was the macaque (*Macaca* sp., Cercopithecidae) and it showed no interest in the figs (Compton, S. G., pers. comm.) and only one mammal, a squirrel (*Callosciurus caniceps*, Sciuridae) was regularly observed eating them. Bulbuls (Pycnonotidae) and squirrels (Sciuridae) are known to be able to adapt to live in many habitat types, including anthropogenic areas (Corlett, 1998). The study sites are open for tourism purposes (with tourists attracted to the waterfalls) and the mammalian fauna associated with these fig trees is likely to be more diverse in more isolated areas.

Frugivore feeding behaviour affects their seed handling quality. Frugivores which swallow whole figs are considered more likely to be high quality seed dispersers rather than frugivores the bite or peck at the fruits to break down the figs into several smaller parts before feeding on them (Peh & Chong, 2003). All the birds observed in this study were mainly swallowers if the figs consumed by them were not larger than their gape width. Bulbuls are the most likely important seed dispersal agents of fruiting trees in the Oriental Region (Corlett, 1998) as well as at the study sites, and several studies have suggested that ingestion by bulbuls promotes seed germination of many plant species (Weir, 2004; Linnebjerg et al., 2009). Moreover, bulbuls disperse most ingested seeds disproportionately far away from parent trees (Weir & Corlett, 2007; Khamcha et al., 2014; Kerdkaew, 2014). The benefits of having figs eaten by bulbuls are in contrast to feeding by squirrels and rats, which are likely to be mainly seed predators because of their chewing behaviour, though no explicit studies of squirrels and fig seed survival appear to have been published. Fig seeds ingested by rats show lower survival and germination rates, but small numbers of seeds are dispersed intact (Staddon et al., 2010).

This is one of the pioneer studies of how fish interact with riparian fig trees in South East Asia. The major cyprinid fish species in the riparian forest of western Thailand is the blue mahseer (*Neolissochilus stracheyi*, Cyprinidae). Figs that fell from the trees into the water were rapidly eaten by this fish if they were present in the area. In the rainy season, figs falling from large fig trees (*F. racemosa* and *F. oligodon*) tended to fall mainly on the water, where they could be carried downstream or eaten by the fish. When water levels were lower, fewer figs would fall in the water, and this form of dispersal is likely to be less important. This relationship is not detected in the smaller riparian shrub species (*F. ischnopoda* and *F. montana*), probably because of where they were growing. The population size of Blue mahseer at the Erawan site was larger than at Kratengjeng. Illegal fishing and fish trapping were observed at Kratengjeng and this is the likely explanation. This suggests that these riparian fig trees not only have fewer large mammals to disperse their seeds than in the past, but also fewer fish to disperse them.

Cyprinidae fishes are generally seed predators rather than dispersers because of their strong pharyngeal teeth (Boedeltje et al., 2015) and if interactions with *F. montana* seeds are typical then fish are unlikely to be large scale dispersers of fig seeds in western Thailand streams even where the fish are abundant. They may nonetheless move small numbers of seeds upstream. When its seeds were ingested by Blue mahseer and Red-tailed tinfoil (*Babonymus altus*, Cyprinidae) they were mostly destroyed, irrespective of the size of the fish. This is in contrast to some other studies, where the size of the fish influences the likelihood of seed destruction. Larger *Cyprinus carpio* (Cyprinidae) have stronger jaws and jaw muscles than juveniles and have a higher bite force which can destroy seeds (Boedeltje et al., 2015). In contrast, seeds of the aquatic plants were more likely to be dispersed intact by larger individuals of *Colossoma macropomum* (Serrasalmidae) in Peru (Anderson et al., 2009). Both the Thai cyprinids can growth larger than the size range that was tested, and seed retrieval rates may be different among the largest individuals present in the streams. Although few *F. montana* seeds survived after being ingested by these cyprinids, the surviving seeds germinated faster than the non ingested seeds. It seems that some seeds may be scarified when passing through the fish guts, but others are more damaged (Horn et al., 2011).

Some fig tree species have extensive jelly around their seeds. Examples include *F. awkeotsang* (Grubert, 1974), *F. rosulata* (Compton, S. G., pers. comm.) and *F. oligodon*. When possible roles of the jelly inside female *F. oligodon* figs were examined it was found that fig seeds covered by the jelly totally failed to germinate. However, some seeds were still viable after removing the jelly and around half of them could still be germinated. This suggests that the jelly protects the seeds from rapid germination by blocking water and oxygen from reaching the seeds (Heydecker & Orphanos, 1968; Witztum et al., 1969). In *F. awkeotsang,* an anti-fungal compound was extracted from the jelly (Li et al., 2003), and this may also be the case with the jelly of *F. oligodon*. Most of its seeds without jelly that were treated by soil-extract water could not be germinated, suggesting that the jelly provided protection from soil contaminants such as microbes or allelopathic compounds. Large numbers of fallen figs sometimes accumulated beneath *F. oligodon* and also *F. racemosa* parent trees. These would probably be eventually carried downstream as waters rose during the rainy season, and the jelly may allow seeds in figs on the ground to survive long enough to take advantage of dispersal by the water.

