



HAL
open science

Figs of Madagascar, their wasps, their frugivores, their importance for humans

Jean-Yves Rasplus, Yildiz Aumeeruddy-Thomas, Astrid Cruaud, Finn Kjellberg, Verohanitra M. Rafidison, Doyle Mckey, Martine Hossaert-Mckey

► **To cite this version:**

Jean-Yves Rasplus, Yildiz Aumeeruddy-Thomas, Astrid Cruaud, Finn Kjellberg, Verohanitra M. Rafidison, et al.. Figs of Madagascar, their wasps, their frugivores, their importance for humans. Goodman, S. M. The new natural history of Madagascar, Princeton University Press, pp.617-634, 2022, 9780691222622. hal-04188347

HAL Id: hal-04188347

<https://hal.science/hal-04188347>

Submitted on 25 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Figs of Madagascar, their wasps, their frugivores, their importance for humans

In Goodman, S. M. (ed.) 2022. The new natural history of Madagascar. Princeton, Princeton University Press. ISBN 9780691222622, pp 617-634

Jean-Yves Rasplus, Yildiz Aumeeruddy-Thomas, Astrid Cruaud, Finn Kjellberg, Verohanitra M.

Rafidison, Doyle McKey, and Martine Hossaert-McKey

Jean-Yves Rasplus

Centre de Biologie pour la Gestion des populations (CBGP), INRAE, CIRAD, IRD, Montpellier SupAgro, Univ Montpellier, Montpellier, France; email: jean-yves.rasplus@inrae.fr

Yildiz Aumeeruddy-Thomas

Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France; email: Yildiz.AUMEERUDDY-THOMAS@cefe.cnrs.fr

Astrid Cruaud

Centre de Biologie pour la Gestion des populations (CBGP), INRAE, CIRAD, IRD, Montpellier SupAgro, Univ Montpellier, Montpellier, France; email: astrid.cruaud@inrae.fr.

Finn Kjellberg

Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France; email: Finn.KJELLBERG@cefe.cnrs.fr

Verohanitra M. Rafidison

Department of Biology and Plant Ecology, Faculty of Sciences, University of Antananarivo, Antananarivo 101, Madagascar; email: verohani@yahoo.fr

Doyle McKey

Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France; email: Doyle.MCKEY@cefe.cnrs.fr

Martine Hossaert-McKey

Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, Univ Montpellier, EPHE, IRD,
Montpellier, France; email: Martine.HOSSAERT@cnrs-dir.fr

Introduction

In this contribution, we discuss not only the natural history and biogeography of Malagasy fig trees (Moraceae, *Ficus*) but also that of some of their associated insects. We then address fig frugivory and its importance in different habitats on the island. We illustrate how chemical ecology is crucial to better understand fig-fig wasps and fig-frugivore interactions. Finally, we present the importance of figs to humans. This chapter is based on different herbarium collections and internet databases, as well as on a review of published and unpublished data concerning the evolutionary ecology of fig-wasp interactions, the phenology of figs, frugivory, and the ethnobiology of *Ficus*. We use the terms “Madagascar” for the island of Madagascar in the strict sense; Malagasy Region for the group composed of Madagascar and surrounding archipelagos (Comoros, Seychelles including Aldabra, and Mascarenes); “continental Africa” for the African subregion (thus excluding the Malagasy Region); and “Afrotropical (biogeographic) region” for sub-Saharan continental Africa plus the Malagasy Region.

The Genus *Ficus* and its Pollination by Mutualistic Wasps

Ficus is a pantropical genus of about 850 species (Berg and Corner 2005) characterized by the production of figs, which are urn-shaped receptacles each containing numerous unisexual flowers. Fig plants are well known for their obligate mutualism with agaonid wasps, which are their unique pollinators. Each *Ficus* species is associated with one to seven species of pollinating wasps (Chalcidoidea: Agaonidae), which mostly develop at the expense of seeds of a single *Ficus* species (Wiebes 1963). The genus *Ficus* is subdivided into six subgenera (namely *Ficus*, *Sycomorus*, *Sycidium*, *Synoecia*, *Pharmacosyceae* and *Urostigma*) all of them, excepted *Synoecia*, occurring in the Afrotropical region. Subgenera are subdivided into sections and the subgenus *Urostigma*

contains 5 sections, of which sections *Urostigma* and *Galoglychia* occur in the Afrotropics. Very few agaonid wasp species are associated with two or more species of figs and this mostly happens in the Neotropics. The genus *Ficus* is morphologically diverse, comprising free-standing trees, (hemi)-epiphytes (stranglers), shrubs, and creepers (Rasplus et al. 2020). Size and morphology of figs and leaves are highly variable among species. Leaf morphology is also variable among conspecifics, as well as within single individuals, which complicates identification.

In this pollination mutualism between *Ficus* and agaonids, female wasps enter the closed central cavity of the fig through the ostiole (an opening located at the distal part of the fig) by crawling through the ostiolar bracts. The architecture of the bracts limits the entrance into the fig of non-adapted insects (Cook and Rasplus 2003). Once inside the fig, wasps lay eggs by inserting their ovipositor through the styles of some flowers and can pollinate either actively or passively (Kjellberg et al. 2001). Often, once they have laid eggs, female wasps cannot escape and die in the fig cavity. Flowers in which eggs have been laid are transformed into galls in which larvae of the new generation of wasps develop. Other female flowers that do not contain larvae develop seeds. By the time the wasp offspring emerge from the galls into the central cavity of the fig, male flowers (which produce pollen) have reached maturity. Male wasps emerge first and mate with females that are still enclosed in their galls. Then, females emerge and either actively collect pollen which they load into thoracic structures called pollen pockets (Kjellberg et al. 2001) (active pollination: two-thirds of fig species worldwide) or are dusted with pollen by the natural dehiscence of the anthers (passive pollination: one-third of the species). Finally, males dig tunnels through the fig wall and the short-lived female wasps fly away from their natal fig. They are attracted by chemical compounds emitted by receptive figs into which they enter, and the cycle is repeated (Hossaert-McKey et al. 2010). In order to maintain this reproductive cycle, fig trees of the appropriate species

with receptive figs should be present all year around; this is the reason why fig species are mainly found (with some notable exceptions) under tropical or subtropical climates.

About half of the species worldwide, and most Afrotropical species, are monoecious. In these species, each fig contains both staminate (male) and pistillate (female) flowers and produces pollen, pollinators and seeds (Cook and Rasplus 2003). Each fig contains both short-styled female flowers in which wasps preferentially lay their eggs and long-styled flowers in which wasps cannot oviposit. Thus, short-styled flowers mostly produce wasps and long-styled flowers mostly produce seeds. The other half of the world's fig species are gynodioecious. In these species, which are exclusively found in the Old World, mainly in the Oriental region, male function (pollen and pollinator production), and female function (seed production) are each performed by separate individual trees. In about half of the individual trees, figs contain only long-styled female flowers in which wasps are not able to lay eggs because of their very long styles, much longer than the wasps' ovipositors. In these individuals, wasps pollinate the flowers and often die within the fig. Consequently, these trees produce only seeds, but neither pollinators, nor pollen: such trees are morphologically and functionally female (Berg 1984). The other one-half of tree individuals produce figs with shorter styled female flowers, frequently organized in two layers, as well as male flowers. The wasps are thus able to lay eggs in all ovaries, and their offspring will disseminate the pollen to other trees. These individual trees produce pollen and pollinating-wasps, but (almost) no seeds; although morphologically hermaphroditic, such trees are functionally male.

Malagasy Species of *Ficus* and Fig Wasps

Most *Ficus* species on Madagascar were first described by Perrier de la Bâthie (1928, 1952) or by earlier botanists. Berg (1986) later revised their taxonomy and produced detailed descriptions of

Malagasy species, but see also Berg and Wiebes (1992) and Rafidison et al. (2011). Malagasy *Ficus* belong to four subgenera (Table 1). Some allochthonous species have also been introduced to Madagascar in historic times, either for their edible fruits (e.g., *F. carica*) or as ornamentals (e.g., *F. elastica*, *F. pumila*) (Turk 1995) mostly without their pollinating wasps.

Comparatively to southeast Asia (Corner 1965), Madagascar was considered to be depauperate in *Ficus* species (Goodman and Ganzhorn 1997), but species richness on the island appears similar to that observed in drier parts of Africa, at least at regional or local scales (see Berg 1990; Rasplus et al. 2003), although this still needs to be formally tested. About two-thirds of the Malagasy fig species are associated with relatively humid vegetation, and the remainder with drier habitats; these proportions are comparable to those observed in continental Africa (Berg 1990).

Although Berg's (1986) revision clarified the taxonomic status of most species, a few changes are required. Indeed, Berg considered *F. sakalavarum* (subgenus *Sycomorus*) as a subspecies of *F. sycomorus*, but several lines of evidence suggest that it is a valid species (Kerdelhué et al. 1999; Rafidison et al. 2011), including morphological characters (figs and leaves), as well as their distinct pollinating and non-pollinating wasps (Kerdelhué 1997). Ripe figs of *F. sakalavarum* are larger than those of *F. sycomorus*, the size difference being larger than that indicated by Berg (1986) and Berg and Wiebes (1992; see Table 1). The report of *F. bojeri* from northern Madagascar by Berg (1986) is probably erroneous and specimens previously identified under this name belong in fact to *F. brachyclada* (Rafidison et al. 2011).

As a consequence, we consider that the fig flora of Madagascar comprises 24 species (Table 1), including seven species from subgenus *Sycomorus*, most of them endemics. However, a thorough analysis of species in the subgenus *Sycidium* (*F. brachyclada* and *F. politoria*, Figure

2A and 2B) will most probably reveal that in their current configuration they constitute a species complex comprised of several more species.

Pollinators of 14 of the 24 Malagasy fig species are described, which means that at least 40% of the agaonid species still await description. The pollinators of five rare or localized species still need to be discovered (*F. ampana*, *F. assimilis*, *F. bivalvata*, *F. marmorata*, and *F. torrentium*). With the exception of *F. sycomorus* and *F. politoria*, most of the Malagasy *Ficus* host a single pollinator species (Table 2; Berg and Wiebes 1992). Most pollinator species are endemic to the Malagasy Region, and most genera are also present in continental Africa, with the exception of the pollinator of *F. humberti*, which belongs to a new genus of Agaonidae and of *Maniella bergi* (previously included in *Platyscapa*), which belongs to an otherwise strictly Oriental and Australasian genus. The four *Ficus* species that occur both on Madagascar and continental Africa share the same agaonid species (though in two of the four cases different subspecies are described).

Ficus sycomorus and *F. politoria* are each associated with multiple species of agaonids on Madagascar (J.-Y. Rasplus, unpublished data). *Ficus sycomorus* is associated with two *Ceratosolen* species, namely *C. arabicus* and *C. galili*, which occur in sympatry throughout the whole geographical range of their host (Madagascar and continental Africa). More importantly, only *C. arabicus* pollinates its host. *Ceratosolen galili*, even though it has fully developed pollen pockets, does not exhibit pollination behavior, and is therefore described as a ‘cuckoo wasp’ (Compton et al. 1991), that is to say a parasite of the *F. sycomorus* – *C. arabicus* mutualism. *Ficus politoria* is associated with at least three different pollinator species (J.-Y. Rasplus, unpublished data). Finally, two Malagasy subgenus *Sycomorus* species (*F. botryoides* and *F. trichoclada*), appear to be pollinated by a same pollinator species, *C. blommersi*.

