Interactions Between Figs and Gall-Inducing Fig Wasps: Adaptations, Constraints, and Unanswered Questions

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The ancient interaction between figs (*Ficus*, Moraceae) and their pollinating fig wasps is an unusual example of a mutualism between plants and gall-inducing insects. This review intends to offer fresh perspectives into the relationship between figs and the diversity of gall-inducing sycophiles which inhabit their enclosed globular inflorescences that function as microcosms. Besides gall-inducing pollinators, fig inflorescences are also inhabited by other gall-inducing wasps. This review evaluates the state of current knowledge on gall-induction by fig wasps and exposes the many lacunae in this area. This review makes connections between fig and gall-inducing wasp traits, and suggests relatively unexplored research avenues. This manuscript calls for an integrated approach that incorporates such diverse fields as life-history theory, plant mate choice, wasp sexual selection and local mate competition, plant embryology as well as seed and fruit dispersal. It calls for collaboration between researchers such as plant developmental biologists, insect physiologists, chemical ecologists and sensory biologists to jointly solve the many valuable questions that can be addressed in community ecology, co-evolution and species interaction biology using the fig inflorescence microcosm, that is inhabited by gall-inducing mutualistic and parasitic wasps, as a model system.

Keywords: *Ficus*, fig wasps, gall induction, microcosm, multitrophic interactions, mutualism, parasitism

INTRODUCTION

Gall-inducing insects are usually plant parasites (Espírito-Santo and Fernandes, 2007; Oliveira et al., 2016; Miller and Raman, 2019). Sometimes, however, they are beneficial to plants, as in brood-site pollination mutualisms where plants trade insect development sites against seed production (Sakai, 2002; Borges, 2016). Yet, such mutualisms persist only if partner exploitation is controlled (Borges, 2015b; Dunn, 2020). Most mutualisms involving galling insects are specific, and often exhibit co-diversification, co-speciation, and co-evolution (Cruaud et al., 2012; Wang et al., 2019). This specificity mandates adaptations at many levels including unusual life history traits, e.g., 30-year diapause in yucca moth larvae to match the flowering phenology of yucca host-plant populations (Powell, 2001).

In the brood-site pollination mutualism between figs and wasps, a single pollinator wasp larva usually occupies each uniovulate galled flower within a multi-flowered closed inflorescence (Janzen, 1979; Wiebes, 1979). Pollinating fig wasps usually belong to family Agaonidae: subfamilies

Agaoninae, Kradibiinae, Tetrapusiinae (Kjellberg et al., 2005; Heraty et al., 2013; Farache et al., 2017). The fig inflorescence or syconium is also occupied by non-pollinating parasitic gall-inducing wasps in the Sycophaginae (Agaonidae), Otitesellinae, and Epichrysomallinae (Pteromalidae; Heraty et al., 2013; Farache et al., 2017, 2018b). There is extreme sexual dimorphism in adult fig wasps, with the males usually being wingless and completing their life cycle within their natal syconium (Weiblen, 2002). The fig–fig wasp mutualism is a classic example of co-diversification (Cruaud et al., 2012; Wang et al., 2019), with much greater congruence in phylogenies between figs and their pollinators, and between pollinators and competing gallers, than between figs and their galler parasites (Wang et al., 2019); the latter incongruence may signify host switches, duplications, and association losses (Yang et al., 2015; Wachi et al., 2016).

Although the fig–galler fig wasp interaction has been extensively investigated (Cook and Rasplus, 2003; Kjellberg et al., 2005; Herre et al., 2008; Borges, 2015a; Dunn, 2020), vital mechanisms governing fig and fig wasp biology remain to be discovered. This review will propose possible correspondences between traits of figs and gall-inducing wasps, relevant to the mutualism or its exploitation. This review provides fresh insights and suggests new questions that await answers.