The taste of the jelly is not sweet (Compton, S. G., pers. comm.). Terrestrial vertebrate frugivores had no interest in the jelly and fed on the fig pulp, so the jelly is unlikely to be produced as a reward for frugivores. Although at least four species of ant (*Crematogaster* sp., *Pheidole* sp., *Philidris* sp. and *Oechophylla smaragdina*, Formicidae) were found around ripe female *F. oligodon* figs, these ants did not feed on the jelly of *F. oligodon* but only the fig pulp.

Gene flow of plants reflects pollination and seed dispersal processes across large spatial scales (Chen et al., 2008). The extensive gene flow achieved by monoecious fig trees is primarily as a result of pollinator movements between trees, which can be longer than 160 km (Ahmed et al., 2009). It is suggested that pollen flow of dioecious fig trees is more limited (Harrison, 2003; Zhao et al., 2014), but low genetic differentiation ($F_{ST} = 0.050$) and a high genetic diversity was found in *F. montana* populations in western Thailand. Other dioecious fig species, such as *F. pumila* (Liu et al., 2013), *F. hirta* (Yu & Nason, 2013) and *F. sarmentosa* (Wang et al., 2018) also show low genetic differentiation among different geographical sites ($F_{ST} < 0.10$). Thus, these dioecious figs may also extend their pollen flow range by long distance movement of pollinators assisted by wind. Moreover, evidence of possible long distance pollen flow between *F. montana* populations can be inferred by the low genetic differentiation of its pollinator, *Kradibia* (= *Liporrhopalum*) *tentacularis,* between the coastal mainland and archipelago of Indonesia, but more restricted pollinator gene flow among populations within the mainland (Zavodna et al., 2005a).

Gene flow assisted by seed dispersal appears to be limited to short distances in *F. montana* because high chloroplast DNA differentiation was detected in the western Thailand populations. Many *F. montana* figs fall down to the ground or water because ripe female figs are rarely fed on by frugivores. The main terrestrial frugivores feeding on *F. montana* figs are several bulbul species (Pycnonotidae). Bulbuls are recognised as important seed dispersers across East Asia (Corlett, 1998), and seeds of many plants species are still viable after passing a bulbul’s guts (Weir, 2004). Bulbuls have small home range size and are known as short distance seed dispersers, and most seeds will be deposited within 100 m of parent trees (Peh & Ong, 2002; Tanasarnpaiboon, 2008; Khamcha et al., 2012; 2014; Kerdkaew, 2014). Thus most *F. montana* seeds consumed by small birds like bulbuls will be dispersed within the local area. Although *F. montana* may gain some long distance seed dispersal by flowing water currents, seeds in fallen figs ingested by local fishes are mostly destroyed, further reducing the likelihood of long distance seed dispersal.

The global database of vertebrate fig-eaters of Shanahan et al. (2001) was updated by reviewing research articles from 2001 to 2017, including data from this thesis, and obtaining a large number of records from the global bird database, Handbook of the Birds of the World Alive (del Hoyo et al., 2017). The majority of updated frugivore records were from dietary studies of non-volant mammals, birds and fruit bats. A greater improvement of fig species records has occurred in the Neotropics and Afrotropics than Asia.

The data make clear that fig trees are keystone resources for frugivores, especially the hemi-epiphytic *Urostigma* stranglers. However, the ability of many species of vertebrates to disperse the seeds of fig trees can aid their spread if the tree is invasive. One *Urostigma* fig tree, *F. microcarpa,* is recognised as a widely invasive species (Caughlin et al., 2012). *F. microcarpa* is native to Indo-Malaya, East Asia, and Northern Australia (The Plant List, 2018). Because one of its pollinators (*Eupristina verticillata*) is widely introduced (Wang et al., 2015), this species successfully produces seeds wherever the trees have been planted, including several islands, North and South America and Europe (Ramírez, 1988; Nadel et al., 1992; Starr et al., 2003; Asner et al., 2008; Caughlin et al., 2012; Wang et al., 2015).Wherever viable seeds are produced there are numerous species of birds that eat the figs and spread invasions further.

Clearly, figs are eaten by wide range of vertebrate frugivores, including fish, reptile, bird and mammal. This supports the statement that ‘Everybody eats figs’ (Janzen, 1979). This does not mean that all figs are eaten by all the local frugivores. The variety of fig traits (size, colour, texture, odour and vertical stratification), in combination with the different morphological, behavioural and physiological characters of frugivorous animals, can generate disperser syndromes where birds, non-volant mammals or bats are more likely to eat the figs of a particular species (Shanahan, 2000; Lomáscolo et al., 2010; CHAPTER 3). Fig traits that favour birds are small size, being more colourful, having shorter peduncles, less smelly and being positioned on branches, whereas bat syndrome fig trees produce larger figs, mostly on the trunk, with longer peduncles, a light colour and strong odour (Lomáscolo et al., 2010).

