Wetenschappelijke literatuur over de vijg

Deze lijst is bedoeld om docenten die de leeractiviteit *Plant in de kamer* (onderbouw- en bovenbouwversie) willen uitvoeren toegang te verschaffen tot achtergrondinformatie. Wellicht dat een enkel artikel ook bruikbaar is voor leerlingen in bovenbouw vwo.

De lijst bevat vooral veel-geciteerde onderzoeksartikelen (de aantal keren dat ze geciteerd zijn *Times cited heb ik* vastgesteld in dec 2018 via Web of Science). Maar ook enkele weinig-geciteerde artikelen zijn opgenomen: sommige heel recente en andere interessante oudere. Ook zijn enkele review-artikelen opgenomen. Ik schat in dat hiermee de hoofdlijnen van het (ecologisch) onderzoek naar de Ficus in beeld zijn.

Een aantal van de opgenomen artikelen zijn vrij toegankelijk via bijvoorbeeld Google Scholar. In het geval het niet lukt om een gewenst artikel te vinden, neem gerust contact op met Marcel Kamp: m.kamp@docentenacademie.ru.nl. Van Borges e.a. (2018) heb ik via een vertaalmachine een Nederlandse versie gemaakt, die helemaal achteraan staat. Dit artikel biedt een snelle ingang in het onderwerp. Het Nederlands is niet van grote schoonheid!)

Onderwerpen die aan bod komen zijn:

- mutualisme tussen vijg en vijgewesp; en tussen vijgenwesp en nematoden
- parasitisme van vijg door *non-pollinating fig wasp NPFW: cospeciation*
- het gebrek aan succes van bedrog (cheating) in mutualisme
- de vijg als voedselbron voor mensen, de vijgenboom als cultureel en religieus centrum
- de plaats van de vijg in het voedselweb in de natuur, speciaal in relatie tot vleermuizen en zaadverspreiding
- het Allee-effect: Bij te kleine populatie kunnen voortplantingspartners elkaar niet vinden wat kan leiden tot uitsterven.
- geneeskrachtige werking van de latex en schors van luchtwortels oa tegen kanker: het perspectief van ethnopharmacology
- uitsterven van Ficussoorten vanwege droogte door El Nino
- verschillen t.a.v. verspreidingsstrategie tussen eenhuizige en tweehuizige vijgensoorten
- de functie van latex bij bescherming tegen virusziekte
- latex en mutualisme vijg-vijgenwesp
- lokken met geuren door de vijg van vijgenwespen
- functie van kleuren-zien van primaten bij zoeken van slecht onderscheidbare vruchten o.a. vijgen
- foerageergedrag van binturongs die vooral vijgen eten
- luchtreiniging binnenshuis door Ficus
- bescherming in plaats van jacht op fruit-etende vleermuizen
- het dieet van chimpansees en gorilla’s
- endemische vijgensoorten en hun bedreiging

Anstett, M. C., HossaertMcKey, M., & Kjellberg, F. (1997). Figs and fig pollinators: Evolutionary conflicts in a coevolved mutualism. *Trends in Ecology & Evolution, 12*(3), 94-99. Times cited 112.
Figs and fig wasps form one of the best known examples of species-specific mutualism and coevolution. Recent experiments and observations have led to a better understanding of the evolutionary processes involved in the origin and maintenance of species interactions. The observed fine-tuned traits involve not only coevolution but also selection acting on only one of the partners. Furthermore, some of the 'fine-tuned traits' appear to be preadaptations - traits that existed before the mutualism was established.

Borges, R. M., Compton, S. G., & Kjellberg, F. (2018). Fifty years later, figs and their associated communities. *Acta Oecologica-International Journal of Ecology, 90*, 1-3.
Dit korte goed toegankelijke artikel bevat een review van 50 jaar vijgenonderzoek en een blik op de toekomst. Onderwerpen: 1. Inleiding ; 2. Vijgdiversificatie; 3. Vertebraten en vijgen; 4. Vijgenwespen; 5. Geleedpotigen, andere ongewervelde dieren en vijgenbescherming; 6. Concluderende lijnen

Chen, J., Su, Y. C., Chen, G. Q., & Wang, W. D. (1999). Ethnobotanical studies on wild edible fruits in southern Yunnan: Folk names; Nutritional value and uses. *Economic Botany, 53*(1), 2-14. Times cited: 111.
The climate of Yunnan province ranges from humid tropical to subtropical. Wild edible fruits form an important dietary component of the ethnic groups in the south of Yunnan Province, which is famous for its rich diversity in both biological resources and ethnic culture, and A list of 123 different fruits is presented, which includes the folk names used by Dai, Hani, Bulang, Jinuo, and others; distribution; uses and the nutritional contents of 52 different species (edible part percentage, moisture, total sugar, titratable acid, vitamin C, crude fat, crude fiber; starch, and soluble tannin).

Chen, S. F., Shen, T. J., Lee, H. C., Wu, H. W., Zeng, W. T., Lu, D. J., et al. (2017). Preference of an insular flying fox for seed figs enhances seed dispersal of a dioecious species. *Biotropica, 49*(4), 511-520. Times cited: 1.
Interactions among multiple species form complex networks of interdependences and are considered primary factors in the generation and maintenance of biodiversity. Pteropodid bats are keystone species that provide important ecosystem services of pollination and seed dispersal in the tropics and subtropics. In this study, we investigated the utilization and preference of food resources by the insular frugivorous flying fox Pteropus dasymallus. We found that fig species constituted the major portion of the diet of the flying fox (94.6%). When foraging, the flying fox preferred seed figs from female trees over gall figs from male trees in functionally dioecious fig species. Germination experiments showed a significantly higher percentage of germination for fig seeds in feces than those from pellets and ripe figs (feces: 80.2%, pellets: 23.4%, ripe figs: 32.9%). Considering the active selection of seed figs and avoidance of gall figs by foraging flying foxes, we suggest that the abundance of seed figs accurately represents food availability for dioecy. This preference for seed figs or viable seeds can effectively promote the survival of pollinating wasps and might reinforce the evolution of dioecism in figs. In addition, the effects of gut passage on seed germination, in combination with the capacity of flying foxes to travel long distances, may substantially contribute to the efficiency of flying foxes as seed dispersers.

Chun, S. C., Yoo, M. H., Moon, Y. S., Shin, M. H., Son, K. C., Chung, I. M., et al. (2010). Effect of Bacterial Population from Rhizosphere of Various Foliage Plants on Removal of Indoor Volatile Organic Compounds. *Korean Journal of Horticultural Science & Technology, 28*(3), 476-483. Times cited: 10.
Total bacterial populations were cultured from the Hydroball cultivation media in the rhizospheres of 9 different plants including Hedera helix L. and Dracaena deremensis

cv. Warneckii Compacta, etc. These cultured bacterial populations were studied to test if the bacterial populations in the plant growing pots may play a role on removal of volatile organic compounds (VOCs) such as benzene and toluene in the air. To meet this objective, first, we tested the possibility of removal of VOCs by the cultured total bacteria alone. The residual rates of benzene by the inoculation of total bacterial populations from the different plant growth media were significantly different, ranging from 0.741-1.000 of Spathiphyllum wallisii 'Regal', Pachira aquatica, Ficus elastica, Diejfenbachia sp. 'Marrianne' Hort., Chamaedorea elegans, compared to the control with residual rate of 0.596 (LSD, P=0.05). This trend was also similar with toluene, depending on different plants. Based on these results, we inoculated the bacterial population cultured from P. aquatica into the plant-growing pots of P. aquatica, F. elastica, and S. podophyllum inside the chamber followed by the VOCs injection. The inoculated bacteria had significant effect on the removal of benzene and toluene, compared to the removal efficacy by the plants without inoculation, indicating that microbes in the rhizosphere could play a significant role on the removal of VOCs along with plants.

Compton, S. G., Wiebes, J. T., & Berg, C. C. (1996). The biology of fig trees and their associated animals. *Journal of Biogeography, 23*(4), 405-407. Times cited: 20.
Kort review met Nederlandse expert Wiebes. Nog steeds interessante samenvattting.