Associated Non-pollinating Insects

In addition to its mutualistic partner, each fig species hosts a variety of non-pollinating fig wasps (NPFWs) that also develop in the flowers. Each of these wasps is mostly associated with one or a few species of figs, and each fig species hosts a community of NPFWs (Jousselin et al 2008). These communities are relatively small in dioecious species (up to six species of NPFWs developing on a single fig species) but can be highly diversified in monoecious figs (up to 44 species of NPFWs on *F. microcarpa* in Asia) (Kerdelhué and Rasplus 1996a, 1996b). Most species of NPFW are still undescribed and their biology poorly studied. Some are gall-makers and oviposit in the fig ovules, while others are parasitoids, hyperparasitoids or inquilines (their larvae develop at the expense of the gall tissue induced by another wasp species), and lay eggs in gall-transformed ovaries that already contain a larva of a pollinator or a gall-maker. Some species are like the pollinator in that they enter into the fig through the ostiole (e.g., Sycophaginae and Sycoecinae on Madagascar) and oviposit in the ovaries. But most species of NPFW oviposit from outside of the fig, through the fig wall, using long or coiled ovipositors (Sycoryctinae, Otitesellinae, Epichrysomallinae, Ormyridae or Eurytomidae on Madagascar). Many open questions remain about numerous aspects of the ecology and evolution of NPFW, as well as their phylogeny and biogeography and their impact on the mutualism remains to be thoroughly studied.

Various other groups of insects also develop inside figs. Among these, the drosophilid fly genus *Lissocephala* has undergone a highly specialized radiation on *Ficus* in the African region (Lachaise et al. 1996). These flies develop in the fig, taking advantage of the fig – fig wasp mutualism without affecting any of the mutualistic partners. This genus is present in the Malagasy Region with strong affinities with continental Africa as compared to the Oriental – Australasian region (Lachaise et al. 1996). Tropical species of the weevil genera *Curculio* and *Omophorus*

(Coleoptera: Curculionidae) are also specialized on figs (Rasplus et al. 2003). In this case, however, the development of the beetle larva in the fig cavity destroys seeds and wasp galls, and the impact on the mutualism is thus negative for both partners. On Madagascar for instance, more than 50% of the crop (up to 100%) in a given tree of *F. botryoides* (Figure 3C), *F. polyphlebia* (Figure 3D), and *F. tiliifolia* (Figure 3D), can be parasitized by weevil larvae (A. Dalecky, unpublished data). Ants (Formicidae) patrol receptive figs and capture wasps, as well as ripe figs to collect seeds (both were observed for *F. tiliifolia*), and in *F. botryoides* ant nests can be found in the cauliflorous inflorescences (A. Dalecky, unpublished data; see also Cushman et al. 1998 for data including Malagasy *Ficus*).

Biogeographical Considerations

Distribution maps (Figures 1) are tentative because data on the distribution of several rare *Ficus* species are scarce; some species have been only recently described and are still poorly known (see Berg 1986; Berg and Wiebes 1992); and the different regions of Madagascar have not been sampled with the same intensity. Some species are probably restricted to the moist evergreen forests of the Eastern, Central and/or Sambirano Domains (sensu Humbert 1955). These include *F. polyphlebia*, *F. botryoides*, *F. torrentium*, *F. antandronarum*, *F. politoria*, *F. brachyclada*, and *F. bivalvata*. Some species are probably restricted to the Southern and Western Domains, including *F. marmorata* and *F. humberti* (Figure 2F). Other species are found across the island: *F. sakalavarum*, *F. tiliifolia*, *F. lutea*, *F. reflexa*, *F. polita*, and *F. pachyclada* (Figure 3A).

Seven of the 24 *Ficus* species of Madagascar are also present on surrounding islands (Table 1), and only 15 species are endemic to Madagascar. The nearby islands also host four other species (all endemic to the Malagasy Region) not present on Madagascar: *F. densifolia* (Seychelles and

Mascarenes, with one doubtful citation of this species for Madagascar), *F. lateriflora* (Mascarenes), *F. mauritiana* (Mascarenes), and *F. karthalensis* (Comoros) (Berg and van Heusden 1985; Berg and Wiebes 1992). Possibly another species may occur in the Comoro Islands, *Ficus* cf. *tiliifolia* (F. Kjellberg, unpublished data). In total, 86.2% (25 of 29) of the fig species are endemic to the Malagasy Region.

None of the Malagasy figs are found in any other biogeographic region than Africa. For most of the island's species that were included in a phylogenetic analysis (Cruaud et al. 2012; Harrison et al., 2012), their closest relative occurs in the Afrotropics (*Sycidium*, *Sycomorus*, and all *Galoglychia* species), with the following exceptions. *Ficus madagascariensis* appears to be sister to *F. densifolia* (Mascarenes) plus all other *Ficus* belonging to section *Urostigma*, which mostly occur in Asia (Chantarasuwan et al. 2016), but this requires confirmation, as another possible explanation is that this species originates from an early colonization event from Asia. *Ficus menabeensis* (Figure 2E) is the sole representative of the section *Conosycea* on Madagascar and is sister to *F. glaberrima*, a species occurring from India to Java. *Ficus humberti* is very probably a misclassified section *Galoglychia* species, thus originating from Africa (J.-Y. Rasplus, unpublished data). *Ficus assimilis* may also have colonized Madagascar from southeast Asia, as its closest relative, the rare *F. albipila*, occurs widely from Sumatra to Australia (Corner 1985).

Several subgenus *Sycomorus* species are endemic to Madagascar and may represent a local radiation. However, none of the phylogenetic studies has yet included a representative sampling of this Malagasy group of species. Harrison et al. (2012) analyzed several species of this group, and they did not group in a unique radiation.

Reconstructing the history of Madagascar colonization by the different fig clades is a difficult task. Indeed, the timing of the origin of the crown *Ficus* has been debated for the past 15

years, with phylogenies supporting a Late Cretaceous origin [60.0–101.9 Mya, Cruaud et al. 2012] and others an early Cenozoic origin [40.8–56.0 Mya, Zhang et al. 2019]. This huge uncertainty is probably due to differences in calibration scheme (stem vs crown, log-normal vs uniform, secondary calibration of the root, etc.). However, evidence from the agaonid wasps supports a late Cretaceous origin of the crown *Ficus*. Two lines of evidence are consistent with this hypothesis: 1) agaonid divergence from their closest relatives has been estimated at 90 Mya using 37 fossils of Hymenoptera to calibrate and UCE markers (Branstetter et al. 2018); 2) a fossil discovered in the Insect Bed of the Bembridge (Isle of Wight, UK) and belonging to the wasp clade that pollinates *Galoglychia* fig trees [*Archaeagaon minutum* (Donisthorpe 1920)] has been dated back to about 34 Mya (Compton et al. 2010). This age is 10 Mya older than the age estimates for stem *Galoglychia* in the early Cenozoic hypothesis and hence supports the Late Cretaceous origin hypothesis.

Fig trees and their pollinating wasps have independently colonized Madagascar at least eight times (Cruaud et al. 2012; Chantarasuwan et al. 2016). Using a Late Cretaceous hypothesis, the timing of these different colonization events ranges from ca. 36 Mya to 5 Mya. The most ancient colonization events appear to be those of *F. menabeensis* (36 Mya) and of the ancestor of the subgenus *Sycomorus* lineage (33 Mya). The colonization of Madagascar by the subgenus *Sycidium* may also be relatively ancient (ca. 20 Ma) as well as the colonization by subgenus *Urostigma* species. This last event is problematic as the position of *F. densifolia* differs between studies, being sister to all Oriental species of the section in Chantarasuwan (2016), but nested within Oriental species and sister to *F. religiosa* in other studies.

In contrast, colonization of Madagascar by Afrotropical species of section *Galoglychia*, through the crossing of the Mozambique Channel, is recent (less than 10 Mya). Some *Galoglychia*

species may have been introduced recently by humans. However, leaf prints of *Ficus* aff. *polita* found in clays at Benenitra along the Onilahy River and dating at least from the early Quaternary, suggest this species has colonized Madagascar before humans (Perrier de la Bâthie 1928).

This tempo of colonization of Madagascar by figs is confirmed by the timing inferred from dated phylogenies of fig wasps. The oldest colonization of agaonids appears to be those of *Ceratosolen* species pollinating subgenus *Sycomorus* fig trees (ca 33 Mya, with a radiation around 25 Mya) and of *Maniella bergi*, the pollinator of *F. menabeensis* (between 29 and 12 Mya). Again, colonizations of Madagascar by pollinators of section *Galoglychia* species (from Africa) are more recent events (less than 12 Mya). Results for the few Malagasy non-pollinating fig wasps for which we have a time estimate of their colonization of Madagascar are consistent with those for figs and pollinating wasps.

Successful colonization of islands by fig trees is not easy, as it necessitates colonization by compatible partners (*Ficus* and pollinating wasp). Pollination shifts between non-sister host species are relatively rare events in the Old World. Therefore, the colonizing fig tree requires pollination by its own pollinator or by a closely related species that must be i) attracted by the odors of a non-host fig, ii) capable of entering the fig (despite of co-adaptation of head and ostiole lengths), and iii) capable of using the female flowers (co-adaptation of ovipositor and style lengths). While fig seeds can be dispersed over rather long distances by frugivorous mammals (i.e. fruit bats) or birds (pigeons and parrots), the wasps only live two or three days and are blown by the wind. Nevertheless, long-distance dispersal of fig wasps, up to tens of kilometers and sometimes over 100 km, has been observed (McKey 1989; Ahmed et al. 2009). The mutualistic interaction may constitute an important constraint to colonize islands, compared to less specific pollination systems.

Colonization of Madagascar from the Oriental region (India) may have occurred through island hopping across the western Indian Ocean. Indeed, a series of islands emerged over the past 65 Mya (Chagos Plateau, Saya de Malha Bank, and Nazareth Bank) through which species belonging to subgenera *Sycidium*, *Sycomorus* and *Conosycea* may have reached the Mascarenes, Madagascar, and subsequently Africa but such a scenario still requires validation.

Fig Frugivory

In the obligate mutualism between figs and agaonid wasps, each partner provides an essential resource to the other. At any time of the year within a breeding population of fig trees, emerging wasps from a tree with ripening figs need to find a tree with receptive figs if the local population is to be maintained. Considering that pollinating wasps probably cannot survive for more than 2-4 days and that flowering is relatively synchronous within a fig tree, between-tree flowering asynchrony in a population of fig trees is a key feature that maintains local populations of pollinator(s) (Janzen 1979; McKey 1989; Herre 1996). In turn, flowering asynchrony means that ripe figs of a given species are found year-round and may constitute a critical resource for frugivores, especially during lean periods of low fruit availability (Korine et al. 2000). Fruiting asynchrony among trees, as well as the large crops of some fig trees, the pulpy nature of the ripening inflorescences make figs a keystone resource for frugivore communities in Neotropical and Oriental tropical forests (Janzen 1979; Terborgh 1986). However, figs do not appear to have a key role in maintaining frugivore populations in some other tropical rainforests (Gautier-Hion and Michaloud 1989) and this could be the case in Madagascar (Goodman and Ganzhorn 1997).