Frugivore groups interact with fig trees to different degrees. Among birds, mynahs (Sturnidae), pigeons (Columbidae), bulbuls (Pycnonotidae) and parrots (Psittasidae) show frequent interactions with fig trees. These birds could be important seed dispersers of fig trees, but some pigeons and most parrots act mainly as seed predators rather than dispersers. A high rate of interaction with fig trees is also found in Old World monkeys (Cercopithecidae), Old World fruit bats (Pteropodidae) and New World fruit bats (Phyllostomidae) and all of these groups are probably effective seed dispersal agents, but despite the increase in fig feeding records in recent years, the relative effectiveness of seed dispersal by different animals remains largely unknown.

8.1 Further research

Although this thesis provides some valuable insights into the ecology of riparian *Ficus* in western Thailand, and in particular their interactions with frugivores, it is inevitable that further studies are needed to fill in knowledge gaps and to examine questions raised by the results that still have not been examined.

The tropical forest of western Thailand is part of the Indo-Burmese biological hotspots for plant and animal diversity (Conservation International, 2018). To date it is reported that there are 119 *Ficus* species distributed in Thailand (Pattharahirantricin, 2008), and 22 of these were recorded in a single study plot in Kanchanaburi Province (Chantarasuwan et al., 2007). The roles of these fig tree species in ecosystem functioning should be a key research theme. Fig trees are good study subjects for investigating coevolution and co-adaptation involving plants and their pollinator and frugivore counterparts (Ramírez, 1974; Wiebes, 1979; Herre, 1989; Shanahan, 2000; Lomáscolo et al., 2010). They also support many herbivorous insects, e.g. Lepidopteran caterpillars (Cheanban et al., 2017), and their figs are the centre of interactions involving a wide range of other invertebrates including non-pollinator fig wasps (West & Herre, 1994), phoretic mites and nematodes (Jauharlina, 2014) and flies (MacGowan & Compton, 2018).

The relative productivity of fruits among fig trees and non-fig plants is another interesting research question in this tropical region. Fig trees should not be studied in isolation. The reproductive phenology of other forest trees determines fluctuations in the overall level of food resources available to frugivore and the relative importance of fig trees at different times of the year. It will also determine the foraging behaviour of the frugivores. At a community level, the bipartite network approach can be applied to the study of *Ficus* and frugivore interactions to reveal how important fig trees are to the vertebrate community. It is suggested that these network studies give crucial information for biological conservation and management (Corlett, 2017).

Examining the extent that frugivores are effective seed dispersers is another key study central to an understanding of interactions among fig trees and frugivores. There are several studies that have investigated the roles of different frugivores in seed dispersal of fig trees, but more intensive and extensive studies are needed. For example, in this thesis, the common riparian specialist bird, Blue-whistling thrush (*Myoponus caeruleus*, Muscicapidae) was found to be a fig consumer in riparian forest of western Thailand. However, to date, the role of this bird species for seed dispersal of other riparian fig trees is completely unknown. Further studies focusing on its biology and life history, such as ranging behaviour and diet, and also how this species handles fig seeds after ingestion would help fill this knowledge gap.

Cyprinidae fishes are not the only fig-eaters in riparian forests of western Thailand. Several species of catfishes (Order: Siluriformes) are also commonly found (Wutthisin et al., 2011). The Pangasiidae catfishes (*Pangasius* spp.) are recognized as fig-eaters elsewhere, and fig seeds can be found in their guts (Baird, 2007). However, fig seed survival after ingestion by catfishes is largely unstudied in South East Asia. Comparing the seed dispersal effectiveness of these fishes with cyprinids would reveal more clearly the role of fish as seed dispersers or seed predators of riparian plants in the region.

The jelly surrounding mature seeds of *F. oligodon* has the effect of delaying seed germination, which preserves the viability of the seeds. This will allow the seeds more time to be dispersed and allow them to be dispersed further away from their parent plants. Further studies should address whether the jelly offers the seeds any protection when passing through frugivore guts. Like *F. oligodon, F. rosulata* occupies riparian habitats in Thailand and produces large quantities of jelly. Also like *F. oligodon*, dispersal by water is probably important for this species. *F. awkeotsang* is not closely related to *F. oligodon,* and occupies a different habitat, but also produces lots of jelly. An understanding of broader ecological and phylogenetic correlates of production of large quantities of jelly would also be useful in the future.

The extensive gene flow in *F. montana* is predominantly achieved by the movement of pollinators carried by air currents, but gene flow mediated by seed dispersal seems extremely limited. Further investigations should focus on gene flow of other riparian fig tree species, together with comparative gene flow of their pollinators and the animals that disperse their seeds. Unlike some of the other riparian fig trees, this species is not likely to have suffered a decline in the number of vertebrate species that disperse its figs. Densities of the small birds that eat its figs may have declined however, in response to disturbance from humans. There are also many man-made weirs in the riparian forest of western Thailand and two big dams have been built for irrigation and hydro-electric purposes. These will block movements of fish and figs floating down stream. The effect of these constructions on gene flow of riparian fig trees such as *F. montana* will be an interesting future research question in western Thailand.

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