Cook, J. M., & Segar, S. T. (2010). Speciation in fig wasps. *Ecological Entomology, 35*, 54-66. Times cited: 60.
A single fig species has one to four pollinator species and also hosts up to 30 non-pollinating wasp species. Most wasps show a high degree of host-plant specificity and are known from only a single fig species. However, in some cases wasps may be shared across closely related fig species. 3. There is impressive morphological co-evolution between figs and fig wasps and this, combined with a high degree of partner specificity, led to the expectation that figs and pollinators have cospeciated extensively. Comparison of deep phylogenies supports long-term codivergence of figs and pollinators, but also suggests that some host shifts have occurred. 4. Phylogenies of more closely related species do not match perfectly and may even be incongruent, suggesting significant roles for processes other than strict cospeciation. Combined with recent evidence on host specificity patterns, this suggests that pollinator wasps may often speciate by host shifts between closely related figs, or by duplication (the wasp speciates but the fig doesn't). The frequencies and biological details of these different modes of speciation invite further study. 5. Far less is known about speciation in non-pollinating fig wasps. Some lineages have probably co-evolved with figs and pollinators for most of the evolutionary history of the symbiosis, while others appear to be more recent colonisers. Many species appear to be highly host-plant specific, but those that lay eggs through the fig wall without entering the syconium (the majority of species) may be subject to fewer constraints on host shifting than pollinators. There is evidence for substantial host shifting in at least one genus, but also evidence for ecological speciation on the same host plant by niche shifts in other cases. 6. Finally, recent work has begun to address the issue of 'community phylogeny' and provided evidence for long-term co-divergence of multiple pollinating and non-pollinating wasp lineages with their host figs.

Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution, 14*(10), 405-410. Times cited: 896.
The Allee effect describes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction. The importance of this dynamic process in ecology has been under-appreciated and recent evidence now suggests that it might have an impact on the population dynamics of many plant and animal species. Studies of the causal mechanisms generating Allee effects in small populations could provide a key to understanding their dynamics.

Dufay, M., & Anstett, M. C. (2003). Conflicts between plants and pollinators that reproduce within inflorescences: evolutionary variations on a theme. *Oikos, 100*(1), 3-14. Times cited: 88.

The high diversity of mutualisms has probably limited the development of a general theory about their evolution and their stability. Here we review conflicts of interests occurring in the 13 known nursery pollination systems, where pollinators reproduce within the inflorescence they pollinate. We found three main conflicts of interest between mutualists that correspond to the following evolutionary questions: 1) Why do plants not kill their pollinators' larvae? 2) Why do pollinators visit deceptive flowers? and 3) Why do pollinators pollinate? We show that the reproductive system of the plant is strongly correlated not only with the set of conflicts of interests that actually occur but also with the proximal resolution of these conflicts. In many cases the evolutionary stability of nursery pollination mutualisms relies on the avoidance of intra-specific competition among pollinator larvae. This stabilizing factor could perhaps also explain the absence of overexploitation in other mutualisms.

el-Din, S. H. S., El-Lakkany, N. M., Mohamed, M. A., Hamed, M. M., Sterner, O., & Botros, S. S. (2014). Potential effect of the medicinal plants Calotropis procera, Ficus elastica and Zingiber officinale against Schistosoma mansoni in mice. *Pharmaceutical Biology, 52*(2), 144-150. Times cited 6.

Context: Calotropis procera (Ait.) R. Br. (Asclepiadaceae), Ficus elastica Roxb. (Moraceae) and Zingiber officinale Roscoe (Zingiberaceae) have been traditionally used to treat many diseases. Objective: The antischistosomal activity of these plant extracts was evaluated against Schistosoma mansoni. Materials and methods: Male mice exposed to 80 +/- 10 cercariae per mouse were divided into two batches. The first was divided into five groups: (I) infected untreated, while groups from (II-V) were treated orally (500 mg/kg for three consecutive days) by aqueous stem latex and flowers of C. procera, latex of F. elastica and ether extract of Z. officinale, respectively. The second batch was divided into four comparable groups (except Z. officinale-treated group) similarly treated as the first batch in addition to the antacid ranitidine (30 mg/kg) 1 h before extract administration. Safety, worm recovery, tissues egg load and oogram pattern were assessed. Results: Calotropis procera latex and flower extracts are toxic (50-70% mortality) even in a small dose (250 mg/kg) before washing off their toxic rubber. Zingiber officinale extract insignificantly decrease (7.26%) S. mansoni worms. When toxic rubber was washed off and ranitidine was used, C. procera (stem latex and flowers) and F. elastica extracts revealed significant S. mansoni worm reductions by 45.31, 53.7 and 16.71%, respectively. Moreover, C. procera extracts produced significant reductions in tissue egg load (similar to 34-38.5%) and positively affected oogram pattern. Conclusion: The present study may be useful to supplement information with regard to C. procera and F. elastica antischistosomal activity and provide a basis for further experimental trials.

Farache, F. H. A., Cruaud, A., Rasplus, J. Y., Cerezini, M. T., Rattis, L., Kjellberg, F., et al. (2018). Insights into the structure of plant-insect communities: Specialism and generalism in a regional set of non-pollinating fig wasp communities. *Acta Oecologica-International Journal of Ecology, 90*, 49-59. Times cited: 2.

Insects show a multitude of symbiotic interactions that may vary in degree of specialization and structure. Gallinducing insects and their parasitoids are thought to be relatively specialized organisms, but despite their ecological importance, the organization and structure of the interactions they establish with their hosts has seldom been investigated in tropical communities. Non-pollinating fig wasps (NPFW) are particularly interesting organisms for the study of ecological networks because most species strictly develop their offspring within fig inflorescences, and show a multitude of life history strategies. They can be gall-makers, cleptoparasites or parasitoids of pollinating or of other non-pollinating fig wasps. Here we analysed a

set of non-pollinating fig wasp communities associated with six species of Ficus section Americanae over a wide area. This allowed us to investigate patterns of specialization in a diverse community composed of monophagous and polyphagous species. We observed that most NPFW species were cleptoparasites and parasitoids, colonizing figs several days after oviposition by pollinators. Most species that occurred in more than one host were much more abundant in a single preferential host, suggesting specialization. The food web established between wasps and figs shows structural properties that are typical of specific antagonistic relationships, especially of endophagous insect networks. Two species that occurred in all available hosts were highly abundant in the network, suggesting that in some cases generalized species can be more competitive than strict specialists. The Neotropical and, to a lesser extent, Afrotropical NPFW communities seem to be more generalized than other NPFW communities. However, evidence of host sharing in the Old World is quite limited, since most studies have focused on particular taxonomic groups (genera) of wasps instead of sampling the whole NPFW community. Moreover, the lack of quantitative information in previous studies prevents us from detecting patterns of host preferences in polyphagous species.

Galindo-Gonzalez, J., Guevara, S., & Sosa, V. J. (2000). Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology, 14*(6), 1693-1703. Times cited: 186.

Bats are abundant and effective seed dispersers inside the forest, but what happens when a forest is fragmented and transformed into pasture? The landscape at Los Tuxtlas, Mexico, originally rainforest, is greatly fragmented and covered with pastures. We analyzed the seed rains produced by frugivorous bats and birds under isolated trees in pastures in the fragmented landscape and the contribution of this process to vegetational recovery. We surveyed bats and obtained fecal samples under isolated trees in pastures. We also collected seed rain below the canopy of 10 isolated Ficus trees, separating nocturnally dispersed seeds from diurnally dispersed seeds. We caught 652 bats of 20 species; 83% of captures were frugivores. The most abundant species were Sturnira lilium (48%), Artibeus jamaicensis (18%), Carollia perspicillata (12%), and Dermanura tolteca (11%). Fecal samples contained seeds of 19 species in several families: Piperaceae (50%), Moraceae (25%), Solanacea (12%), Cecropiaceae (10%), and others (3%). Sturnira lilium was the most important disperser bat in pastures. Seed rain was dominated by zoochorous species (89%). We found seed diversity between day and night seed captures to be comparable, but we found a significant interaction of disperser type (bird or bat) with season. Seven plant species accounted for 79% of the seed rain: Piper auritum (23%), Ficus (hemiepiphytic-strangler tree) spp. (17%), Cecropia obtusifolia (10%), P. amalago (10%), Ficus (free-standing tree) spp. (8%), P. yzabalanum (6%), and Solanum rudepanum (5%). Bats and birds are important seed dispersers in pastures because they disperse seeds of pioneer and primary species (trees, shrubs, herbs, and epiphytes), connect forest fragments, and maintain plant diversity. Consequently, they might contribute to the recovery of woody vegetation in disturbed areas in tropical humid forests.