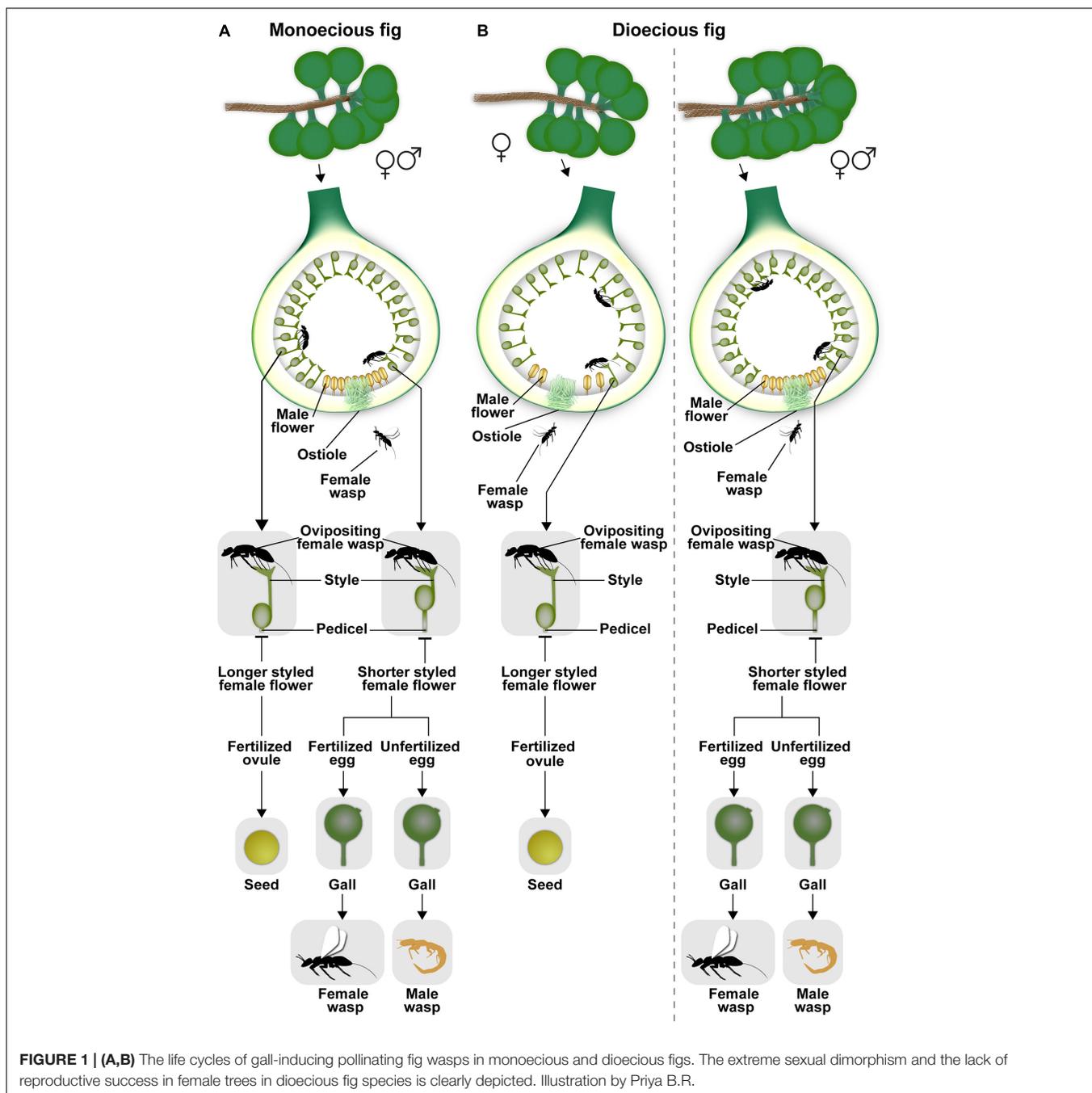## *FICUS* (MORACEAE) INFLORESCENCE TRAITS

Fig flowers or inflorescence tissues, that are exploited by galling wasps, are hidden within a globoid or urn-shaped inflorescence called a syconium. This enclosed fig inflorescence likely originated from the invagination of a flat flower-bearing capitulum (Thorogood et al., 2018; Clement et al., 2020). The fig–fig wasp mutualism, which probably arose in Eurasia, is dated at 75+ mya (Cruaud et al., 2012; Rasplus et al., 2020), but a more recent date of 41–56 mya is suggested (Zhang et al., 2019) which matches the 49 my age of fig wasps (Peters et al., 2018).

The urn-shaped fig inflorescence with its compressed internodes (Verkerke, 1989) is closed off by an involucre of bracts, leaving a single opening or ostiole. Usually, female pollinators entering through the tight-fitting ostiole suffer wing and antennal breakage and other injuries; consequently, such females, called foundresses, can usually visit only a single syconium within which they soon die. Syconia can be axillary, cauliflorous, or geocarpic being subtended on subterranean stolons (Baijnath and Ramcharun, 1983). Syconia range in size from a few mm in diameter (e.g., *Ficus tsjahela* in south India, RM Borges, pers. observ.) to 21 × 18 cm (*Ficus dammaropsis* from Papua New Guinea; Ezedin and Weiblen, 2019). Syconia contain tens (e.g., 50 in *Ficus mathewsii*) to thousands of flowers (e.g., 7000 in *Ficus pumila*) (Verkerke, 1989). Fig species are either monoecious (52%) with plants bearing syconia containing individual male and female flowers, or gynodioecious (48%) with plants bearing syconia with either only functional female flowers (female trees) or those with male and female flowers ("male" trees) (Basso-Alves et al., 2014; Rasplus et al., 2020; **Figure 1**). In monoecious species, all syconia give rise to seeds, pollen,