Compared to other large islands in the Old World, Madagascar (587,041 km²) is slightly smaller (75%) than Borneo (743,330 km²) or New Guinea (775,210 km²) but exhibits a much lower

diversity of *Ficus* species (24 species versus about 150 and 157 species, respectively). At the local scale, the richness of Madagascar sites rarely exceeds more than 12 species of fig trees, while sites in Borneo and Papua can reach over 80 and 65 species, respectively. Africa is comparable to Madagascar, they share section *Galoglychia* and were colonized by most fig lineages (section *Oreosyceae* and subgenera *Sycidium* and *Sycomorus*) with the notable exception of section *Conosyceae* that only reached Madagascar. Some of the well-studied African sites also exhibit higher richness of figs, with about 30 species locally, compared to well-studied Malagasy sites (Harrison 2005). The low richness of fig species in Madagascar could easily be explained by the isolation of the island in deep geological time, the low number of fig colonization events, as well as the low level of subsequent local diversification of fig lineages that reached Madagascar. Finally, Madagascar is globally drier than Borneo and New Guinea, which may also explain the lower richness of *Ficus*.

Compared to other tropical areas, Madagascar is also noteworthy for its relative paucity in frugivores (Table 4). Malagasy figs are eaten by several vertebrates, including lemurs, birds (pigeons, parrots, and bulbuls), bats, small rodents, and presumably introduced bush-pigs (Perrier de la Bâthie 1928; Turk 1995; Goodman et al. 1997) (Table 4). The non-volant mammalian frugivore fauna is dominated by lemurs and lacks ungulates, squirrels, and large rodents (Dewar 1984). Furthermore, among landbirds only ca. 10% of the species occurring on Madagascar are at least partially frugivorous (Razafindratsima 2014).

Densities of fig trees have received little attention on Madagascar, but appear to be low, at least for hemiepiphytic species, as observed in other tropical regions (Harrison 2005). Free-standing members of the subgenera *Sycomorus* and *Sycidium* species can be locally more abundant, especially along streams. Therefore, in Malagasy ecosystems, the contribution to food

resource availability by figs, at least across seasons, appears relatively limited and globally low compared to fruit resources produced by other trees. It is possible that fig densities on the island are too low to allow their functioning as keystone species during the season of low availability of fruits, but better estimates of fig densities are required.

Reproductive phenology data for Malagasy fig species are also scarce. Dalecky et al. (2003) reported the phenologies of *F. brachyclada* and *F. politoria* over two years and of *F. botryoides*, *F. polyphlebia*, and *F. tiliifolia* over a single year in the moist evergreen forest of Ranomafana National Park (600-1100 m altitude). Stages of fig maturity were recorded following Galil and Eisikowitch (1968), and fig abundance was noted on a semi-quantitative scale. All surveyed fig trees produced relatively small crops (< 10 figs per tree) that may be able to sustain fig wasp populations but are of limited importance for large frugivores. At Ranomafana, figs are available almost year-round (Dalecky et al. 2003) and the lack of fruiting individuals of some species (i.e. *F. politoria*) during some periods (july-november) may be artefactual due to insufficient sample size and local search for figs. In dioecious figs, wasps may locally be extinct after period of strong drought (Harrison, 2000) but can recolonize the area from nearby trees. In the moist evergreen forests of the island, ripe-fig availability varied seasonally, with the summer months (December-February) most productive, and winter (June-August) the least (Hemingway and Overdorff 1999). Peak of fig production was in summer and did not correspond with maximum fig feeding in lemurs. At Ranomafana, during the season other fruits became scarcer, all lemur species fed on figs, but in the dry deciduous forests of the north there is concentrated fig fruiting during the winter months and they are extensively fed upon by fruit bats (S. M. Goodman, unpublished data). Elsewhere on the island, few studies have been conducted to explore the importance of figs. In Madagascar, figs were found to be among the most important food sources for bats (Bollen and van Elsacker 2002)

and for lemurs. However, most Malagasy frugivores exhibit a highly diverse diet, thereby dispersing a wide array of fruiting trees, among which fig trees represent only a small portion. This is different from what happens in Africa, where species richness patterns of figs and avian frugivores are linked via strong resource–consumer interactions (Kissling et al. 2007).

Few quantitative data on feeding by frugivorous vertebrates on figs are available for Madagascar (but see Goodman et al. 1997; Dalecky et al. 2003). In Ranomafana most lemur populations commonly exploited strangler fig species (Dalecky et al. 2003). Despite an overall similarity in species composition in the diets of these lemurs, there were notable differences in the quantity of figs consumed (Table 3), from 35.4% of overall feeding time in *Eulemur fulvus* to 3.1% in the folivore *Haplemur griseus*. However, figs were clearly among the preferred fruit resources for *H. griseus*, comprising 23.1% of fruit feeding time. This species also feeds on *Ficus* leaves. There are a few cases of extreme specialization of frugivores on fig resource, but none are known from Madagascar (Shanahan et al. 2001). In Malagasy habitats, no frugivores have specialized on fig species and most species appear to be generalists (Table 4).

Most species of Malagasy frugivores are not dependent on figs to survive during the lean season, as would be expected from classical descriptions of keystone resources. Most of these animals are generalists and can easily shift their diets, which might be result from the seasonality of fruit availability. Frugivorous lemurs are also frequently folivorous and increase leaf consumption during periods of lower fruit availability (i.e. *Propithecus*). Only two lemur genera, *Varecia* and *Eulemur*, are considered to be mainly frugivorous and therefore may in some cases be dependent on fig trees that fruit during the period of fruit scarcity. *Eulemur* at Andringitra were shown to depend heavily on *Ficus* (nearly exclusively *F. lutea*) during the winter months when fruits are scarce (including the studied *Ficus* species) (Dalecky et al. 2003). This site may represent

to date the best candidate location for a role of *Ficus* as a keystone resource for frugivores. Further phenological surveys are necessary to evaluate the importance of *Ficus* to the frugivore community on the island, comparing patterns in the moist evergreen, semi-deciduous and dry deciduous forests. Among the community of Malagasy vertebrate frugivore species, a few species can be considered as seed predators (rodents, *Coracopsis* parrots), whereas most other species are seed dispersers (Bollen et al. 2004).

Studies on Malagasy frugivores have mostly focused on the feeding ecology and the role of mammals (lemurs and bats) in dispersal (Dew and Wright 1998; Ganzhorn et al. 1999; Bollen and van Elsacker 2002; Bollen et al. 2004). On the island, size of ripe figs ranges from ca. 4 mm (*F. antandronarum*) to over 50 mm in *F. sakalavarum*, one of the two *Ficus* species with the largest ripe figs in the Afrotropical region. Within forest fragments, large and medium-sized figs are mostly dispersed by frugivorous lemurs with large home ranges (> 100 ha) and long daily distances traveled (Bollen et al. 2004). Frugivorous bats, as well as *Alectroenas* and *Treron* fruit pigeons and *Hypsipetes madagascariensis* Madagascar Bulbul, are probably the most important dispersers of seeds across forest fragments (Bollen and Van Elsacker 2002).

Seeds of *Ficus* are small (1 to 2 mm long in Malagasy species) (Vololona and Goodman 2019) and appear to germinate faster after they passed through the digestive tract of their dispersers (Oleksy et al. 2017). Deposition of seeds in feces may have complex effects on post-dispersal predation as well as on the probability of germination in favorable sites. On Madagascar, this has been demonstrated for seeds of *F. assimilis*, *F. polita*, *F. grevei*, and *F. lutea* after ingestion by *Pteropus rufus* (Bollen and van Elsacker 2002; Oleksy et al. 2017) and for seeds of *F. brachyclada* and *F. menabeensis* after ingestion by *Eidolon dupreanum* (Picot et al. 2007). Germination success is also increased, as shown for seeds of *F. rubra* ingested by *Rousettus madagascariensis*

(Andrianaivoarivelo et al. 2011). Other Malagasy frugivorous mammals (Dew and Wright 1998) and birds (Razafindratsita and Zack 2009) also have positive effects on seed germination.

Hence, despite the lack of fig specialists, certain frugivores depend on *Ficus* in some seasons, as proposed in other tropical forests (McKey 1989). Globally *Ficus* may not play a role of staple year-round food in Malagasy forest habitats. However, the role of *Ficus* during lean periods needs further documentation and may be of importance for different endemic species on the island.

Chemical Ecology of Fig Pollination and Seed Dispersal

Chemical signaling is crucial at two stages of the fig's life cycle: when receptive figs must attract their specific pollinators, and when mature figs must attract frugivores that will disperse their seeds. Many studies show that pollinating fig wasps are attracted by volatile organic compounds emitted by figs at receptivity (Grison-Pigé et al. 2002; Hossaert-McKey et al. 2010). Maximum distances from which wasps can detect receptive figs are not known, but scent plumes produced by flowers emitting VOCs (including VOCs present in fig emissions) are typically detectable by insects over distances of a few hundreds of metres (Fuentes et al. 2016). Moreover, each fig wasp species is usually only attracted by the odor of its own host fig (Proffitt et al. 2009; Souto-Vilarós et al. 2018). Specificity is often ensured by qualitative differences in the compounds present (mainly monoterpenes, sesquiterpenes, shikimic compounds, and some fatty acid derivatives) and by quantitative differences in the relative proportions of major and minor common compounds. In very few species the odor is composed of rare compounds as a private sensory channel (Chen et al. 2009) between the fig and its pollinating wasp. In a few examples, it has also been shown that non-pollinating fig wasps locate their host species by using the volatile compounds that are emitted by figs during the stage of development at which each species can oviposit within the fig (Proffitt et al. 2007). Further research is required to investigate the function of fig scents in the

attraction of non-pollinating fig wasps. Scents as cues for host location are also important to explain why wasps still continue to visit female figs, in which they cannot reproduce (see above). In some dioecious species (Hossaert-McKey et al. 2016), it has been shown that male and female figs at receptivity produce the same volatile organic compounds and in similar proportions, and that fig wasps are not able to discriminate between figs of the two sexes, supporting the hypothesis of chemical mimicry (Ashman 2009).

Finally, scents are important cues in fig-frugivore interactions, mainly in the case of mammalian frugivores (Borges et al. 2008; Hodgkison et al. 2013; Soler et al. 2018). The volatile compounds emitted by figs differ between the receptive phase and dispersal phase of figs of the same species, although both are composed mainly of fatty acid derivatives and terpenes.

On Madagascar, chemical mediation of fig interactions with their mutualistic partners remains to be studied. Odors of receptive figs have been investigated in only two species, the monoecious species *F. botryoides* and one of the three dioecious species present on the island, *F. pachyclada*. This last species is characterized by a high proportion of 2-heptanone (an odorant ketone), associated with some minor compounds such as 6-methyl-3-hepten-2, benzaldehyde, and α -cedrene. The olfactory signal emitted by figs of *F. botryoides* is mainly composed of monoterpenes such as (E)-ocimene, ρ -cymene and sabinene (C. Soler, unpublished data). Finally, only one species has been studied at the dispersal phase, *F. lutea*. In this species, the volatile organic compounds are emitted by ripe figs, both on the island and in South Africa, and in both cases odors of ripe fruits were comprised of about 50% fatty acid derivatives (such as undecane, (Z)-3-hexenol, (E)-2-hexenol). The main difference between the two sites was the significantly higher proportion of sesquiterpenes (α -bergamotene, β -caryophyllene and α -copaene) emitted by this fig on Madagascar. Detailed studies of such intraspecific variation in fruit scent should help

determine if among possible causes such as isolation by distance, and insular isolation, the very peculiar fauna of Madagascar frugivores could be a driving force.