Harrison, R. D. (2000). Repercussions of El Nino: drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society B-Biological Sciences, 267*(1446), 911-915. Times cited 103.

Figs (Ficus spp.) and their species-specific pollinators, the fig wasps (Agaonidae), have coevolved one of the most intricate interactions found in nature, in which the fig wasps, in return for pollination services, raise their offspring in the fig inflorescence. Fig wasps, however, have very short adult lives and hence are dependent on the near-continuous production of inflorescences to maintain their populations. From January to March 1998 northern Borneo suffered a very severe drought linked to the El Nino-Southern Oscillation event of 1997-1998. This caused a

substantial break in the production of inflorescences on dioecious figs and led to the local extinction of their pollinators at Lambir Hills National Park, Sarawak, Malaysia. Most pollinators had not recolonized six months after the drought and, given the high level of endemism and wide extent of the drought, some species may be totally extinct. Cascading effects on vertebrate seed dispersers, for which figs are often regarded as keystone resources, and the tree species dependent on their services are also likely. This has considerable implications for the maintenance of biodiversity under a scenario of climate change and greater climatic extremes.

Harrison, R. D., & Rasplus, J. Y. (2006). Dispersal of fig pollinators in Asian tropical rain forests. *Journal of Tropical Ecology, 22*, 631-639. Times Cited: 59.
Fig pollinators (Agaonidae, Chalcioidea) lay their eggs in fig inflorescences (Ficus, Moraceae). Reproductive success for both partners is thus largely dependent on the dispersal of these tiny wasps. Some are known to cover substantial distances (> 10 km) using wind above the canopy. However, fig ecology is extremely varied, and hence one might also expect a diversity of pollinator dispersal strategies. We studied fig pollinator dispersal in Sarawak (2001 and 2004) and Peninsular Malaysia (2003). The results indicate substantial differences in dispersal ecology between the pollinators of monoecious and dioccious figs. Monoccious-fig pollinators were common, and species composition and rank abundances were similar between years despite short sampling periods. Substantial temporal and spatial variation in their production is thus smoothed out by long-distance dispersal. Some species whose hosts do not occur at our Sarawak site and are rare throughout Borneo were caught, suggesting exceptionally long-distance dispersal in these species. Conversely, few dioecious-fig pollinators were caught and species overlap between years was low. Dispersal range in many dioecious-fig pollinators may be more restricted. At a finer scale, among genera pollinating monoccious figs we found marked differences in flight behaviour (height and time-of-dispersal). We relate these findings to the ecology of their hosts, and discuss the implications for fig-fig-pollinator coevolution.

Harrison, R. D., & Yamamura, N. (2003). A few more hypotheses for the evolution of dioecy in figs (Ficus, Moraceae). *Oikos, 100*(3), 628-635. Times cited: 45.
In figs (Ficus, Moraceae) there are two breeding systems: monoecy is the ancestral condition but approximately half the 750 odd species are functionally dioecious. Three hypotheses have been proposed for the evolution of dioecy in figs, invoking seasonality (Kjellberg et al. 1987), the reduction of non-pollinating wasp species (Kerdelhue and Rasplus 1996), and the persistence of pollinator populations within small groups of trees (Kameyama et al. 1999). However, there are two major problems with these ideas. Firstly, dioecy has probably evolved only twice (Weiblen 2000), which severely limits our ability to test between alternative hypotheses. Secondly, it is very simple to suggest ways in which dioecy can evolve from monoecy (Charnov 1982). To illustrate this problem, and enlarge on some recent progress in our understanding of functionally dioecious figs, we are proposing a few more hypotheses.

Herre, E. A., Jander, K. C., & Machado, C. A. (2008). Evolutionary Ecology of Figs and Their Associates: Recent Progress and Outstanding Puzzles. *Annual Review of Ecology Evolution and Systematics, 39*, 439-458. Times cited: 169.
Over the past decade a proliferation of research has enriched and dramatically altered our understanding of the biology of figs, their pollinator wisps, and the myriad of other organisms that depend oil them. Ecologically, this work underscores the crucial role that fig fruits play in sustaining and shaping tropical frugivore communities. More generally, this work addresses several key issues in evolutionary ecology, including evolution of breeding systems (shifts between monoecy and dioecy), factors that promote the stability of mutualisms, precision of adaptation, and trajectories of community assembly and coevolution in systems with multiple interacting partners. Moreover, both the pollinating and nonpollinating wasps

associated with figs provide unparalleled opportunities for examining how different population structures call differentially affect sex allocation, kill selection, the evolution of parasite virulence, and many fundamental parameters of population genetics (e.g., levels of genetic variation and rates of silent and nonsilent base Substitutions).

Jander, K. C., & Herre, E. A. (2010). Host sanctions and pollinator cheating in the fig tree-fig wasp mutualism. *Proceedings of the Royal Society B-Biological Sciences, 277*(1687), 1481-1488. Times cited: 87.

Theory predicts that mutualisms should be vulnerable to invasion by cheaters, yet mutualistic interactions are both ancient and diverse. What prevents one partner from reaping the benefits of the interaction without paying the costs? Using field experiments and observations, we examined factors affecting mutualism stability in six fig tree-fig wasp species pairs. We experimentally compared the fitness of wasps that did or did not perform their most basic mutualistic service, pollination. We found host sanctions that reduced the fitness of non-pollinating wasps in all derived, actively pollinated fig species (where wasps expend time and energy pollinating), but not in the basal, passively pollinated fig species (where wasps do not). We further screened natural populations of pollinators for wasp individuals that did not carry pollen ('cheaters'). Pollen-free wasps occurred only in actively pollinating wasp species, and their prevalence was negatively correlated with the sanction strength of their host species. Combined with previous studies, our findings suggest that (i) mutualisms can show coevolutionary dynamics analogous to those of 'arms races' in overtly antagonistic interactions; (ii) sanctions are critical for long-term mutualism stability when providing benefits to a host is costly, and (iii) there are general principles that help maintain cooperation both within and among species.

Janzen, D. H. (1979). How to be a fig. *Annual Review of Ecology and Systematics, 10*, 13-51. Times cited: 523.

Goed leesbaar en beroemde samenvatting van kennis van de vijg 40 jaar geleden.

Lansky, E. P., Paavilainen, H. M., Pawlus, A. D., & Newman, R. A. (2008). Ficus spp. (fig): Ethnobotany and potential as anticancer and anti-inflammatory agents. *Journal of Ethnopharmacology, 119*(2), 195-213. Times cited: 112.

This review explores medieval, ancient and modern sources for ethnopharmacological uses of Ficus (fig) species, specifically for employment against malignant disease and inflammation. The close connection between inflammatory/ infectious and cancerous diseases is apparent both from the medieval/ancient merging of these concepts and the modern pharmacological recognition of the initiating and promoting importance of inflammation for cancer growth. Also considered are chemical groups and compounds underlying the anticancer and anti-inflammatory actions, the relationship of fig wasps and fig botany, extraction and storage of fig latex, and traditional methods of preparing fig medicaments including fig lye, fig wine and medicinal poultices.

Leigh, E. G. (2010). The evolution of mutualism. *Journal of Evolutionary Biology, 23*(12), 2507-2528. Times cited: 86.