and wasps; however, in gynodioecious species, syconia on female trees give rise to only seeds while those on "male" trees give rise to only wasps (**Figure 1**). This sex-limited seed or wasp production in dioecious species is related to the longer style lengths of flowers in female trees which prevent female wasps from depositing eggs at the level of the ovule, resulting in zero reproductive success for foundress females entering syconia on female trees (**Figure 1**). In syconia of monoecious figs and of male trees in gynodioecious species, there is extreme protogyny, i.e., female flowers develop first and the interval between female and male flower development can be several weeks or months. This is likely an adaptation to the brood-site pollination mutualism, since one generation of pollinators brings in pollen to fertilize female flowers, but the next generation of pollinators that develops within the syconium carries pollen out of the syconium. Very recently, gynomonoecy was discovered in *Ficus umbrae* in Papua New Guinea (Ezedin and Weiblen, 2019); in this case, plants bear syconia with female flowers and non-functional male flowers as well as syconia with fully functional male and female flowers. Monoecy appears ancestral in *Ficus* (Weiblen, 2000; Rasplus et al., 2020); gynodioecy apparently appeared once, and monoecy has reappeared at least twice in gynodioecious clades (Ezedin and Weiblen, 2019; Rasplus et al., 2020). Unisexuality in *Ficus* flowers is achieved by stamen absence *ab initio* in female flowers, and by pistil absence *ab initio* or abortion in male flowers (Basso-Alves et al., 2014).

Glands on ostiolar bracts release volatiles (Souza et al., 2015; Hu et al., 2020) that attract pollinators to pollen-receptive syconia (Hossaert-McKey et al., 2010; Borges, 2016, 2018). The ostiole usually shuts after pollinators enter, but loosely arranged bracts sometimes allow the now wingless female pollinators to exit and visit other syconia on the same plant (Hu et al., 2010). The ostiole may also re-open at the wasp dispersal stage (Verkerke, 1989) so that the next generation of pollen-carrying females exit through the ostiole rather than through a passage through the syconium wall excavated by wingless males. Bracts may bear stomata (Verkerke, 1989) and secretory glands whose exudates seal the ostiole or contribute to antibiotic-containing fluid in the syconium lumen (Machado et al., 2013). The syconium wall has multi-layered parenchyma with sclerified cells and abundant latex-producing laticifers, and is covered externally by trichomes; these collectively constitute frontline defenses against parasitic gall-inducers or other herbivorous insects (Machado et al., 2013; Fan et al., 2019).

Monoecious figs have imperfect heterostyly, i.e., flowers are arranged in multiple layers with style lengths that are either normally distributed or have a positively skewed distribution; flower pedicel lengths often vary such that all stigmas reach the same level (Kathuria et al., 1995; Ganeshaiah et al., 1999) to form a fused synstigma by the coherence of groups of stigmas (Teixeira et al., 2021; **Figure 2**). The synstigma is typical of actively pollinated fig species (see later). Dioecious figs have perfect heterostyly; syconia on male trees have short-styled flowers, while those on female trees are long-styled (**Figure 1**). The synstigma allows pollen deposited at one location within this fused network to grow down a distant style at another location (Teixeira et al., 2021; **Figure 2**). This is analogous

FIGURE 1 | (A,B) The life cycles of gall-inducing pollinating fig wasps in monoecious and dioecious figs. The extreme sexual dimorphism and the lack of reproductive success in female trees in dioecious fig species is clearly depicted. Illustration by Priya B.R.

to the hyperstigma of *Tambourissa* (Monimiaceae) in which flowers are located within an invaginated cup (reminiscent of a syconium) closed by a mucilaginous hyperstigma (Endress, 1979). The reasons for apparent convergence in these traits need further investigation. The *Ficus* stigma is of the dry type (Heslop-Harrison and Shivanna, 1977), and must be punctured or gnawed by the pollinator ovipositor or mouthparts to initiate secretion of germination fluids (Ramírez-Benavides, 2007). Each flower has a single bitegmic ovule surrounded by two integuments (Galil et al., 1970; Baijnath and Naicker, 1989). The nucellus of each