Figs and Humans

In this section, we present knowledge and practices of Malagasy people related to fig species, their symbolic meanings, roles in Malagasy history, as well as practical uses and linkages to vernacular taxonomy and naturalist knowledge of *Ficus* species. We use case studies conducted by ethnoecologists especially among the Betsileo and the Merina and data from other regions, both from literature (e.g., Perrier de la Bâthie 1928; Boiteau and Allorge 1998; Samyn 1999; Beaujard 2017) and from our field observations.

To set the scene, those who travel to Madagascar with a strong interest in figs will come across children on the road or in small villages in the Central Highlands who systematically recall a short poem used in schools to learn how to count, which goes as follows: *Isa ny amontana* (*one*, *F. lutea*), *roa ny aviavy* (*two*, *F. polita*), *telo fangady* (*angady*, the Malagasy typical spade used in rice fields). This poem probably diffused across portions of the island during the period when the Merina attempted to extend their control over more than two-thirds of the land and a large share of the population of Madagascar in the early nineteenth century (Kottak 1977). This poem was a means of associating these two *Ficus* species to the Merina culture and the symbolic importance of these plants to the royal family (Razafiarivony 2006; Aumeeruddy-Thomas et al. 2018). Andrianapoinimerina (about 1745 to 1810), one of the best known of the kings from this period, used to deliver his public speeches to the people under a *F. lutea* which is still present at his ancient residence, Rova Ambohimanga, near Antananarivo. In addition, the Merina planted *F. lutea* well beyond its natural area of distribution, as one of their symbols to mark new territories over which they gained control (Aumeeruddy-Thomas et al. 2018; Rafidison et al. 2020).

Betsileo inhabitants still plant *F. lutea* in front of their houses and many are among the ancient members of Betsileo noble class who had close relationships with the Merina kings (e.g., Harper 2003). Investigations of the 12 sacred hills surrounding Antananarivo, directly related to the former royal families, found planted and spontaneously planted *F. lutea* and *F. polita*, which today still represent symbols of power and sacredness or *hasina*, a concept used by many Malagasy cultural groups that relates simultaneously to the power of nature and its sacred dimension (Aumeeruddy-Thomas et al. 2018) (see Figure 3A). However, in some parts of Madagascar, other trees are of greater symbolic importance. Nevertheless, Sakalava living in the western lowlands do plant or protect some *Ficus* species on their lands, such as *F. sycomorus*, for medicinal uses of the bark, for its edible fruits.

Studies by Turk (1995) assembled a list of names in Malagasy for fig species, to which we add new data (Table 5), but such vernacular names are lacking from certain areas of the island. Variations in naming of the same *Ficus* species are apparent, a situation common in vernacular taxonomy in most traditional and modern societies throughout the world, as names vary from one ethnic group to another (and even within ethnic groups), indicating linguistic and cultural identity. In Madagascar, linguistic diversity is high due to ancient influences of Austronesian and African languages and local dialects therefore introduce variations in naming (e.g. Beaujard 2011). Most vernacular *Ficus* names on the island are linked to uses, origin or biological aspects (Table 5). All names collected to date refer to names referring to the species level and can be associated to a species in scientific naming, with some regional variations. For example, *F. lutea* in Antananarivo is called *amontana*, while the same species for the Betsileo is *amonta* (Rafidison et al. 2020). Naming intraspecific variation is rare and is known for *F. tilifolia*, named *voara* or *ara*. This tree is highly appreciated for its fruits by the Betsileo, who recognize two varieties, *voara bekobo* or

voara malefaka in villages near Fianarantsoa. The names refer to the shape and taste of fruits of the two varieties (Figure 3D).

The following physical characteristics of different *Ficus* are used jointly or separately to distinguish the species and are most often linked to uses, ecology or beliefs:

1) The white latex flowing abundantly from t cut bark -- *Ficus* latex is used in different portions of the island for hunting birds or for medicinal purposes, and is believed to improve water retention in soils and to improve breast feeding by women (Rafidison 2013, Rafidison et al. 2016, Aumeeruddy-Thomas et al. 2018). *Ficus reflexa*, named *nonoko* or *laza*, meaning literally ‘feeding breast’, is named after this particular characteristic, although other species used by groups other than the Betsileo or Merina may be called *nonoka* in analogy to *F. reflexa*.

2) Use of the fibrous bark of *Ficus* to make ropes or barkcloth (called *fato*) -- The bark of both *voara*, *F. tiliifolia*, or *fompoha*, *F. botryoides* are used to make *fato* (MBG Tropicos database, Turk 1995, Rafidison 2013, Rafidison et al. 2016, 2020).

3) The shape and quality of the fruits, including the presence or not of internal insects -- Some people talk of parasites that affect the fruit (e.g., *F. lutea* in Antananarivo) but not to the role of these insects in the pollinating process (Aumeeruddy-Thomas et al. 2018; Rafidison et al. 2020). Two species, *F. botryoides* (Figure 3C) and *F. trichoclada* (Figure 2C), are both named *fompoha*. *Fompoha* literally means “to blow” and refers to the gesture of blowing on the opened ostiole to produce a small cloud of tiny insects. Children are very good observers of the presence of insects and know how to clear away the insect debris before consuming fruits (Figure 3B). The fruits of many species are locally eaten by people as snacks (Rafidison et al. 2020). The cauliflorous habit is also recognized as a trait characteristic of some *Ficus* species and more generally where the fruit is located on the tree is a trait that is used locally to distinguish *Ficus* species (Figure 3C).

4) The leaves are also a feature well identified in certain species groups -- *Ficus politoria* and *F. brachyclada* bear the same name due to a particular leaf characteristic; they have rough leaves and are both called either *kivozy* or *ampaly*, meaning literally scabrous. These leaves are often used to polish wood.

5) Their ease of propagation from woody cuttings – This technique is frequently used to make living hedges. The Betsileo use *F. reflexa* and *F. lutea* in such hedges for cattle (*zebu*) corrals. Such structures serve multiple functions, protecting against soil erosion and with supernatural power to protect cattle as well as people from evil spirits, while bringing happiness and well-being (Figure 3E).

6) The hemi-epiphytic or hemi-epilithic (growing on rocks) habit characteristic of some *Ficus* species is linked to beliefs regarding the sacred nature of these plants. They are believed to have been planted by intangible creatures and symbolize the sacred power of nature (*hasina*) due to their capacity to grow on “natural” rocks, steles (megaliths), tombs or cliffs (Figure 3F) without requiring any visible soil substratum.

As a result of their multiple values, several *Ficus* species are planted and for these, as well as those growing naturally near villages are protected (Table 1 (Figure 3G) (Rafidison et al. 2020). These trees constitute an attractive resource for frugivores, and may thereby increase seed rain of various plant species and facilitate and accelerate succession, serving an important conservation role.

Subject editors: Laurent Gautier and Steven M. Goodman

References cited

Ahmed, S., Compton, S. G., Butlin, R. K., and Gilmartin, P. M. 2009. Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences of the USA* 106(48): 20342-20347.

- Andrianaivoarivelo, R. A., Ramilijaona, O. R. Racey, P. A., Razafindrakoto, N., and Jenkins, R. K. B. 2011. Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928 (Chiroptera: Pteropodidae) in eastern Madagascar. *Mammalia* 75: 69-78.
- Ashman, T. L. 2009. Sniffing out patterns of sexual dimorphism in floral scent. *Functional Ecology* 23: 852-862.
- Aumeeruddy-Thomas, Y., Rafidison, M. V., Kjellberg, F., and Hossaert-McKey, M. 2018. Sacred hills of Imerina and the voyage of *Ficus lutea* Vahl (Amontana) in Madagascar. *Acta Oecologica* 90: 18-27.
- Beaujard, P. 1988. Plantes et médecine traditionnelle dans le sud-est de Madagascar. *Journal of Ethnopharmacology* 23: 165-265.
- Beaujard, P. 2011. The first migrants to Madagascar and their introduction of plants: Linguistic and ethnological evidence. *Azania* 46: 169-189.
- Beaujard, P. 2017. *Histoire et voyages des plantes cultivées à Madagascar avant le XVIème siècle*, Paris: Karthala.
- Berg, C. C. 1984. Floral differentiation and dioecism in *Ficus* (Moraceae). In *Minisymposium on figs and fig insects*, eds. F. Kjellberg, F. and G. Valdeyron, G., pp 15-25. Montpellier: CNRS.
- Berg, C. C. 1986. The *Ficus* species (Moraceae) of Madagascar and the Comoro Islands. *Bulletin du Muséum national d'Histoire naturelle, Paris, 4^e série, 8, section B, Adansonia* 1: 17-55.
- Berg, C. C. 1990. Distribution of African taxa of *Ficus* (Moraceae). *Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg* 23: 401-405.
- Berg, C. C., and Corner, E. J. H. 2005. Moraceae - *Ficeae*. *Flora Malesiana*, Series I, 17(2): 1-70.
- Berg, C. C., and van Heusden, E. C. H. 1985. Moracées. *Flore des Mascareignes*, famille 164: 1-21.
- Berg, C. C., and Wiebes, J. T. 1992. *African fig trees and fig wasps*. Amsterdam: Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen.
- Berlin, B., Breedlove, D. E., and Raven, P. H. 1968. Covert categories and folk taxonomies, *American Anthropologist* 70: 291-299.
- Boiteau, P., and Allorge, L. 1998. *Plantes médicinales de Madagascar*. CD-ROM.: Lune Rouge s.a.
- Bollen, A., and van Elsacker, L. 2002. Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropterologica* 4: 33-47.
- Bollen, A., van Elsacker, L., and Ganzhorn, J. U. 2004. Relations between fruits and disperser assemblages in a Malagasy littoral forest: A community-level approach. *Journal of Tropical Ecology* 20: 1-14.
- Borges, R., Bessière, J.-M., and Hossaert-McKey, M. 2008. The chemical ecology of seed dispersal in monoecious and dioecious figs. *Functional Ecology* 22: 484-493.
- Branstetter, M. G., Danforth, B. N., Pitts, J. P., Faircloth, B. C., Ward, P. S., Buffington, M. L., Gates, M. W., Kula, R. R., and Brady, S. G. 2017. Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. *Current Biology* 27: 1019-1025.
- Burrows, J., and Burrows, S. 2003. *Figs of southern and south central Africa*. Hatfield, South Africa: Umdaus Press.
- Chantarasuwan, B., Ronsted, N., Kjellberg, F., Sungkaew, S., and van Welzen, P. C. 2016. Palaeotropical intercontinental disjunctions revisited using a dated phylogenetic hypothesis