Like altruism, mutualism, cooperation between species, evolves only by enhancing all participants' inclusive fitness. Mutualism evolves most readily between members of different kingdoms, which pool complementary abilities for mutual benefit: some of these mutualisms represent major evolutionary innovations. Mutualism cannot persist if cheating annihilates its benefits. In long-term mutualisms, symbioses, at least one party associates with the other nearly all its life. Usually, a larger host harbours smaller symbionts. Cheating is restrained by vertical transmission, as in Buchnera; partner fidelity, as among bull-thorn acacias and protective ants; test-based choice of symbionts, as bobtail squid choose bioluminescent bacteria; or sanctioning nonperforming symbionts, as legumes punish nonperforming nitrogen-fixing bacteria. Mutualisms involving brief exchanges, as among plants and seed-

dispersers, however, persist despite abundant cheating. Both symbioses and brief-exchange mutualisms have transformed whole ecosystems. These mutualisms may be steps towards ecosystems which, like Adam Smith's ideal economy, serve their members' common good.

Marinho, C. R., Pereira, R. A. S., Peng, Y. Q., & Teixeira, S. P. (2018). Laticifer distribution in fig inflorescence and its potential role in the fig-fig wasp mutualism. *Acta Oecologica-International Journal of Ecology, 90*, 160-167. Times cited: 1.
Although in Moraceae the presence of laticifers is considered to be a synapomorphy, little is known about the distribution and morphology of this type of secretory structure in the reproductive organs of its species. Ficus, the largest genus of Moraceae, is characterized by an inflorescence known as syconium and by an obligate mutualistic interaction with pollinating wasps. The objectives of the present study were to evaluate the distribution and morphology of laticifers in syconia of 36 species belonging to different Ficus sections and to survey traits of taxonomic and adaptive value for the group. Syconia containing flowers in a receptive state were collected, fixed and processed for anatomical analysis. All species studied have branched laticifers distributed in the syconium receptacle, in the ostiolar bracts and in the pedicel of staminate flowers. Almost all species show laticifers in the pedicel of shorter-styled flowers. Laticifers also occur in the pedicel of longer-styled flowers in most Ficus sections, except F. curtipes (Conosycea section) and more than 75% of the studied species of the Americanae section. Laticifers are observed in the sepals of 25 of the 36 species studied and occasionally in the pistil. The presence of laticifers in the pedicel of shorter-style flowers and its absence in the pistil suggest that the distribution of this secretory structure in the fig flower was selected by pressures imposed by the fig-fig wasp mutualism. The laticifers in the pedicel of shorter-styled flowers may confer protection to the developing wasp larvae against natural enemies. However, the absence of laticifers in the pistil of most Ficus species studied was probably selected by the mutualistic relationship with the agaonid pollinating wasps since the latex could interfere with oviposition through the style, with the larval development of the pollinating fig wasps, and the emergence of pollinator offspring from their galls.

Mbosso, E. J. T., Nguedia, J. C. A., Meyer, F., Lenta, B. N., Ngouela, S., Lallemand, B., et al. (2012). Ceramide, cerebroside and triterpenoid saponin from the bark of aerial roots of Ficus elastica (Moraceae). *Phytochemistry, 83*, 95-103. Times cited: 13.
Three compounds, ficusamide (1), ficusoside (2) and elasticoside (3), were isolated from the bark of aerial roots of Ficus elastica (Moraceae), together with nine known compounds, including four triterpenes, three steroids and two aliphatic linear alcohols. The chemical structures of the three compounds were established by extensive 1D and 2D NMR spectroscopy, mass spectrometry and by comparison with published data. The growth inhibitory effect of the crude extract and isolated compounds was evaluated against several microorganisms and fungi. The cytotoxicity against human cancer cell lines was also assessed. Ficusamicle (1) displayed a moderate in vitro growth inhibitory activity against the human A549 lung cancer cell line and a strong activity against Staphylococcus saprophyticus, while elasticoside (3) showed a potent activity on Enterococcus faecalis.

McCormick, A. C., Unsicker, S. B., & Gershenzon, J. (2012). The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends in Plant Science, 17*(5), 303-310. Times cited: 159.
Plants respond to herbivore attack by emitting complex mixtures of volatile compounds that attract herbivore enemies, both predators and parasitoids. Here, we explore whether these mixtures provide significant value as information cues in herbivore enemy attraction. Our survey indicates that blends of volatiles released from damaged plants are frequently specific depending on the type of herbivore and its age, abundance and feeding guild. The sensory perception of plant volatiles by

herbivore enemies is also specific, according to the latest evidence from studies of insect olfaction. Thus, enemies do exploit the detailed information provided by plant volatile mixtures in searching for their prey or hosts, but this varies with the diet breadth of the enemy.

Melin, A. D., Khetpal, V., Matsushita, Y., Zhou, K., Campos, F. A., Welker, B., et al. (2017). Howler monkey foraging ecology suggests convergent evolution of routine trichromacy as an adaptation for folivory. *Ecology and Evolution, 7*(5), 1421-1434. Times cited: 4.

Primates possess remarkably variable color vision, and the ecological and social factors shaping this variation remain heavily debated. Here, we test whether central tenants of the folivory hypothesis of routine trichromacy hold for the foraging ecology of howler monkeys. Howler monkeys (genus Alouatta) and paleotropical primates (Parvorder: Catarrhini) have independently acquired routine trichromacy through fixation of distinct mid- to long-wavelength-sensitive (M/LWS) opsin genes on the X-chromosome. The presence of routine trichromacy in howlers, while other diurnal neotropical monkeys (Platyrrhini) possess polymorphic trichromacy, is poorly understood. A selective force proposed to explain the evolution of routine trichromacy in catarrhinesreliance on young, red leaveshas received scant attention in howlers, a gap we fill in this study. We recorded diet, sequenced M/LWS opsin genes in four social groups of Alouatta palliata, and conducted colorimetric analysis of leaves consumed in Sector Santa Rosa, Costa Rica. For a majority of food species, including Ficus trees, an important resource year-round, young leaves were more chromatically conspicuous from mature leaves to trichromatic than to hypothetical dichromatic phenotypes. We found that 18% of opsin genes were MWS/LWS hybrids; when combined with previous research, the incidence of hybrid M/LWS opsins in this species is 13%. In visual models of food discrimination ability, the hybrid trichromatic phenotype performed slightly poorer than normal trichromacy, but substantially better than dichromacy. Our results provide support for the folivory hypothesis of routine trichromacy. Similar ecological pressures, that is, the search for young, reddish leaves, may have driven the independent evolution of routine trichromacy in primates on separate continents. We discuss our results in the context of balancing selection acting on New World monkey opsin genes and hypothesize that howlers experience stronger selection against dichromatic phenotypes than other sympatric species, which rely more heavily on cryptic foods.

Nakabayashi, M., & Ahmad, A. H. (2018). Short-term movements and strong dependence on figs of binturongs (Arctictis binturong) in Bornean rainforests. *European Journal of Wildlife Research, 64*(6). Times cited: 0.

We evaluated short-term movements of three radio-collared binturongs in relation to food distribution in Bornean rainforests, in addition to the basic ecological information on their home-range size and diet. Mean 95% fixed kernel and 95% MCP home-range size were 4.24 +/- 0.79km(2) and 1.54 +/- 0.89km(2), respectively (mean +/- SD). We recorded 13 fig Ficus species and four non-fig species as their foods. Fig trees accounted for 87.5% of the feeding sites of the three collared binturongs, and 87.9% including uncollared individuals. Our results suggested that binturongs' short-term movements were strongly affected by food distribution, especially figs. They feed on various fig species and may remember the location and fruiting periods of fig trees. They may use the biggest fig species, F. punctata, as a fallback food when other foods are scarce. Although this is the first systematic study to describe movement and feeding habits of binturongs, further studies are needed to understand their ecology so that proper measures can be designed for their conservation.

Park, S. A., Kim, M. G., Yoo, M. H., Oh, M. M., & Son, K. C. (2010). Comparison of Indoor CO2 Removal Capability of Five Foliage Plants by Photosynthesis. *Korean Journal of Horticultural Science & Technology, 28*(5), 864-870. Times cited: 3.