ovule is crassinucellate (i.e., massive and well developed), and therefore can serve as food, especially for gallers (Verkerke, 1989). Each ovule is either anatropous, i.e., its micropyle (entrance to the ovule) is bent downward toward the point of basal attachment to the funiculus (**Figure 2**), or hemi-anatropous, i.e., with its micropyle at right angles to the funiculus (Galil et al., 1970; Verkerke, 1987). Owing to anatropy, pollen tubes have to grow down the style and curve around to enter the micropyle (**Figure 2**), a long path which may lend itself to pollen tube competition. Possibly due to the high specificity
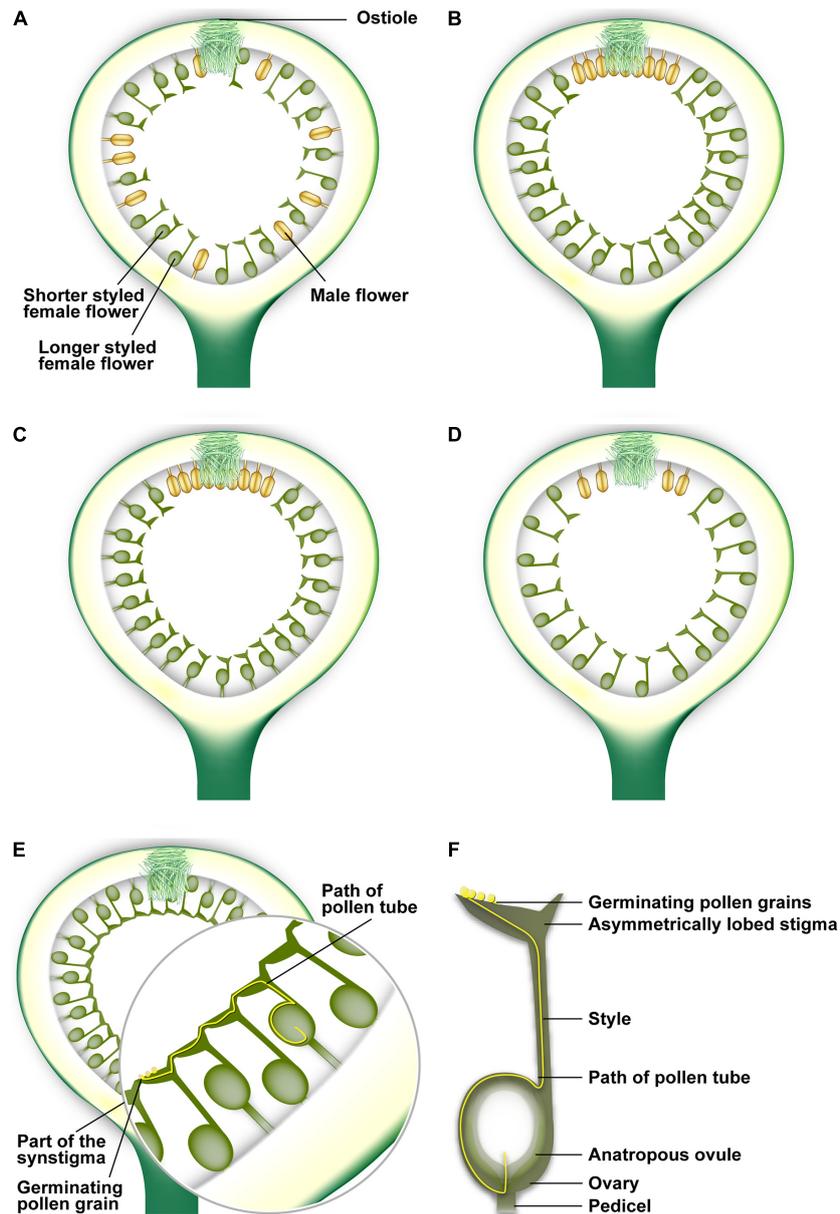
FIGURE 2 | Arrangement of flowers within fig syconia. (A) Passively pollinated syconia usually have male flowers interspersed with female flowers throughout the syconium. (B) Actively pollinated syconia usually have few male flowers near the ostiolar opening. (C) Distribution of short-styled female flowers and a few male flowers in a syconium on a male tree in a gynodioecious fig species. (D) Distribution of long-styled female flowers in a syconium on a female tree in a gynodioecious fig species. (E) The synstigma in the syconium of an actively pollinated fig species showing longer-styled flowers with short pedicels and shorter-styled flowers with long pedicles. The potential path of a pollen tube taken in a synstigma is also shown. (F) The potential path taken by a pollen tube after germinating on an asymmetrically lobed stigma and traversing down the style to enter the micropyle of an anatropous ovule. Illustration by Priya B.R.

between figs and pollinators, *Ficus* lacks self-incompatibility systems that recognize pollen genotypes (Hossaert-McKey and Bronstein, 2001; Ramírez-Benavides, 2007); this may explain why hybridization potential is frequently recognized between different *Ficus* "species" (Wei et al., 2014; Ghana et al., 2015a).