- with nearly complete species level sampling of *Ficus* subsect. *Urostigma* (Moraceae). *Journal of Biogeography* 43: 384-397.
- Chen, C., Song, Q. S., Proffit, M., Bessière, J.-M., Li, Z. B., and Hossaert-McKey, M. 2009. Private channel: A single unusual compound assures specific pollinator attraction in *Ficus semicordata*. *Functional Ecology* 23: 941-950.
- Compton, S. G. 1992. New records of *Ficus* species and their pollinators on Grand Comore. *Bothalia* 22(1): 46-47.
- Compton, S. G., Holton, K. C., Rashbrook, V. K., Van Noort, S., Vincent, S. L., and Ware, A. B. 1991. Studies of *Ceratosolen galili*, a non-pollinating Agaonid fig wasp. *Biotropica* 23(2): 188-194.
- Compton, S. G., Ball, A. D., Collinson, M. E., Hayes, P., Rasnitsyn, A. P., and Ross, A. J. 2010. Ancient fig wasps indicate at least 34 Myr of stasis in their mutualism with fig trees. *Biology Letters* 6: 838-842.
- Cook, J. M., and Rasplus, J.-Y. 2003. Mutualists with attitude: Coevolving fig wasps and figs. *Trends in Ecology and Evolution* 18: 241-248.
- Corner, E. J. H. 1965. Check-list of *Ficus* in Asia and Australasia, with keys to identification. *Garden's Bulletin of Singapore* 21: 1-186.
- Corner, E. J. H. 1985. Essays on *Ficus*. *Allertonia* 2: 125-168.
- Cruaud, A., Rønsted, R., Chantarasuwan, B., Siang Chou, L., Clement, W., et al. 2012. An extreme case of plant-insect co-diversification: Figs and fig-pollinating wasps. *Systematic Biology* 61: 1029-1047.
- Cushman, J. H., Compton, S. G., Zachariades, C., Ware, A. B., Nefdt, R. J. C., and Rashbrook, V. K. 1998. Geographic and taxonomic distribution of a positive interaction: Ant-tended homopterans indirectly benefit figs across southern Africa. *Oecologia* 116: 373-380.
- Dalecky, A., Kerdelhué, C., Johnson, S., Razafindratsita, V. R., Grassi, C., Razafiarimalala, A. C., Overdorff, D. J., and Rasplus, J.-Y. 2003. Moraceae, *Ficus* and associated fauna. In *The natural history of Madagascar*, eds. S. M. Goodman and J. P. Benstead, pp. 322-334. Chicago: The University of Chicago Press.
- Decary, R. 1946. Plantes et animaux utiles de Madagascar. *Annales du Musée colonial de Marseille*, 54ème année, 6ème série, 4: 1-234.
- Dew, J. L., and Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30: 425-437.
- Dewar, R. E., and Richard, A. F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences to the USA* 104(34): 13723-13737.
- Dury, S. 1991. Approche ethnobotanique des *Ficus* au Nord du Cameroun. Ph.D. thesis, Ecole Nationale Agronomique de Montpellier.
- Fuentes, J.D., Chamecki, M., Roulston, T., Chen, B., Kenneth, R., and Pratt, K.R. 2016. Air pollutants degrade floral scents and increase insect foraging times. *Atmospheric Environment* 141: 361-374.
- Galil, J., and Eisikowitch, D. 1968. Pollination ecology of *Ficus sycomorus* in east Africa. *Ecology* 49: 260-269.
- Ganzhorn, J. U., Fietz, J., Rakotovo, E., Schwab, D., and Zinner, D. 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology* 13: 794-804.
- Goodman, S. M., and Ganzhorn J. U. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Revue d'Ecologie (Terre et Vie)* 52: 321-329.

- Goodman, S. M., Ganzhorn, J. U., and Wilmé, L. 1997. Observation at a *Ficus* tree in Malagasy humid forest. *Biotropica* 29: 480-488.
- Gautier, D. 1996. *Ficus* (Moraceae) as part of agrarian systems in the Bamileke Region (Cameroon). *Economic* 50(3): 318-326.
- Gautier-Hion, A., and Michaloud, G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70(6): 1826-1833.
- Global Biodiversity Information Facility (GBIF). 2020. GBIF home page. Available at <https://www.gbif.org>.
- Grisson-Pigé, L., Bessièrre, J.-M., and Hossaert-McKey, M., 2002. Specific attraction of fig-pollinating wasps: Role of volatile compounds released by tropical figs. *Journal of Chemical Ecology* 28: 283-295.
- Harper, J. 2003. Memories of ancestry in the forests of Madagascar. In *A landscape memory and history*, eds. P. J. Stewart and A. Strathern, pp. 89-107. London: Pluto Press.
- Harrison, R. D. 2000. Repercussions of El Niño: Drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society B* 267: 911-915.
- Harrison, R. D. 2005. Figs and the diversity of tropical rainforests. *Bioscience* 55: 1053-1064.
- Harrison, R. D., Ronsted, N., Xu, L., Rasplus, J.-Y., and Cruaud, A. 2012. Evolution of fruit traits in *Ficus* subgenus *Sycomorus* (Moraceae): To what extent do frugivores determine seed dispersal mode? *PLoS One* 7: e38432.
- Hemingway, C. A., and Overdorff, D. J. 1999. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. *Biotropica* 31(2): 354-364.
- Herre, E. A. 1996. An overview of studies on a community of Panamanian figs. *Journal of Biogeography* 23(4): 593-607.
- Hodgkison, R., Ayasse, M., Häberlein, C., Schulz, S., Zubaid, A., Mustapha, W. A. W, Kunz, T. H., and Kalko, E. K. V. 2013. Fruit bats and bat fruits: The evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics. *Functional Ecology* 27: 1075-1084.
- Hossaert-McKey, M., Soler, C., Schatz, B., and Proffit, M. 2010. Floral scents: Their roles in nursery pollination mutualisms. *Chemoecology* 20: 75-88.
- Hossaert-McKey, M., Proffit, M., Soler, C., Chen, C., Bessièrre, J.-M., Schatz, B., and Borges, R. M. 2016. How to be a dioecious fig: Chemical mimicry between sexes matters only when both sexes flower synchronously. *Scientific Reports* 6: 21236.
- Humbert, H. 1955. Les territoires phytogéographiques de Madagascar. In *Colloques internationaux du Centre National de la Recherche Scientifique, LIX: les divisions écologiques du monde, moyen d'expression, nomenclature, cartographie*, Paris, 1954. *Année Biologique*, 3ème série, 31: 439-448.
- Janzen, D. H. 1979. How to be a fig. *Annual Review of Ecology and Systematics* 10: 13-51.
- Johnson, S., and Wyner, Y. 2000. Notes on the biogeography of *Eulemur fulvus albocollaris*. *Lemur News* 5: 25-28.
- Jousselin, E., van Noort, S., Rasplus, J.-Y., Rønsted, N., Erasmus, C., and Greeff, J. 2008. One tree to bind them all: Host conservatism in a fig wasp community unraveled by cospeciation analyses among pollinating and non-pollinating fig wasps. *Evolution* 62: 1777-1797.
- Kerdelhué, C. 1997. Les communautés de Chalcidiens sycophiles associées aux figuiers du sous-genre *Sycomorus*: écologie et évolution. Ph.D. Thesis, Institut National Agronomique Paris-Grignon.

- Kerdelhué, C. and Rasplus, J.-Y. 1996a. Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* 75: 3-14.
- Kerdelhué, C. and Rasplus, J.-Y. 1996b. The evolution of dioecy among *Ficus* (Moraceae): An alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. *Oikos* 77(1): 163-166.
- Kerdelhué, C., Le Clainche, I., and Rasplus, J.-Y. 1999. Molecular phylogeny of the *Ceratosolen* species pollinating *Ficus* of the subgenus *Sycomorus sensu stricto*: Biogeographical history and origins of the species-specificity breakdown cases. *Molecular Phylogenetics and Evolution* 11(3): 401-414.
- Kissling, W. D., Rahbek, C., and Böhning-Gaese, K. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society B: Biological Sciences* 274: 799-808.
- Kjellberg, F., Jouselin, E., Bronstein, J. L., Patel, A., Yokoyama, J., and Rasplus, J.-Y. 2001. Pollination mode in fig wasps: The predictive power of correlated traits. *Proceedings of the Royal Society of London, B*, 268: 1113-1121.
- Korine, C., Kalko, E. K. V., and Herre, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123: 560-568.
- Lachaise, D., Harry, M., and Solignac, M. 1996. Affinités biogéographiques des Drosophilidae de Madagascar et des îles de l'océan indien. In *Biogéographie de Madagascar*, ed. W. R. Lourenço, pp. 467-478. Paris: Editions ORSTOM.
- Lahann, P. 2007. Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *Journal of Zoology* 271(1): 88-98.
- Martin, E., Ratsimisetra, L., Laloë, F., and Carrière, S. M. 2009. Conservation value for birds of traditionally managed isolated trees in an agricultural landscape of Madagascar. *Biodiversity and Conservation* 18(10): 2719-2742.
- Martin, E., Viano, M., Ratsimisetra, L., Laloë, F., and Carrière, S. M. 2012. Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. *Agriculture, Ecosystems & Environment* 149(1): 1-9. <https://doi.org/10.1016/j.agee.2011.12.005>
- MBG. No date. *Missouri Botanical Garden's Tropicos database*. Available at <http://mobot.mobot.org/Pick/Search/pick.html>
- McKey, D. B. 1989. Population biology of figs: Applications for conservation. *Experientia* 45: 661-673.
- MNHN. No date. *Catalog of vascular plants*. Muséum national d'Histoire naturelle, Paris' database. Available at <http://www.mnhn.fr/base/sonnerat.html>
- Oleksy, R., Giuggioli, L., McKetterick, T. J., Racey, P. A., and Jones, G. 2017. Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. *PLoS ONE* 12(9): e0184023.
- Perrier de la Bâthie, H. 1928. Les *Ficus* de Madagascar. *Archives de Botaniques, II, Bulletin mensuel* 8-9: 137-180.
- Perrier de la Bâthie, H. 1952. *Ficus* Tourn. ex L. *Flore de Madagascar et des Comores* 55: 40-71.
- Picot, M., Jenkins, R. K. B., Ramilijaona, O. Racey, P. A., and Carrière, S. M. 2007. The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar. *African Journal of Ecology* 45(4): 645-650. (doi:10.1111/j.1365-2028.2007.00788.x)

- Proffit, M., Schatz, B., Borges, R. M., and Hossaert-McKey, M. 2007. Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. *Journal of Animal Ecology* 76: 296-303.
- Proffit, M., Chen, C., Soler, C., Bessière, J.-M., Schatz, B., and Hossaert-McKey, M. 2009. Can chemical signals responsible for mutualistic partner encounter promote the specific exploitation of nursery pollination mutualisms? – The case of figs and fig wasps. *Entomologia Experimentalis et Applicata* 131: 46-57.
- Rakotomalaza, P. J., and Messmer, N. 1999. Structure and floristic composition of the vegetation in the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 94: 51-96.
- Rafidison, V. M. 2013. Ethnobiologie et écologie des *Ficus* des terroirs Betsileo et du corridor Ranomafana – Andringitra. P.H.D. thesis, Doctorat en Sciences de la vie. Faculté des Sciences, Université d'Antananarivo.
- Rafidison, V. M., Rabevohitra, R., Aumeeruddy-Thomas, Y., Hossaert-McKey, M., Rasplus, J.-Y., and Kjellberg, F. 2011. Notes taxonomiques et identification des *Ficus* malgaches. *Acta Botanica Gallica* 158(4): 453-472.
- Rafidison, V. M., Rakotoanadahy, B., Rakototomaro, J. F., Rafanomezantsoa, E., Rasabo, E., Rakotozafy, R., and Aumeeruddy-Thomas, Y. 2016. Pratiques et connaissances naturalistes des communautés Betsileo: lisière du corridor forestier Andringitra-Ranomafana, Madagascar. In *Indigenous and local knowledge of biodiversity and ecosystem services in Africa*, eds. M. Roué, N. Césard, Y. C. Adou Yao, and A. Oteng-Yeboah, pp. 96-107. Paris: UNESCO. http://climatefrontlines.org/sites/default/files/ipbes/IPBES_in_Africa_2015.pdf
- Rafidison, M. V., Rakouth, B., Carrière, S. M., Kjellberg, F., and Aumeeruddy-Thomas, Y. 2020. Local knowledge, practices and uses relating to isolated *Ficus* trees in Betsileo rural landscapes in Madagascar. Implications for biodiversity conservation. *Biodiversity Conservation* 29: 1027–1058.
- Rasplus, J.-Y., Harry, M., Perrin, H., Chassagnard, M. T., and Lachaise, D. 2003. Les *Ficus* (Moraceae) et l'entomofaune des figues (Hym. Agaonidae; Pteromalidae, Torymidae, Eurytomidae; Dipt. Drosophilidae; Col. Curculionidae) du Mont Nimba en Guinée. *Memoires du Muséum national d'Histoire naturelle* 190: 107-182.
- Rasplus, J.-Y., Rodriguez, L. J., Sauné, L., Peng, Y.-Q., Bain, A., et al. 2020. Exploring systematic biases, rooting methods and morphological evidence to unravel the evolutionary history of the genus *Ficus* (Moraceae). *bioRxiv*. doi: <https://doi.org/10.1101/2020.04.15.042259>.
- Razafiarivony, M. 2006. Compter et réfléchir avec l'arbre dans la poésie orale traditionnelle malgache. In *L'Arbre et l'Homme* (Ed.), Recueil de textes sur la conception de l'arbre dans la culture malgache. Regards sur la Science. Antananarivo, Institut des Civilisations.
- Razafindratsima, O. H. 2014. Seed dispersal by vertebrates in Madagascar's forests: Review and future directions. *Madagascar Conservation & Development* 9(2): 90-97.
- Razafindratsita, V., and Zack, S. 2009. Frugivory and facilitation of seed germination by the Velvet Asity, *Philepitta castanea* (Müller, 1776), in the rainforest understory of Ranomafana National Park, Madagascar. *Malagasy Nature* 2: 154-159.
- Samyn, J. M. 1999. *Plantes utiles des hautes terres de Madagascar*. Antananarivo: Graphoprint.