This study was conducted to determine the effects of foliage plants on reducing indoor carbon dioxide (CO2). Five foliage plants such as Hedera helix L., Ficus benjamina L., Pachira aquatica, Chamaedorea elegans, and Ficus elastica were selected and cultivated in two different growth medium (peatmoss and hydroball). Each plant was placed in an airtight chamber and then treated with the combinations of two different CO2 concentrations (500 or 1,000 ppm) and two different light intensities (50 or 200 mu mol . m(-2) . S-I). The change of CO2 concentration (ppm) in the airtight chamber during day and night was measured and then converted into the photosynthetic rate (mu mol CO2 . m(-2) . s(-1)). As the results, each foliage plant reduced CO2 level in the airtight chamber for one hour by photosynthesis. Pachira aquatica and Ficus elastica absorbed CO2 more effectively compared to the other plants. The plants exposed to higher CO2 concentration (1,000 ppm) and higher light intensity (200 mu mol . m(-2) . s(-1)) showed more effective CO2 elimination rate and photosynthetic rate. The plants that have wide leaves and big leaf areas such as Pachira aquatica, Hedera helix L., and Ficus elastica showed higher photosynthetic rate than the other plants that have smaller leaves. Released CO2 concentration by respiration of the plants during the night was very low compared to the absorbed CO2 concentration by photosynthesis during the day. There was no significant difference between peatmoss and hydroball medium on reducing CO2 concentration and increasing photosynthetic rate. In conclusion, this study suggested that foliage plants can effectively eliminate indoor CO2. Optimum environmental control in relation to photosyntheis and usage of right indoor foliage plants having lots of leaves and showing active photosynthesis even under low light intensity like indoor light condition would be required to increase the elimination capacity of indoor CO2.

Proffit, M., Schatz, B., Borges, R. M., & Hossaert-Mckey, M. (2007). Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. *Journal of Animal Ecology, 76*(2), 296-303. Times cited 51.

1. The parasitic chalcidoid wasps associated with the species-specific and obligatory pollination mutualisms between Ficus spp. and their agaonid wasp pollinators provide a good model to study the functional organization of communities. 2. However, communities of non-pollinating fig wasps (NPFWs) remain little characterized, and their functioning and evolutionary dynamics are still poorly understood. 3. We studied the communities of NPFWs associated with the monoecious F. racemosa and the dioecious F. hispida. Associated with these two fig species are a total of seven wasp species belonging to three genera. These species present contrasts in life history traits and in timing of oviposition. The species studied are thus broadly representative of the communities of NPFWs associated specifically with fig-pollinator mutualisms. 4. In our study systems, there is temporal segregation of oviposition time among members of NPFW communities. 5. We tested the role of volatile chemicals in the attraction of NPFWs associated with these two fig species, and tried to determine if chemical mediation can explain the organization of the communities. 6. We conducted odour choice tests using a Y-tube olfactometer. All the NPFWs studied were shown to use volatile chemicals produced by the fig to locate their host. Furthermore, the signals used by each species depended on the phenological stage of the fig they exploit. 7. Results demonstrated that the pattern of oviposition results from the utilization of volatile signals produced by figs that vary in their composition at different stages of fig development. Thus, chemical mediation allows resource partitioning in the NPFW communities associated with fig-pollinator mutualisms, and suggests hypotheses to explain coexistence in other parasite communities.

Shi, Y. X., Mon, A. M., Fu, Y., Zhang, Y., Wang, C., Yang, X. F., et al. (2018). The genus Ficus (Moraceae) used in diet: Its plant diversity, distribution, traditional uses and ethnopharmacological importance. *Journal of Ethnopharmacology, 226*, 185-196. Times cited: 0.

Ethnopharmacological relevance: A new field of enthnopharmacology has opened, where pharmacological studies draw their attention from the conventional only-medicine approach towards the dietary dimension. The uses of Ficus species in the human diet have been extensively documented by ethnobotanical field surveyors. Overlap commonly exist between the dietary and medicinal selection of Ficus species but not for choices of the plant parts and development stages, which leave a large space for ethnopharmacological study. Aims of the study: 1) To review published works on the dietary uses of Ficus species and their food-medicine overlap based on traditional uses, and 2) to spark interest in ethnopharmacological studies on the dietary uses of Ficus species. Materials and methods: Data was collected and analyzed from many sources, including published and unpublished ethnobotanical field surveys, taxonomic and distribution information, international journals, books, thesis, floras, reports and professional databases. The possible biases arising from data sources are assessed to make sure that the dataset are global representative. Results: A total of 132 Ficus species are reported for dietary uses, including one subspecies and four varieties. Those species are found across all of the six subgenera of the genus Ficus. For distribution, 98 species from the Indo-Australasian region, 27 species from the African tropics (with one species, F. palmata, from both the two regions) and 8 from the Neotropics. The parts most commonly used are the figs (i.e. syconium or fruits) (110 species) and leaves (67 species), in various growth stages. It is also found that the certain plant parts of 78 species are used both for dietary and medicinal purpose. Among which the figs are frequently cited in the treatment of diarrhea and oligogalactia, the leaves in the treatment of diarrhea, stomach complaintsas, antidote and diabetes, the latex in the treatment of intestinal worms and wounds, and the barks in the treatment of diarrhea. Conclusions: We demonstrate that throughout its area of distribution, the genus Ficus is generally used as a dietary plant, although use of a individual species seems uncommon. Furthermore, we highlight the diet-medicine overlap of the uses of this genus, which should enable further understanding of the potential for broader health benefits, rather than limiting studies in this genus to its only-medicinal properties.

Singaravelan, N., Marimuthu, G., & Racey, P. A. (2009). Do fruit bats deserve to be listed as vermin in the Indian Wildlife (Protection) & Amended Acts? A critical review. *Oryx, 43*(4), 608-613. Times cited: 7.

Of the 13 species of fruit bats occurring in India, the Indian flying fox Pteropus giganteus, the dog-faced fruit bat Rousettus leschenaultii and the greater short-nosed fruit bat Cynopterus sphinx are distributed throughout the country. They usually live in trees (P. giganteus), temples and caves (R. leschenaultii) and foliage (C. sphinx) and feed on fruits such as fig Ficus spp., Singapore cherry Muntingia calabura, Indian almond Terminalia catappa, mango Mangifera indica, guava Psidium guajava as well as leaves, nectar and pollen. The other 10 species live at sea level and at altitudes Of > 2,000 in and their distribution and foraging activities may be restricted mainly to forests. Two of them, the Nicobar flying fox Pteropus faunulus and Salim Ali's fruit bat Latidens salimalii are endemic. Although details of their foraging activity are poorly known, there is no evidence that they visit commercial fruit orchards. They feed on wild fruits and disperse seeds widely, contributing to forest regeneration. Although P. giganteus, R. leschenaultii and C. sphinx feed on commercial fruits, their role in pollination and seed dispersal of economically important plants such as kapok Ceiba pentandra, mahua Bassia latifolia and petai Parkia spp. is important. Sacrificial crops such as M. calabura can be used at orchards to reduce the damage bats cause to commercial fruit. Because the ecological services provided by bats are not appreciated by the public and conservation planners, all fruit bat species with one exception are still categorized as vermin and included as such in Schedule V of the Indian Wildlife (Protection) Act, 1972 and amended Acts. It is now appropriate for the Government of India to revisit

this issue and consider removing these pollinators and seed dispersers from the list of vermin in the Wildlife (Protection) Act.

Souto-Vilaros, D., Proffit, M., Buatois, B., Rindos, M., Sisol, M., Kuyaiva, T., 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*(6), 2256-2273. Times cited: 0.

1. In the fig (Moraceae) and fig-wasp (Agaonidae) mutualism, scent is believed to be of primary importance in pollinator attraction and maintenance of species specificity. Scent divergence between closely related Ficus species seems sufficient in promoting reproductive isolation through pollinator behaviour, starting the process of speciation. 2. We investigated volatile organic compound (VOC) variation from figs in several Ficus species endemic to Papua New Guinea. Sister species of section Papuacyse and subspecies of Ficus trichocerasa substitute each other along the continuously forested Mt. Wilhelm elevational gradient. We placed these species in a phylogenetic context to draw conclusions of scent divergence between close relatives. In addition, pollinator response to VOCs emitted by figs of different species was tested. 3. Volatile profiles differed significantly between focal species, although with a varying degree of overlap between (sub)species and elevations. Pollinators were generally attracted to VOCs emitted only by their hosts except in one case where pollinating fig wasps were also attracted to the sister species of its host. Wasp morphological traits, however, indicate that it is mechanically impossible for this species to oviposit in figs of this atypical encounter. 4. Synthesis. This study demonstrates that while scent is an effective signal for partner recognition, there are multiple barriers which help maintain prepollination isolation in fig and pollinating fig-wasp interactions. Speciation along this elevational gradient is reinforced by divergence in key reproductive isolation mechanisms on both sides of the mutualism.