Syconia are well endowed with latex, which is often effective against herbivory (Ramos et al., 2019). Although laticifers occur throughout the syconium wall, they are precisely distributed in floral tissues (Marinho et al., 2018). For example, laticifers are absent from pistils, which will develop either into seeds or support gall-inducing pollinator larvae, and also do not occur in stamens; however, they are present in ostiolar bracts, sepals, and flower pedicels (Marinho et al., 2018). Inappropriate localization of latex could interfere with pollination, oviposition, stamen excision and safe exit from galls and may explain their precise distribution (Marinho et al., 2018). Moreover, laticifer

distribution may also restrict galler larvae to single galls derived from uniovulate flowers, since movement between galls and feeding on extra-gall tissue could result in severance of laticifers resulting in entrapment in latex. How restricted feeding within a single gall has affected larval and adult size is unknown. Latex leakage is prevented by callose and suberin in laticifer walls (Teixeira et al., 2020) and rapid occlusion of laticifers on damage (Shi et al., 2019). Inflorescence laticifers are unlikely to be a synapomorphy in Moraceae as hitherto believed since laticifers occur within the inflorescence and other plant tissues in Urticaceae and Moraceae (Marinho and Teixeira, 2019); however, in non-*Ficus* species within Moraceae, laticifers also occur in the ovary and style (Marinho and Teixeira, 2019) whereas they are absent from such tissues in *Ficus* suggesting that the syconium may be the only brood-site in a latex-rich host plant wherein laticifer distribution is specifically adapted to the mutualism with gall-inducing pollinators.

Another trait critical to the mutualism between figs and galler fig wasps is flowering phenology (Addicott et al., 1990). *Ficus* flowers aseasonally, usually showing a neutral response to photoperiod; flowering is usually synchronous within plants (Gates and Nason, 2012; Krishnan and Borges, 2014). However, at the northern limit of its sub-tropical range and in fig species located in temperate regions, e.g., *Ficus carica* in southern Europe, flowering phenology matches seasonal temperature fluctuations and may also include over-wintering syconia that keep pollinators alive through the winter (Kjellberg et al., 1987; Zhao T. T. et al., 2014; Chen et al., 2015). While the molecular basis of short- or long-day flowering is known (Singh et al., 2017), that for day-neutral flowering, as generally occurs in *Ficus*, is barely understood (Lu et al., 2020). In *Ficus carica,* which has a 5-month fruiting period before entering winter dormancy, *FcFT1*, a *FLOWERING LOCUS T*-like gene, and *FcLFY*, a homolog of the *FLORICAULA/LEAFY* gene, are involved in inflorescence differentiation (Ikegami et al., 2013; Ma et al., 2020).

Syconium development times also vary between species; wasp and seed development phases can range from 15 to 100 days (Ramírez-Benavides, 1974) and this may be dependent on syconium size. Since syconia are largely animal-dispersed (Shanahan et al., 2001), they must become attractive to fruit dispersers only after pollinators have left the syconium; ripening prior to pollinator dispersal would result in pollinators being consumed by frugivores. Some fig fruit, however, ripen slowly while others ripen very rapidly; the reasons for these differences are barely investigated (Borges et al., 2011).

TRAITS OF GALL-INDUCING FIG WASPS

Pollinator Wasps

Female pollinator wasps have morphological adaptations that facilitate entry between the ostiolar bracts into the syconium (van Noort and Compton, 1996). If only a single foundress wasp enters a syconium, her offspring will experience sib-mating. Therefore, pollinators must tolerate some level of inbreeding (Greeff et al., 2009) since syconia with only single foundresses do occur. The offspring of fig wasps with their

haplo-diploid breeding system (unfertilized eggs developing into males; fertilized eggs developing into females; **Figure 1**) experience local mate competition (LMC) (Hamilton, 1967) since the syconium is an enclosed mating arena. The first foundress has a female-biased offspring sex ratio, while the offspring ratio of late-entering foundresses is more male-biased (Kjellberg et al., 2005). Eggs destined to be males are laid first followed by females (Raja et al., 2008); females modulate egg-laying decisions based on their own clutch sizes and those of competing foundresses (Greeff and Newman, 2011). How they achieve this is unknown, although they may estimate egg load remaining after each bout of oviposition (Raja et al., 2008; Zhang et al., 2020). Fighting between foundresses results in fewer eggs laid by the weaker competitor (Moore and Greeff, 2003).