- Shanahan, M., So, S., Compton, S. G., and Corlett, R. T. 2001. Fig-eating by vertebrate frugivores: A global review. *Biological Reviews* 76: 529-572.
- Soler, C. C., Proffit, M., Bessière, J.-M., Hossaert-McKey, M., and Schatz, B. 2012. Evidence for intersexual chemical mimicry in a dioecious plant. *Ecology Letters* 15: 978-985.
- Soler, C., Schatz, B., Bessière, J.-M., and Hossaert-McKey, M. 2018. Geographic variation of fruit scents in a dispersion mutualism, the case of *Ficus lutea*. *Acta Oecologica* 90: 46-48.
- Souto-Vilarós, D., Proffit, M., Buatois, B., Rindos, M., Sisol, M., et al. 2018. Pollination along an elevational gradient mediated both by floral scent and pollinator compatibility in the fig and fig-wasp mutualism. *Journal of Ecology* 106: 2256-2273.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. In *Conservation biology*, ed. M. Soule, pp. 330-344. Sunderland, Massachusetts: Sinauer Associates.
- Turk, D. 1995. *A guide to trees of Ranomafana National Park and central eastern Madagascar*. Antananarivo: USAID.
- Vololona, J., and Goodman, S. M. 2019. Morphométrie des fruits et des graines de *Ficus* (Moraceae) de la forêt sèche de la Réserve Spéciale d'Ankarana, Madagascar. *Malagasy Nature* 13: 52-59.
- Wiebes, J. T. 1963. Taxonomy and host plant preference of Indo-Australian fig wasps of the genus *Ceratosolen* (Agaonidae). *Tijdschrift voor Entomologie* 106: 1-112.
- Zhang, Q., Onstein, R. E., Little, S. A., and Sauquet, H. 2019. Estimating divergence times and ancestral breeding systems in *Ficus* and Moraceae. *Annals of Botany* 123: 191-204.

Figures and Tables

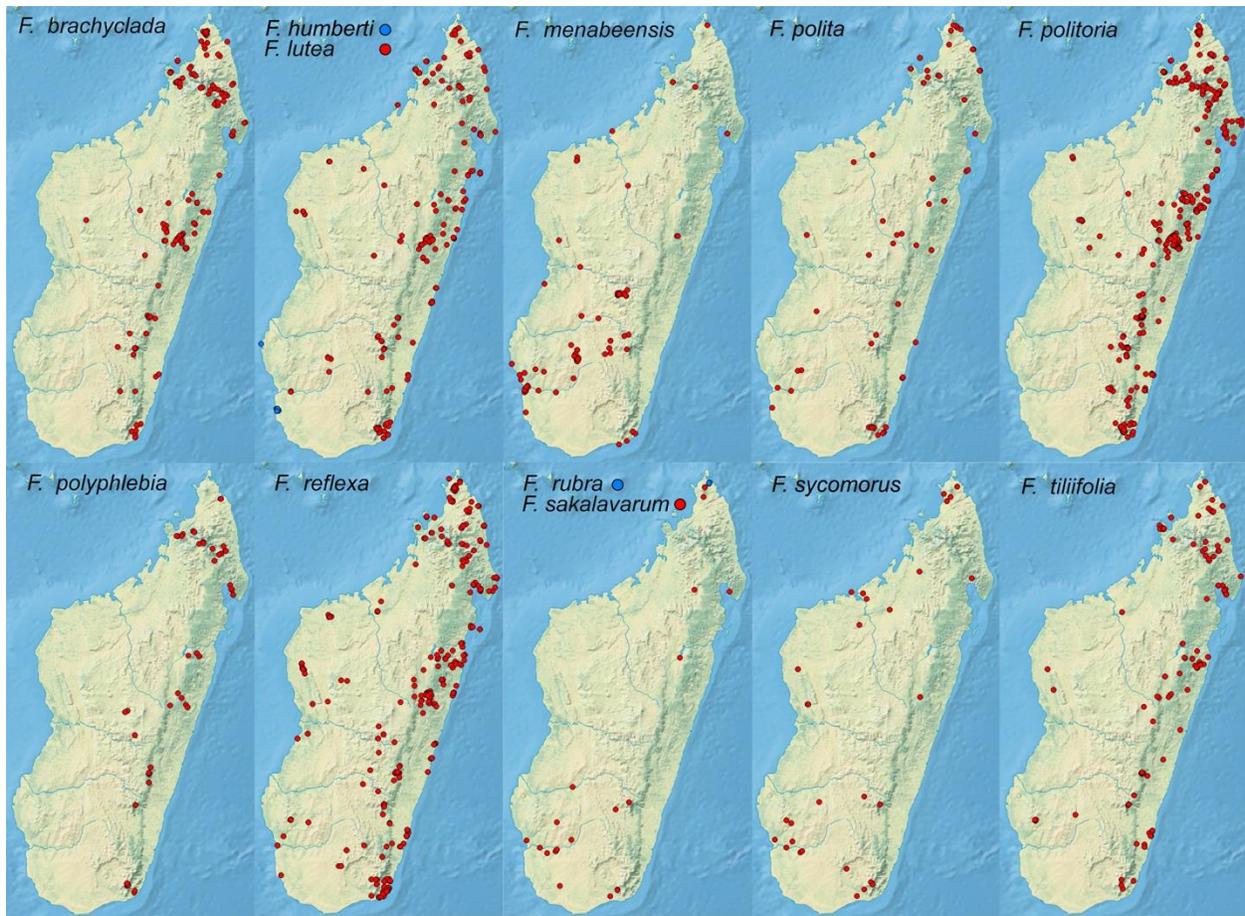


Figure 1. Distribution of some *Ficus* species in Madagascar. Occurrences were retrieved from our samples, the literature, and the GBIF database (GBIF.org, 2020). Identifications were previously verified and sometimes corrected.



Figure 2. Malagasy *Ficus*. **A)** *F. pachyclada*, **B)** *F. politoria* (photo by J.-Y. Rasplus), **C)** *F. trichoclada*, **D)** *F. polyphlebia*, **E)** *F. menabensis*, and **F)** *F. humberti*. Photos A, C-E by F. Kjellberg, B by J.-Y. Rasplus, and F by Dr. Bing Liu at Institute of Botany, Chinese Academy of Sciences.)



Figure 3. Different cultural aspects of *Ficus* on Madagascar. **A)** *F. lutea* at the Rova Ambohimanga, Antananarivo, a tree of the 12 wives of the Merina King Andrianamipoimerina; **B)** children collecting fruits *F. botryoides*, *Fompoha*, Fianarantsoa; **C)** *F. botryoides* in the Botanical Garden of Tsimbazaza, Antananarivo, with Martine Hossaert-McKey collecting samples; **D)** *F. tiliifolia*, local variety *voara bekobo*, literally “the *voara* with thick lips” due to the unusual protuberant aspect of the ostiole; **E)** Finn Kjellberg collecting samples of *F. reflexa* planted by large cuttings around a zebu corral; **F)** *F. reflexa* growing on a stele and Jean-Marie explaining the sacred nature of the stone and of the plant; and **G)** isolated tree of *F. lutea* in agricultural lands, Ambohimahamasina, near Ambalavao. Photo A-G, by Yildiz Aumeeruddy-Thomas.

Table 1. Ecological characteristics of Malagasy *Ficus* species. Classification generally follows Berg (1986) and Berg and Wiebes (1992). References: Perrier de la Bâthie (1952b), Berg (1986), Berg and Wiebes (1992), Compton (1992), Turk (1995), MBG (Tropicos database), MNHN (Catalog of Vascular Plants), Rafidison et al. (2011, 2020), C. Kerdelhué and J.-Y. Rasplus (unpublished data), many new observations by F. Kjellberg and V. Rafidison (unpublished data). Note: ‘Protected’ means seedlings and trees growing spontaneously are protected; ‘Planted’ always means ‘planted by cuttings’ in column ‘Distribution’ below (based on observations made only in central, eastern, and western provinces in Madagascar)

	<i>Ficus</i> (most frequently used synonym)	Mating system ^a	Life-form	Height up to (m) ^b	Mode of fig insertion ^c	Maximum Syconia diam. (cm) ^{b, d}	Habitat	Elevation ^b	Distribution ^e
Subgenus <i>Sycidium</i>	<i>F. pachyclada</i> Baker	d	Tree	25 (-35)	R	1.5 D	Forest, often along rivers, marshes and sea coast	50-1090 (- 1150)	M, Co
	<i>F. brachyclada</i> Baker	d	Shrub or treelet	8	C R	1 (-2) F	Understory, often in riparian forest (syntopic with <i>F. brachyclada</i>)	(0-) 300- 1600 (- 2000)	M
	<i>F. politoria</i> Lamarck	d	Shrub or treelet	8	C R	1 F	Understory, abundant in patches, often in riparian forest	0-1700 (2500- 2800)	M
Subgenus <i>Sycomorus</i>	<i>F. sycomorus</i> L.	m	Tree	15 (-30)	C	2.5 F	Woodlands, frequent near streams, and in secondary growth. Possibly planted in some places. ^f	(30-) 70- 150 (- 1250) ^f	M, Co, CA
	<i>F. sakalavarum</i> Baker	m	Tree			8 (-10) F	Riparian forest, locally abundant	Low elevation	M
	<i>F. tiliifolia</i> Baker	m	Tree	20 (-25)		1.5 - 5 F	Forest, sometimes planted	0-1700	M, Co
	<i>F. torrentium</i> H. Perrier	m	Tree	25	C R A	3 (-5) F	Medium altitude moist evergreen forest, along streams	600-1200 (-1424)	M
	<i>F. polyphlebia</i> Baker	m	Shrub or treelet	10	C R A	3 (-6) F	Rupicolous near or in flowing water	(0-) 20- 1200 (- 1315)	M
	<i>F. botryoides</i> Baker	m	Tree	25	C ^g	2 (-3.8) F	Riparian forest	0-1600	M
	<i>F. trichoclada</i> Baker	m	Tree	15	C R A	3 (-4) F	Riparian forest	100-1500	M
Subgenus <i>Pharmacosycea</i> section <i>Oreosycea</i>	<i>F. assimilis</i> Baker	m	Tree	25		1.5 D	Forest	0-1000	M
	<i>F. ampana</i> Berg	m	Shrub, treelet (or tree ?)	(25 ?)		8 D	Unknown	1000-1050	M