Tripathi, S. C., & Sharma, G. (2007). Inhibition of Infectivity of Ridge Gourd mosaic virus by latex of some angiosperms. *Vegetos, 20*(1), 53-54. Times cited: 2.

Inhibition of Infectivity of Ridge Gourd mosaic virus has been studied by taking latex from ten anglospermic plants belonging to different families namely Argemone maxicana (Papavaraceae), Artocarpus integrifolia, Ficus elastica (Moracea), Calotropis procera (Asclepladaceae), Euphorbia hirta, Euphorbia antiquorum, Euphorbia royleana, Jatropha curcas (Euphorbiaceae) and Vinca rosea (Apocyanaceae). The latex from Jatropha curcas showed maximum inhibitory activity for Ridge Gourd mosaic virus.

Van Goor, J., Piatscheck, F., Houston, D. D., & Nason, J. D. (2018). Figs, pollinators, and parasites: A longitudinal study of the effects of nematode infection on fig wasp fitness. *Acta Oecologica-International Journal of Ecology, 90*, 140-150. Times cited: 2.

Mutualisms are interactions between two species in which the fitnesses of both symbionts benefit from the relationship. Although examples of mutualism are ubiquitous in nature, the ecology, evolution, and stability of mutualism has rarely been studied in the broader, multi-species community context in which they occur. The pollination mutualism between figs and fig wasps provides an excellent model system for investigating interactions between obligate mutualists and antagonists. Compared to the community of non-pollinating fig wasps that develop within fig inflorescences at the expense of fig seeds and pollinators, consequences of interactions between female pollinating wasps and their host-specialist nematode parasites is much less well understood. Here we focus on a tri-partite system comprised of a fig (Ficus petiolaris), pollinating wasp (Pegoscapus sp.), and nematode (Parasitodiplogaster sp.), investigating geographical variation in the incidence of attack and mechanisms through which nematodes may limit the fitness of their wasp hosts at successive life history stages. Observational data reveals that nematodes are ubiquitous across their host range in Baja California, Mexico; that the

incidence of nematode infection varies across seasons within- and between locations, and that infected pollinators are sometimes associated with fitness declines through reduced offspring production. We find that moderate levels of infection (1-9 juvenile nematodes per host) are well tolerated by pollinator wasps whereas higher infection levels (>= 10 nematodes per host) are correlated with a significant reduction in wasp lifespan and dispersal success. This overexploitation, however, is estimated to occur in only 2.8% of wasps in each generation. The result that nematode infection appears to be largely benign - and the unexpected finding that nematodes frequently infect non-pollinating wasps - highlight gaps in our knowledge of pollinator-Parasitodiplogaster interactions and suggest previously unappreciated ways in which this nematode may influence fig and pollinator fitness, mutualism persistence, and non-pollinator community dynamics.

Weiblen, G. D. (2002). How to be a fig wasp. *Annual Review of Entomology, 47*, 299-330. Times cited: 259.

In the two decades since Janzen described bow to be a fig, more than 200 papers have appeared on fig wasps (Agaonidae) and their host plants (Ficus spp., Moraceae). Fig pollination is now widely regarded a model system for the study of coevolved mutualism, and earlier reviews have focused on the evolution of resource conflicts between pollinating fig wasps, their hosts, and their parasites. Fig wasps have also been a focus of research on sex ratio evolution, the evolution of virulence, coevolution, population genetics, host-parasitoid interactions, community ecology, historical biogeography, and conservation biology. This new synthesis of fig wasp research attempts to integrate recent contributions with the older literature and to promote research, on diverse topics, ranging from behavioral ecology to molecular evolution.

West, S. A., Herre, E. A., Windsor, D. M., & Green, P. R. S. (1996). The ecology and evolution of the New World non-pollinating fig wasp communities. *Journal of Biogeography, 23*(4), 447-458. Times cited: 114.

We present data on several previously undescribed species from six genera of New World nonpollinating fig wasps. We show that many of these species have a negative effect on the reproductive success of both the pollinator wasps and the host figs. Our results suggest that the two most abundant genera of non-pollinating wasps, the Idarnes and the Critogaster, compete for the same pool of female flowers as the pollinating wasps in the Urostigma and Pharmacosycea figs, respectively. Wasps from the genus Aepocerus induce and develop within large galls, in the Urostigma figs. By draining resources from the fruit these wasps may have a detrimental effect on the production of pollinator wasps and viable seeds. Some of the species investigated are parasitoids of other non-pollinating species. We examine the importance of the various forms of spatial heterogeneity in the parasitism rate that can act to stabilise the host-parasitoid interaction. Finally, we discuss the factors underlying the large variation in the abundance and diversity of the non-pollinating wasps both among and within fruit crops. (1)

Whittaker, R. J., & Jones, S. H. (1994). The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, krakatau, indonesia. *Journal of Biogeography, 21*(3), 245-258. Times cited : 85.

Krakatau provides a case study in tropical forest rebuilding following sterilization of the islands in 1883 by volcanic eruptions. On the basis of historical and recent records, the roles of frugivorous birds and bats in plant colonization and spread are assessed with reference to the interior forest communities. It is established that the islands are within the effective seed-transport range of members of both the avifauna and bat fauna and it is argued that it is parsimonious to assume a role for both taxa in introducing small-seeded species. For instance, the most successful genus of plant colonists, Ficus with twenty-four species, is attractive to both groups of dispersers. Larger seeds which cannot be ingested by bats must have been

introduced by birds, with the exception of diplochorous, primarily sea-dispersed species (or human introductions). The largest-seeded partially-zoochorous species are bat-spread trees. Birds have a dispersal role for a more balanced range of plant growth forms than do bats, for which available records indicate a restriction largely to trees and shrubs. Early this century savanna was predominant, but following the establishment of scattered patches of trees and shrubs, forest closure occurred very rapidly, almost exclusively involving zoochorous trees, notably Ficus spp. For the period 1883-1992 a total of 124 species of plants are identified as probably having been introduced endogenously by birds and bats and a further forty-nine partially zoochorous species have been recorded. Birds and bats are argued to have partially overlapping yet complementary roles as dispersers. The implications of these observations for restoration ecology and forest conservation are discussed.

Wiebes, J. T. (1979). Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics, 10*, 1-12. Times cited: 307.
Klassiek artikel van Nederlandse expert.

Yoon, J. W., Son, K. C., Yang, D. S., & Kays, S. J. (2009). Removal of Indoor Tobacco Smoke under Light and Dark Conditions as Affected by Foliage Plants. *Korean Journal of Horticultural Science & Technology, 27*(2), 312-318. Times cited: 4.
The efficacy of three species of indoor plants (Spathiphyllum spp., Ficus elastica and Syngonium podophyllum) for the removal of environment tobacco smoke (ETS) particulate matter (PM) in the light and dark and changes in physiological responses (photosynthesis, transpiration, respiration) of the plants to ETS was assessed. Cigarette smoke was generated in sealed chambers to give an initial concentration of similar to 182 mu g.m(-3) and after normalization (10 min) the concentrations of various size categories (PM10, PM1.0, and PM0.5) were determined. ETS PM diminished with time due to adsorption and sedimentation. However, the decrease was accelerated by the presence of indoor plants in both the light and dark. Removal efficiency varied among species and was not correlated with leaf area. Spathiphyllum spp. had the highest removal efficacy on a leaf area basis among the species tested in both light and dark conditions, and removal was more efficient in the light than in the dark. In the dark there was little difference in removal efficiency among species or in respiratory rate. The removal efficiency in the light was higher in species with higher photosynthetic rates, suggesting that photosynthesis may be involved in the accelerated removal.