The extreme inter-sexual dimorphism of fig wasps (**Figure 1**) has been selected by mating conditions of the syconium in which the syconium is the mating arena; mating usually occurs only within the syconium (Cook et al., 1997; Weiblen, 2002). Sexual dimorphism in clock gene expression results in males eclosing and leaving their galls earlier (Gu et al., 2014) to gain access to unmated females. In species in which several foundresses enter syconia, resulting in a more balanced offspring sex ratio, males engage in aggressive combat (Greeff et al., 2003).

Pollinator males also cooperate to release pollen-carrying females by collectively tunneling through the syconium wall (Suleman et al., 2012) usually near the ostiole; why the ostiole is avoided as an exit point is unknown. Males may also excise anthers of the unisexual male flowers that have only recently developed due to the extreme protogyny of the syconium; however, anthers may also dehisce spontaneously. Pollen is dusted over females (in passive pollination) or is actively gathered by females into their special thoracic pockets (in active pollination). In passive pollination, the pollen that coats females entering a female-phase syconium will passively adhere to stigmas, while in active pollination, pollinator females will actively unload pollen from their thoracic pockets using special coxal combs and deposit pollen on the stigmas. In *Ficus,* transitions from passive to active pollination have occurred at least five times (Cruaud et al., 2012); however, active pollination may be ancestral (Rasplus et al., 2020). Anther location near the ostiole in many fig species (Basso-Alves et al., 2014) may direct male tunneling activities near the ostiole so that pollen can be loaded on females prior to their departure.

The few reported non-agaonid gall-inducing pollinators [e.g., the pteromalids *Diaziella* (Sycoecinae) and *Lipothymus* (Otitesillinae)] enter through the ostiole like agaonids (Jousselin et al., 2001; Zhang F. et al., 2009). However, these non-agaonids can service only passively pollinated fig species and require agaonid pollinators within the syconium for successful reproduction. They may therefore be considered supplemental pollinators and have converged on agaonid traits for entering the syconium via the ostiole, e.g., flattened head and mandibular appendages (van Noort and Compton, 1996).

Adult pollinators do not feed; males usually die after mating and releasing females from the syconium. Therefore, pollinators are capital breeders that only utilize resource capital

acquired during development; females are pro-ovigenic and eclose with a full complement of mature eggs, a trait that is a likely consequence of their short life spans (usually 24–48 h) (Ghara and Borges, 2010).

Non-Pollinating Gall-Inducing Wasps

Sycophilic non-pollinating gallers also exhibit extreme sexual dimorphism in addition to wingless or winged males, weapon polymorphism and competition for females (Wang et al., 2010; Cruaud et al., 2011). Some gallers enter through the ostiole (especially in the Old World, e.g., *Sycophaga sycomori*), while most oviposit into the syconium from outside. Those entering through the ostiole are usually unable to re-enter other syconia owing to injuries sustained during ostiolar passage while those ovipositing from outside could deposit eggs in multiple syconia. These gallers are often pro-ovigenic capital breeders with short or more extended lifespans of one day to several days (Ghara and Borges, 2010; Elias et al., 2018a). Sometimes, former mutualists have evolved into completely exploitative gallers but at the cost of reduced fitness, e.g., a cheater *Eupristina* species in *Ficus altissima* (Zhao J. B. et al., 2014). If sufficient suitable syconia are unavailable, older females distribute eggs over fewer syconia or oviposit into those that younger females would have avoided (Yadav and Borges, 2018a), indicating that age influences oviposition decisions. Since the female may deposit several eggs into the same syconium under these circumstances, possibly resulting in sib-mating, such wasps also must tolerate inbreeding as do pollinating fig wasps. Females, that oviposit from outside the syconium, use cues, such as chemical footprints left on the syconium surface by previously ovipositing conspecifics, to make oviposition decisions (Yadav et al., 2018). Since several females often oviposit in the same syconium, sex ratios are less likely to be female-biased, leading to the evolution of even greater male competitive ability (Nelson and Greeff, 2009a).