Subgenus <i>Urostigma</i> , section <i>Urostigma</i>	<i>F. madagascariensis</i> Berg	m	Shrub or tree			6 D	Dry deciduous forest and dry spiny thicket (but also present near Toamasina?)	0-50	M
Subgenus <i>Urostigma</i> , section <i>Conosycea</i>	<i>F. menabeensis</i> H. Perrier	m	Shrub or tree	4 (-20)	A	8 D <10 F	Grasslands, dunes, riparian forest, often rupicolous	0-1200 (- 1500)	M
	<i>F. humbertii</i> Berg	m	Shrub	2 (-5)	A	7 D	Unknown	0-80 (-100)	M
	<i>F. lutea</i> Vahl	m	Hemi-epiphytic tree	23	A	2.5 (-3.5) F	In forest, often riparian, marshes, and littoral forest and thicket.	0-1500	M, Co, Se, CA
	<i>F. trichopoda</i> Baker	m	Shrub or tree	10 (-20)		2 F	Wooded grasslands, in marshy places. Sometimes planted near villages	500-1100	M, CA
	<i>F. grevei</i> Baillon	m	Hemi-epiphytic tree	20 (-35)		1.7 D	Dry deciduous forest, often riparian	30-200	M
Subgenus <i>Urostigma</i> section <i>Galoglychia</i>	<i>F. rubra</i> Vahl	m	Hemi-epiphytic tree	8		0.6-1 D	Often rupicolous	(50-) 300- 650 (- 1000)	M, Me, Se, Al, Co
	<i>F. marmorata</i> Baker	m	Shrub or tree, possibly hemi- epiphytic	15		8 D	Forest, rupicolous	0-50 (-300)	M
	<i>F. bivalvata</i> H. Perrier	m	Tree	20 (-30)		2.5 x 1.2 D	Medium altitude moist evergreen forest	1171-1700	M
	<i>F. antandronarum</i> (H. Perrier) Berg	m	Shrub or tree	20		1.3 D	Moist evergreen and riparian forests	0-1600	M, another ssp. in Co
	<i>F. reflexa</i> Thunberg (= <i>F. pyrifolia</i>)	m	Hemi-epiphytic shrub or tree	10 (-30)	A	1.2 D	In various types of forest	0-1700	M, Me. Two other spp. in Se, Co, Al
	<i>F. polita</i> Vahl (= <i>F. megapoda</i>)	m	Hemi-epiphytic or secondarily terrestrial tree	15 (-40)		4 F	Moist evergreen and riparian forests	600-700	M, CA

^a m = monoecious, d = dioecious.

^b Extreme values are given in brackets.

^c C = cauliflorous, R = ramiflorous, A = axillary.

^d D = when dry, F = when fresh.

^e M: Madagascar; Co: Comoros; Se: Seychelles; Me: Mascarenes; Al: Aldabra; CA: continental Africa.

^f May apply both to *F. sycomorus* and *F. sakalavarum*.

^g Large masses of figs and decomposing organic matter, including rotted figs of previous crops (masses up to 80 cm diam.) for *F. botryoides*.

Table 2. Pollinating fig wasps (Agaoninae) associated with *Ficus* in Madagascar. References: Berg and Wiebes (1992), Compton (1992), Kerdelhué (1997), Kerdelhué et al. (1999), as well as unpublished recent samplings. Distribution: M: Madagascar; Co: Comoros; Se: Seychelles; Me: Mascarenes; CA: continental Africa.

<i>Ficus</i>	Agaoninae (pollinators)	Distribution
<i>F. ampama</i>	Unknown	?
<i>F. antandronarum</i>	New species of <i>Elisabethiella</i>	M
<i>F. assimilis</i>	Unknown	?
<i>F. bivalvata</i>	Unknown	?
<i>F. botryoides</i>	<i>C. blommersi</i>	M
<i>F. brachyclada</i>	<i>K. cowani</i>	M
<i>F. grevei</i>	New species of <i>Elisabethiella</i>	M
<i>F. humbertii</i>	New genus/species close to <i>Nigeriella</i>	M
<i>F. lutea</i>	<i>Allotriozone heterandromorphum</i> ^c	M, Co, CA
<i>F. madagascariensis</i>	New species of <i>Platyscapa</i>	M
<i>F. marmorata</i>	Unknown	?
<i>F. menabeensis</i>	<i>Maniella bergi</i> ^b	M
<i>F. pachyclada</i>	New species of <i>Kradibia</i>	M
<i>F. polita</i>	<i>Courtella bekiliensis bekiliensis</i>	M, other ssp. in CA
<i>F. politoria</i>	<i>K. saundersi</i> and new species	M
<i>F. polyphlebia</i>	<i>C. longimucro</i>	M
<i>F. reflexa</i>	<i>E. reflexa</i>	M, Me
<i>F. rubra</i>	<i>N. avicola</i>	Me
<i>F. sakalavarum</i>	<i>C. namorokensis</i>	M
<i>F. sycomorus</i>	<i>Ceratosolen arabicus</i> (pollinator)	M, Co, CA
	<i>C. galili</i> (non-pollinating)	M, Co, CA
<i>F. tiliifolia</i>	<i>C. stupefactus</i>	M ^a
<i>F. torrentium</i>	Unknown	?
<i>F. trichoclada</i>	<i>C. blommersi</i>	M
<i>F. trichopoda</i>	<i>Elisabethiella bergi breviceps</i>	M, other ssp. in CA

^a Not known from *F. cf. tiliifolia* on Grand Comore (Compton 1992), ^b this species was previously classified within *Platyscapa*, however it belongs to another genus, ^c this species is a species complex.

Table 3. Overall fig feeding time (summed for each study) for five lemur populations. Consumption of all *Ficus* species is combined.

Site	Lemur species	% Feeding ^a	% Fruit ^b	Most commonly used species
Veveombe	<i>Eulemur albocollaris</i>	7.7%	11.6%	<i>F. rubra</i>
Andringitra	<i>E. albocollaris/E. rufus</i> hybrid	35.3%	39.0%	<i>F. lutea</i>
Ranomafana	<i>E. rufus</i>	10.8%	13.7%	<i>F. rubra</i>
Ranomafana	<i>E. rubriventer</i>	12.5%	13.7%	<i>F. rubra</i>
Ranomafana	<i>Hapalemur griseus</i>	3.1%	23.1%	<i>F. reflexa</i>

^a Time spent feeding on figs compared to overall feeding time for each lemur population.

^b Time spent feeding on figs compared to total time feeding of fruits for each lemur population.

Table 4. Main frugivorous vertebrates of Madagascar and fig species they consume as reported in the literature. Species marked with an asterisk (*) are introduced to Madagascar.

	<i>F. assimilis</i>	<i>F. botryoides</i>	<i>F. brachyclada</i>	<i>F. grevei</i>	<i>F. humberti</i>	<i>F. lutea</i>	<i>F. marmorata</i>	<i>F. madagascariensis</i>	<i>F. menabeensis</i>	<i>F. pachyclada</i>	<i>F. polita</i>	<i>F. poliphlebia</i>	<i>F. reflexa</i>	<i>F. rubra</i>	<i>F. sakalavarium</i>	<i>F. sycamoros</i>	<i>F. tiliifolia</i>	<i>F. trichopoda</i>	<i>Ficus sp.</i>	N
Columbidae	<i>Alectroenas madagascariensis</i>	X						X						X						3
Columbidae	<i>Nesoenas picturata</i>																X			1
Columbidae	<i>Treron australis</i>													X		X			X	3
Eurylaimidae	<i>Philepitta castanea</i>																		X	1
Psittacidae	<i>Coracopsis nigra</i>													X		X				2
Pycnonotidae	<i>Hypsipetes madagascariensis</i>	X															X		X	3
Sturnidae	<i>Hartlaubius auratus</i>																X		X	2
Zosteropidae	<i>Zosterops maderaspatanus</i>																X		X	2
Cheirogaleidae	<i>Cheirogaleus major</i>										X									1
Cheirogaleidae	<i>Cheirogaleus medius</i>							X												1
Cheirogaleidae	<i>Cheirogaleus sp.</i>	X			X		X							X						4
Cheirogaleidae	<i>Microcebus rufus</i>													X					X	2
Indriidae	<i>Propithecus coronatus</i>													X						1
Indriidae	<i>Propithecus diamema</i>																X			1
Indriidae	<i>Propithecus edwardsi</i>																		X	1
Indriidae	<i>Propithecus verreauxi</i>						X								X				X	3
Lemuridae	<i>Eulemur cinereiceps</i>				X					X			X		X	X			X	5
Lemuridae	<i>Eulemur collaris</i>	X			X									X					X	4
Lemuridae	<i>Eulemur flavifrons</i>																X		X	2
Lemuridae	<i>Eulemur fulvus</i>							X	X				X	X	X	X				5
Lemuridae	<i>Eulemur macaco</i>	X			X				X	X			X	X	X	X				7
Lemuridae	<i>Eulemur mongoz</i>									X						X				2
Lemuridae	<i>Eulemur rubriventer</i>		X	X				X	X	X	X	X	X			X			X	8
Lemuridae	<i>Eulemur rufifrons</i>		X	X	X					X	X	X					X			5
Lemuridae	<i>Eulemur rufus</i>		X	X				X	X	X	X	X					X			6
Lemuridae	<i>Eulemur sanfordi</i>		X	X			X			X		X								4
Lemuridae	<i>Hapalemur griseus</i>		X	X	X		X	X	X	X		X								5
Lemuridae	<i>Lemur catta</i>			X	X	X		X	X	X					X					7
Lemuridae	<i>Varecia rubra</i>																		X	1
Lemuridae	<i>Varecia variegata</i>	X	X		X					X	X	X				X			X	8
Lepilemuridae	<i>Lepilemur sahamalazensis</i>																X			1
Muridae	* <i>Rattus rattus</i>	X						X												2
Nesomyidae	<i>Eliurus webbi/ellermani</i>	X						X						X						3
Pteropodidae	<i>Eidolon dupreanum</i>		X	X	X				X	X	X	X	X	X				X		9
Pteropodidae	<i>Pteropus rufus</i>	X	X	X	X	X	X	X	X	X		X								10
Pteropodidae	<i>Rousettus madagascariensis</i>		X		X					X			X	X						5
		N	9	7	4	3	1	2	7	6	5	12	1	6	16	3	5	15	1	14

Table 5. Local names of Malagasy *Ficus*. References: a - MBG (Tropicos database); b - Turk (1995); c - unpublished observations of authors; d - MNHN (Catalog of Vascular Plants); e - Berg (1986); f - Boiteau and Allorge (1998), Samyn (1999); g - Decary (1946); h - Beaujard (1988); i - Goodman et al. (1997); j - Perrier de la Bâthie (1952b); k - Berg and van Heusden (1985), l - Rafidison et al. (2016, 2020), and m - Aumeeruddy-Thomas et al. (2018). For locations, and when possible, the province for each site is given before the colon. The names of the ethnic group or original language are in italics. The local name from other Indian Ocean islands, when the term is roughly similar to that in Malagasy, is given into square brackets. PN : Parc National, RNI : Réserve Naturelle Intégrale, RS : Réserve Spéciale, SF : Station Forestière.