Borges, Renee M.
Compton, Stephen G.
Kjellberg, Finn

Fifty years later, figs and their associated communities

Acta Oecologica 90 (2018) 1–3

Vijgen (Ficus, Moraceae) zijn een divers geslacht van grotendeels tropisch en subtropische planten. Ze zijn van uitzonderlijk belang, uit oogpunt van ecologie en van natuurbehoud omdat vijgen waarschijnlijk door meer diersoorten worden gegeten dan de vruchten van welke andere planten ook (Shanahan et al., 2001). De vijgen (de vrucht: Syconia) zijn ongebruikelijke protogynische bloeiwijzen cq *infructescences* met een structuur die generalistische bestuivers uitsluit. Elke vijg heeft de vorm van een holle bal waarvan de binnenkant aan de onderkant bekleed is met kleine bloemen. Stuifmeel (pollen) kan alleen een vijg binnengebracht worden via een smalle ingang (een *ostiole*). Het stuifmeel wordt door zeer kleine vijgenwespen (*Agaonidae*) in de vijgen gebracht; die wespjes leggen hun eitjes in de zaadknop (*ovule)* van de vijg. Ovulen die pollen ontvangen maar geen wespeneitje, kunnen zich ontwikkelen tot zaden. De morfologie van volwassen vrouwelijke vijgenwespen vertoont aanpassingen om door de smalle ostiole te kruipen. Ook mannelijke dieren zijn sterk aangepast; ze brengen het grootste deel van hun leven of zelfs hun hele leven door in de vijg. De gastheerspecificiteit is hoog onder Agaoniden, waarbij de meeste soorten geassocieerd zijn met een enkele gastheer Ficus. Ook is het zo dat veel gastheerbomen bestoven worden door één enkele Agaonidsoort. Maar de lijst van soorten met twee of meer bestuivers neemt toe. Behalve de bestuivende vijgenwespen er zijn ook tal van niet-bestuivende soorten (NPFW). Samen met de bestuivers vormen ze gemeenschappen van fytofagen, parasitoïden en secundaire parasitoïden in de vijgen.

Vijftig jaar geleden werd ontdekt dat sommige vijgenbestuivende wespen stuifmeel verzamelen in gespecialiseerde zakjes voordat ze hun “geboortevijgen” verlaten. Ze deponeren dit stuifmeel op de stigma's in de ontvangende vijgen (Ramirez 1969, Galil en Eisikowitch 1969). Deze originele waarnemingen kunnen worden beschouwd als de start van moderne experimentele en evolutionaire studies van vijgenbomen en de met hen geassocieerde dieren. Ficus en vijgenwespen zijn vaak een modelsysteem genoemd waarmee de evolutie van mutualismen is onderzocht . In feite bieden Ficus en de bijbehorende gemeenschappen ook bredere inzichten in de structurering van ecologische gemeenschappen en in de klassieke evolutie van organismen in het algemeen, evenals in de evolutie van ecologisch interacties. Het streven van dit speciale volume van dit tijdschrift was om deze bredere kijk weer te vertellen geven op wat Ficus en hun geassocieerde gemeenschappen ons vertellen over het leven.

Vijgenbiologen kwamen het eerst bij elkaar bij het “vijgenminisymposium " in 1983 waaraan Jacob Galil, Kees Berg en Koos Wiebes deelnamen. De 9e internationale vijgenbijeenkomst werd gehouden in Montpellier, Frankrijk, precies een halve eeuw sinds de baanbrekende publicaties van Ramirez, Galil en Eisikowitch. Het was daarom een bijzonder genoegen dat Dan Eisikowitch aanwezig wasbij de vergadering.

2. Vijgdiversificatie

Ficussoorten en de bestuivende wespen zijn merendeels gecodiversifieerd (Cruaud et al. 2012). De analyse van Ficus-fylogenieën laat zien dat ze passen in een "museummodel" van oude geleidelijke diversificatie met een progressieve accumulatie van soorten in de context van lage uitsterfratio's (Brunn-Lund et al. 2018). Groot tolerantie (r*ange*) en sterke genenstroom (*gene flow*), zelfs in marginale populaties (Wang et al. 2018), kunnen de lage uitsterfpercentages verklaren.
Hoogstwaarschijnlijk komen deze twee eigenschappen voort uit het mutualistische bestuivingssysteem. Verder suggereert de analyse dat neotropische regenwouden de wieg zijn van recente diversificatie van de vijg binnen een pantropisch museummodel.
Dit verschil in diversificatiepatronen, dat een nieuwe betekenis geeft aan de term 'neotropen', wordt hier getoond binnen de context van een pantropisch geslacht. Maar het zou kunnen gelden voor veel tropische geslachten. De fylogenieën suggereren ook dat de verwerving van hemi-epifytisme, en de daarop volgende kolonisatie van een nieuwe ecologische niche, heeft geleid tot een toename in de snelheid van diversificatie. Tenslotte bevestigen fylogenetische studies dat actieve bestuiving diversificatie bevordert, zodat, ondanks herhaaldelijke veranderingen van actieve naar passieve bestuivingen, twee derde van de Ficus-soorten nog steeds actief bestoven worden (Kjellberg et al. 2001).

3. Vertebraten en vijgen

Gezien het feit dat primaten graag vijgen eten (Shanahan et al. 2001), is het geen verrassing dat verschillende soorten Ficus nauwe relaties hebben met mensen; vijgen hebben zelfs vaker een belangrijke spirituele rol in menselijke samenlevingen (Shanahan 2016). Ze worden door veel samenlevingen als magisch gezien omdat ze vruchten (rijpe vijgen) produceren zonder bloemen voort te brengen (hun bloemen zitten verborgen in de vijgen). De wurggroeivorm van sommige vijgensoorten heeft ook bijgedragen aan het idee dat ze over bovennatuurlijke krachten beschikken. Een studie in Madagaskar laat zien hoe het Merinavolk Ficus lutea en Ficus polita gebruikt als symbolen van macht: ze hebben de vijgenbomen op strategische plaatsen geplant om hun gezag te doen gelden en territoria te claimen (Aumerruddy-Thomas et al. 2018). Vijgenbomen zijn vaak aangeplant als sierplanten en heilige bomen in tropische steden, maar stedelijke vijgenbomen zijn soms ook natuurlijke kolonisten (Lok et al. 2013). Dergelijke bomen leveren welkom voedsel voor stedelijke dieren. Sommige stedelijke Ficus-soorten leveren rijpe vijgen gedurende de winter - een waardevolle voedselbron voor stedelijke vogels (Walther et al. 2018). Eenhuizige Ficussoorten staan bekend om hun sterk gesynchroniseerde vruchtrijping. Sommige soorten produceren grote oogsten van kleinbloemige vijgen, die binnen één of twee dagen worden bestoven door vijgenwespen met een synchrone generatiewisseling, daardoor regent het gedurende enkele weken rijpe vijgen die een continue voedselbron vormen voor fruiteters (Chiang et al. 2018). Zo'n vruchtdragende fenologie, zoals gedocumenteerd voor Ficus supisocarpa en *Ficus caulocarpa* (sectie *Urostigma*), is ook te vinden in de beide Amerika's binnen de groep F. *americana* subspecies *guianensis* (sectie *Americanae*) en in sommige Afrikaanse soorten (sectie Galoglychia). Een grotendeels onderbelicht aspect van de interactie tussen Ficus en fruitverspreiders is de geografische variatie in eigenschappen van de vijg die wordt in verband gebracht met de aantrekkelijkheid en de beschikbaarheid van fruit voor vruchteneters , zoals bijvoorbeeld de aanwezigheid van lange uit lopers met vijgen in F. *hainanensis* op het Aziatische continent, maar op korte gespecialiseerde takken op het eiland Hainan, of geografische variatie in rijpe vijgengeur (Soler et al. 2018).