Community Structure of Fig Wasps Occupying the Syconial Microcosm

Worldwide, there is convergence in the community structure of fig wasps occupying fig syconia with a set of small-, medium-, and large-sized gallers and their corresponding parasitoids (Cruaud et al., 2011; Segar et al., 2013; Darwell et al., 2018). There appears to be a limited number of ways in which wasp communities can be assembled in a syconium, and the duration of the window of development time within which a syconium is suitable for oviposition appears to dictate the stability and diversity of its occupants (Venkateswaran and Borges, 2021). Prior to pollinator arrival at the syconium during the pollen-receptive stage, early-arriving gallers induce a few very large galls that protrude prominently into the syconium lumen. Gallers that arrive either just before or concomitant with the pollinators usually induce medium-sized galls or galls of the same size as pollinators. Generally, there is great host-plant specificity, especially among early-arriving gallers (Farache et al., 2018a). A notable exception is *Idarnes flavicollis,* which colonizes syconia during the pollen-receptive phase and exploits at least 6 *Ficus* species (Farache et al., 2018a). This may be due to its ability to recognize a generalizable blend of "*Ficus*" pollinator attraction scent (Proffit et al., 2020) across these species; such a hypothesis has explained polyphagy in fruit flies (Biasazin et al., 2019). The results may also be explained by cryptic *Idarnes* species, each associated with a different *Ficus* species. More research is required to distinguish between these possibilities.

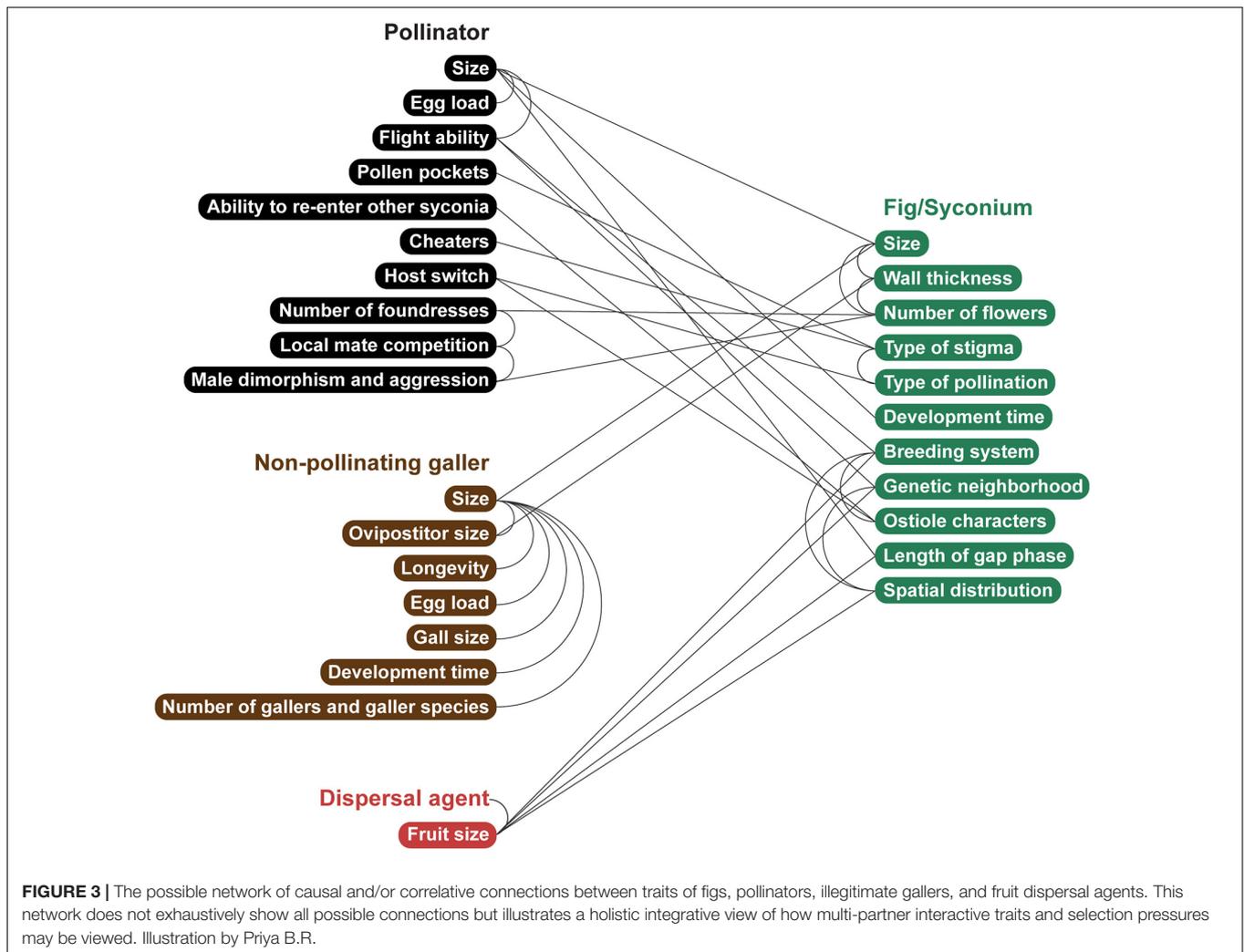# RELATIONSHIP BETWEEN FIG SYCONIUM TRAITS AND TRAITS OF GALL-INDUCING SYCOPHILES