<i>Ficus</i>	Local names	Locations or ethnic groups	References
<i>F. ampana</i>	<i>ampana</i>	Toamasina: Sandrangato	<i>d, e</i>
<i>F. antandronarum</i>	<i>nonoka vaventiravina</i>	Fianarantsoa: PN de Ranomafana	<i>a</i>
	<i>[mandressi angabou on Mayotte]</i>		<i>d</i>
<i>F. assimilis</i>	<i>karay</i>	?	<i>a</i>
	<i>kivozy</i>	Toliara: Manamby	<i>a</i>
	<i>ampany, arostro, fihamy, tsitindrika</i>	?	<i>j</i>
<i>F. botryoides</i>	<i>afompo</i>	Antsiranana: PN de la Montagne d'Ambre	<i>a</i>
	<i>voara rano</i>	Fianarantsoa: PN de Ranomafana	<i>a, b, i</i>
	<i>voara ranoambohitra</i>	Fianarantsoa: PN de Ranomafana	<i>b, c</i>
	<i>voara fopohondahy</i>	Fianarantsoa: PN de Ranomafana	<i>b</i>
	<i>fompoha</i>	Fianarantsoa: Betsileo, Ambohimahamasina, Ambendrana	<i>l</i>
<i>F. brachyclada</i>	<i>ampaly</i>	Antananarivo: SF de Mandraka,	<i>a</i>
	<i>ambaly?</i>	Antsiranana: RS de Manongarivo	<i>a</i>
	<i>ampalifotsy</i>	Antsiranana: PN de Marojejy	<i>a</i>
	<i>mamoakely</i>	Antsiranana: Ambalavoaniho	<i>a</i>
	<i>fotsiditila</i>	Toamasina: Soanierana-Ivongo	<i>a</i>
	<i>famakilela [vaventiravina]</i>	Fianarantsoa: PN de Ranomafana	<i>a, c, i</i>
<i>F. grevei</i>	<i>mandresy</i>	Antsiranana: RS d'Analamerana	<i>a</i>
	<i>fihamy, amota</i>	Sakalava	<i>j</i>
	<i>fiambena</i>	Toliara: Miary	<i>a</i>
<i>F. lutea</i>	<i>nonobe</i>	Toliara: PN d'Andohahela	<i>a</i>
	<i>aviavi?</i>	Toliara: Andranolahy	<i>a</i>

	<i>aviavi(n)dahy</i>	Bestileo	<i>f, j</i>
	<i>aviavindrano</i>	Sakalava	<i>j</i>
	<i>nohondahy</i>	Masikoro	<i>j</i>
	<i>nonoka vaventravina</i>	Fianarantsoa: PN de Ranomafana	<i>b</i>
	<i>amontana (or amotana)</i>	Antsiranana: PN de la Montagne d'Ambre Toamasina?: Manakana Fianarantsoa: PN de Ranomafana Toamasina: PN de Masoala Antanala, Merina	<i>a, b, f, g, i, j, l</i>
	<i>amonta</i>	Antaisaka Fianarantsoa: Betsileo, Ambendrana, Ambohimahamasina	<i>f, j</i> <i>l</i>
	<i>amontana</i>	Antananarivo, Merina, all "rovas" surrounding Antananarivo (e.g., Ambohimanga)	<i>m</i>
	<i>amontambavy</i>	Merina	<i>f</i>
	<i>amontandahy</i>	Merina	<i>f</i>
	'grand figuier des Rovas'	French	<i>f</i>
<i>F. madagascariensis</i>	<i>hampana</i>	Toamasina: Soanierana-Ivongo	<i>d</i>
<i>F. marmorata</i>	<i>lazo</i>	Androy	<i>j</i>
<i>F. menabeensis</i>	<i>hazotsikirova</i>	Toliara: Ankoratsaka	<i>a</i>
<i>F. pachyclada</i>	<i>ampana</i>	Toamasina: Antanandava, Androna	<i>a, j</i>
	<i>apana</i>	Fianarantsoa: PN de Ranomafana	<i>a, i, c</i>
	<i>ampaly</i>	Fianarantsoa: Betsileo,	
	<i>voara</i>	Ambendrana, Ambohimahamasina	<i>j</i>
	<i>voaramongy</i>	Sakalava	<i>j</i>
	<i>ampalibe</i>	Sihanaka	<i>j</i>
	<i>kivozy</i>	Betsimisaraka, Betsileo, Ambendrana, Sahabe	<i>j, l</i>
	<i>kivozo</i>	Fianarantsoa: SF d'Andrambovato	<i>a</i>
<i>F. polita</i>	<i>Aviavy</i>	Sakalava	<i>g, j</i>
	<i>aviavindrano</i>	Sakalava	<i>j</i>
	<i>mandresy</i>	Antanala, Antaimoro, Masikoro?, Antananarivo	<i>h, j, m</i>
	<i>tsaramady</i>	Fianarantsoa: Ambendrana, Ambohimahamasina	<i>l</i>

<i>F. politoria</i>	<i>ambora</i>	Antsiranana: PN de la Montagne d'Ambre	<i>a</i>	
	<i>ampalifotsy</i>	Antsiranana: PN de Marojejy; Toamasina: SF de Tampolo	<i>a</i>	
	<i>marandravy</i>	Toliara: PN d'Andohahela	<i>a</i>	
	<i>ampaly</i>	Toliara: PN d'Andohahela, Fianarantsoa, Betsileo, Ambendrana, Ambohimahamasina Toamasina: Analamay	<i>a, f, l</i>	
	<i>ampaliala</i>	Merina	<i>f</i>	
	<i>ramy rindritra</i>	Toamasina: RS d'Analamazaotra	<i>a</i>	
	<i>ramiraningitra</i>	Tsimihety	<i>f</i>	
	<i>andriambololonkazo</i>	?	<i>f</i>	
	<i>kivozy</i>	Fianarantsoa: Merina, Betsileo Ambendrana, Ambohimahamasina	<i>f, l</i>	
	<i>kivozo</i>	Fianarantsoa: PN de Ranomafana	<i>c</i>	
	<i>horondry</i>	Toamasina: RNI de Betampona	<i>a</i>	
	<i>famakilela</i> (<i>madinidravina</i>)	Fianarantsoa: PN de Ranomafana, SF d'Ampamaherana	<i>a, c, i</i>	
	<i>F. politoria</i> and/or <i>F. brachyclada</i> (under " <i>F. soroceoides</i> ")	<i>ampaly</i>	Fianarantsoa: Betsileo, Ambendrana, Ambohimahamasina	<i>l</i>
		<i>avoza</i>		<i>j</i>
[<i>affouche</i> is used for several fig species in the Mascarenes]			<i>k</i>	
<i>kivozy</i>		Fianarantsoa: Betsileo, Ambendrana, Ambohimahamasina	<i>l</i>	
<i>F. polyphlebia</i>	<i>voara</i>	Toamasina: Antalavia	<i>a</i>	
	<i>voara rano</i>	Antsiranana: PN de Marojejy Fianarantsoa: PN de Ranomafana	<i>a</i> <i>c</i>	
	<i>fopohonona</i>	Fianarantsoa: PN de Ranomafana	<i>a</i>	
	<i>adabo</i>	Antsiranana: Mandrizavona	<i>a</i>	
	<i>sandrohy</i>	Toliara: PN d'Andohahela	<i>a</i>	
	<i>F. reflexa</i>	<i>nonoka</i>	Antsiranana: Ambato Fianarantsoa: Betsileo, Ambendrana, Ambohimahamasina Antananarivo: Merina	<i>a, g, c</i> <i>l</i> <i>m</i>

	<i>nonoka madinidravina</i>	Fianarantsoa: PN de Ranomafana	<i>a</i>
<i>F. rubra</i>	<i>nonoka</i>	?	<i>f</i>
	<i>nonoka siay</i>	Fianarantsoa: PN de Ranomafana	<i>b</i>
	<i>nonoka madinidravina</i>	Fianarantsoa: PN de Ranomafana	<i>b</i>
<i>F. sycomorus</i> <i>and / or</i>	<i>aviary</i>	Fianarantsoa: PN d'Andringitra	<i>a</i>
	<i>hara</i>	Toliara: PN d'Andohahela	<i>a</i>
<i>F. sakalavarum</i>	<i>voara</i>	Fianarantsoa: PN de Ranomafana	<i>i</i>
	<i>adabo</i> [<i>adabou on Mayotte</i>]	Toliara: Analafaly, Miary	<i>a, g, j</i> <i>d</i>
<i>F. tiliifolia</i>	<i>voara</i>	Antsiranana: PN de Marojejy, RNI de Lokobe Fianarantsoa: PN de Ranomafana, Ranomena, Andranobetokana	<i>a, g, i</i>
	<i>voara bekoube</i>	Fianarantsoa Ambendrana	<i>l</i>
	<i>voara malefaka</i>	Toamasina: RS de Nosy Mangabe, Masoala Peninsula	
	<i>voara tenany</i>	Fianarantsoa: PN de Ranomafana	<i>a, b, c</i>
	<i>voarabe</i>	Toamasina: Antalavia	<i>a</i>
	<i>voara mamoohahezana</i> (<i>or mamoatahezana?</i>)	Fianarantsoa: PN de Ranomafana	<i>a, b</i>
	<i>ara</i>	Fianarantsoa: Ambohimahamasina	<i>a</i>
	<i>aravola</i>	Fianarantsoa: location?	<i>a</i>
	<i>voarandambo</i>	Fianarantsoa: PN de Ranomafana	<i>a</i>
	<i>apana?</i>	Fianarantsoa: PN de Ranomafana	<i>c</i>
	<i>F. torrentium</i>	<i>voara</i>	Antsiranana: PN de Marojejy, RS de Manongarivo
<i>ramiringitra</i>		Toamasina: Bezanozano	<i>j</i>
<i>adabo</i>		Antsiranana: RS d'Anjanaharibe-Sud	<i>a</i>
<i>F. trichoclada</i>	<i>fopohana?</i>	Fianarantsoa: Ambatofinandrahana	<i>a</i>
	<i>fopohona?</i>	Fianarantsoa: Ambatofinandrahana	<i>d</i>
	<i>fompohana?</i>	Fianarantsoa: SF d'Ampamaherana	<i>a</i>
	<i>fompoha</i>	Fianarantsoa: Betsileo, Ambendrana,	<i>a</i>
	<i>fopoha?</i>	Ambohimahamasina Toliara: PN d'Andohahela	<i>l</i>
	<i>sandrohy</i>	Toliara: PN d'Andohahela	<i>a</i>

<i>F. trichopoda</i>	<i>zavy</i>	Betsimisaraka, Sakalava	<i>j</i>
	<i>aviavindrano</i>	Merina, Betsileo	<i>J</i>
	<i>aviavy</i>	Fianarantsoa: Betsileo, Ambendrana,	<i>i</i>
	<i>nonoka</i>	Ambohimahamasina Fianarantsoa: PN de Ranomafana	