4. Vijgenwespen

Analyse van de gemeenschappen van niet-bestuivende vijgen (Non Pollinating Fig Wasps NPFW's) en hun structurering binnen briogeografische regio's en tussen continenten biedt inzicht in de manier waarop gemeenschappen zijn gestructureerd, hoe ze werken en wat hun diversificatie drijft. NPFW's staan bekend als specialisten die een enkele Ficus-soort bewonen (McLeish et al. 2012). Een grondige regionale studie in Brazilië, gebaseerd op 100.000 NPFW-exemplaren van morfo-soorten (*morpho-species)* laat zien dat, hoewel de meeste soorten specialisten zijn, er toch weinig strikte specialisten zijn en dat sommige veelvoorkomende soorten echte generalisten zijn (Farache et al. 2018). Dit patroon van generalisme, dat ook is gesuggereerd voor sommige Amerikaanse vijgenbestuivende wespen, komt overeen met de recente diversificatie van Ficus in de neotropen (*Neotropics*). Inderdaad laten voorbeelden van vijgenbestuivende wespensoorten regelmatig zien dat het bestuiven van verschillende niet-zuster Ficus-soorten beperkt blijft tot de Neotropen (Marussich en Machado 2007) en tot subsectie *Chlamidodorae* in sectie *Galoglychia*, die ook recent gediversificeerd (Cornille et al. 2012, McLeish en van Noort 2012).

Een belangrijke uitdaging zal zijn om de trofische structuur te bevestigen en de voedingsgewoonten van de verschillende leden van NPFW-gemeenschappen. Sommige geslachten omvatten *wall gallers*, *flower gallers* en kleptoparasieten (Cruaud et al. 2011, Ghara et al. 2015). Zelfs in een geslacht van parasitoïden, is er ruimte voor variatie, met twee Apocrypta-soorten, één endoparasitoïde en een ectoparasitoïde geassocieerd met *Ficus racemosa* (Yadav en Borges 2018). Veel studies hebben geprobeerd de trofisch structuur af te leiden uit correlaties tussen de aantallen van de verschillende wespensoorten en die van de zaden. Echter, deze correlaties laten hoogstens *informed guesses* toe en moeten worden aangevuld met experimentele gegevens of directe biologische observaties (Segar et al. 2018). Sterfte onder larven van bestuivers bij afwezigheid van parasitisme kan het trekken van conclusies verder compliceren. In twee tweehuizige Ficussoorten is de mortaliteit van de bestuivende larven geschat op ¼ en 1/3 van de larven (Ghana et al. 2012, Yu et al. 2018). Zulke grote aantallen werden niet verwacht.

Vijgen maken hun ontvankelijkheid voor bestuiving kenbaar door een soortspecifieke geur. Aan de vraag hoe deze geur varieert in de ontwikkeling van vijgen, vóór, tijdens en na de ontvankelijkheid, is tot nu toe weinig aandacht besteed, maar het zou een sleutel zijn voor inzicht in hoe de opeenvolging van wespen samenhangt met de opeenvolgende stadia waarin lokale Ficussoorten eieren afzetten (Proffit et al. 2018). Hoe wespen vijgengeuren kunnen detecteren, kan ook een dynamisch proces zijn: een *transcriptome analyse* van genen die betrokken zijn bij de detectie van vluchtige organische stoffen door een bestuivende vijgenwesp liet veranderingen zien na blootstelling aan de geur van receptieve vijgen (Zeng et al. 2018). In vijgenwespen zitten structuren voor de geurperceptie als *sensilla* op antennes. De verdeling en typen van antennale sensilla lijken te variëren, afhankelijk van het gedrag van de wesp bij het zoeken van vijgen en bij het verkennen van het oppervlak van een vijg. Bijvoorbeeld, sommige sensilla correleren met de vraag of de wespen het oppervlak van de vijg aanraken over de hele lengte van de antenne of dat ze op het vijgenoppervlak tikken met de punt van de antennes (Yang et al. 2018). Ook de morfologie van de legboor is een kenmerk dat correleert met de levensgeschiedenis in vijgenwespen (Ghara et al. 2011, Elias et al. 2018); legboren kunnen ook optreden als olfactorische organen (Yadav en Borges 2017).

Bestuiving en eicelbevruchting is een ander facet van de interactie tussen de vijg en de wesp; ze hangt af van een goede match tussen wespengedrag en stigmamorfologie. De eerste beschrijvingen van de stigma's als "samenhangend" of "niet-samenhangend" waren karikaturaal. Nieuwe gegevens over

variatie van vijgensoorten in stigma-arrangement openen mogelijkheden voor gedetailleerd gedragsonderzoek (Teixeira et al. 2018). De hoge larvensterfte gedocumenteerd in twee tweehuizige Ficus-soorten (Ghana et al. 2012, Yu et al. 2018) zou kunnen worden verklaard door een onvolmaakte correlatie tussen *oviposition* in een *ovule* en daadwerkelijke bestuiving en bevruchting van de *ovule* (Jousselin et al. 2001). Onderzoek naar de interactie tussen wespengedrag en de stigmastructuur is de sleutel tot het begrijpen van een dergelijke mismatch.

5. Geleedpotigen, andere ongewervelde dieren en vijgenbescherming

Vijgenmaken het leven mogelijk voor een gevarieerde reeks van ongewervelde dieren, niet alleen voor vijgenwespen. De huidige lijst van niet-vijgenwespen-insecten die zich voeden met vijgen omvat 129 soorten insecten, waaronder 5 ordes en 24 families, en veel van deze zijn vijgenspecialisten (Palmieri et al. 2018). Deze insecten zijn te weinig bestudeerd en van hun effect op de ontwikkeling van vijgen is weinig bekend. Vijgen zijn gastheer voor nematoden die *phoretic* (vastgehecht aan) zijn op bestuivende vijgwespen (Krishnan et al. 2010). Het effect van interacties tussen dergelijke ongewervelden en vijgen kan geografisch zeer variabel zijn: terwijl de nematodensoort *Parasitodiplogaster* een sterk negatief effect bleek te hebben op vijgenbestuivende wespen in Panama (Herre, 1993), had zij slechts een beperkt negatief effect in Baja California (Van Goor et al., 2018).

Een fascinerend kenmerk van veel Ficus-soorten is de synchronisatie van vruchtzetting *binnen* bomen, tegenover de asynchronie *tussen* bomen in dezelfde populaties. *Crop synchronisation* kan worden begunstigd door vele factoren, zoals het vermogen om bestuivers van veraf aan te trekken, of het vermogen om rondtrekkende vruchtenetende dieren aan te trekken Omgekeerd kan juist *tegen* crop-synchronisatie worden geselecteerd door hetzelfde type factoren, zoals het aantrekken van grote aantallen op vijgen gespecialiseerde *lepidoptera's* wier larven zich voeden met ontwikkelende vijgen (Piatscheck et al. 2018).

Omdat vijgen worden blootgesteld aan een groot aantal antagonisten, heeft Ficus vele verdedigingslinies tegen hen geëvolueerd. Moraceae in het algemeen, en Ficus in het bijzonder produceren bijvoorbeeld beschermende latex. De verdeling van *laticifers* in vijgenbloemen laat zien dat ze aanwezig zijn in verschillende delen van de bloemen, maar afwezig in de stijlen; die worden immers aangeraakt door de bestuivers en latex kan de reproductie van bestuivers verstoren (Marinho et al. 2018). De bescherming van planten kan ook indirect zijn. In Ficus benguetensis hebben de vijgen *nectariën* en hun suikersecretie trekt mieren aan die de ontwikkeling beschermen van larven van bestuivende soorten tegen parasitisme door niet-bestuivende vijgenwespen, en mogelijk ook tegen andere vijgenetende insecten (Bain et al. 2018).

6. Concluderende lijnen

Een gemeenschappelijk kenmerk van de studies die in dit volume worden gerapporteerd, is hoe weinigen ze zijn gefocust op de interacties tussen één soort van Ficus en zijn soort bestuiver(s). De meeste studies gaan over interspecifieke netwerken en interactienetwerken. De studie van vijgen en hun geassocieerde gemeenschappen is geleidelijk aan in een nieuw tijdperk terechtgekomen.