In this section, connections are made between fig and wasp traits (**Figure 3**). Here, there is no assumption about causation, and many connections are hypotheses that await testing; these patterns may have been observed in a few species, or not at all; consequently, this section intends to stimulate the focused collection of patterns across the 874 fig species described to date (POWO, 2020).

Syconium Size and Development Time

Syconia can vary from few mm to many cm in diameter between species; smaller syconia likely have smaller and fewer flowers. Smaller flowers are likely able to support smaller wasps which may have intrinsically lower flight ability given the energy expenditure required for flight (Venkateswaran et al., 2018). Figs with small syconia are most often pollinated by smaller wasps (Murray, 1985). Even though fig wasps are largely wind-dispersed, they vary considerably in intrinsic flight ability (Venkateswaran et al., 2018). Figs with smaller syconia may therefore have smaller genetic neighborhoods of wasp-mediated pollen transfer. Smaller syconia, when ripe, are also likely consumed by smaller frugivores with smaller dispersal distances, further contributing to more local gene movement. Since body size and ovipositor size are correlated in agaonids (Murray, 1985), and ovipositor size determines access to precise locations within each flower, it is likely that flower size and body size traits of gallers are closely related (**Figure 3**). The matching of these traits by either exaptive or co-evolutionary processes (Janzen, 1980) needs investigation. It is expected that trait values will stabilize to prevent over-exploitation of the mutualism by pollinators with overly long ovipositors (Murray, 1985).

If ovipositor sizes determine the exploitation of flower sizes by pollinators, then host switches in fig wasps may occur more often between figs and wasps whose flower and ovipositor sizes are compatible. Therefore, host switches may largely involve sister species as has been found in dioecious figs (Yang et al., 2015). Smaller syconia with smaller flower numbers are likely visited by fewer numbers of foundresses. Consequently, larger syconia are likely to have more inter-foundress competition, less male-biased sex ratios and more aggression among males (Nelson and Greeff, 2009a).

Syconium wall thickness may be related to syconium size and may limit exploitation by gall-inducing fig wasps that oviposit from the exterior. Early-arriving gallers have shorter ovipositors and fewer accessible sites compared to those arriving later in syconium ontogeny (Ghara et al., 2014). Ovipositors must

FIGURE 3 | The possible network of causal and/or correlative connections between traits of figs, pollinators, illegitimate gallers, and fruit dispersal agents. This network does not exhaustively show all possible connections but illustrates a holistic integrative view of how multi-partner interactive traits and selection pressures may be viewed. Illustration by Priya B.R.

also have appropriate armature and stiffness to penetrate the syconium wall (Ghara et al., 2011; Elias et al., 2018b). Large syconia with many more flowers likely support greater diversity of gallers compared to smaller syconia. Moreover, syconium development time is also affected by its contents, e.g., purely seed syconia take longer to develop compared to those containing only pollinators and illegitimate gallers (Galil, 1977; Krishnan and Borges, 2014). Furthermore, the duration of the pollen-receptive phase of individual syconia (which is usually only a few days) can be extended to more than 1 month if pollinators fail to enter the syconium (Gu et al., 2012; Zhang et al., 2012). While prolonged pollen-receptivity is likely an adaptation to stochasticity in pollinator arrival, older syconia, that have waited longer for pollinators to arrive, set lighter seeds and have a greater male-biased function (Gu et al., 2012); therefore, waiting for pollinators comes at a cost.

In dioecious figs, there is inter-sexual mimicry in syconium scent (Hossaert-McKey et al., 2016) to ensure equal attraction of pollinators to male and female trees, since pollinators entering syconia on female trees will have no reproductive success (**Figure 1**). However, in most dioecious angiosperms, flower number and size are larger in males (Barrett and Hough, 2013). In gynodioecious fig species, the constraints of intersexual mimicry may have caused syconium size to converge between the sexes, at least at the pollen-receptive stage, so that pollinator attractive scent varies neither in quality nor quantity (Raja et al., 2016) resulting in equal probabilities of visitation to both sexes. Divergence in attraction resulting in unequal probability of visitation to both sexes will destabilize the mutualism.

Ostiolar Traits

The ostiole of the syconium may be permeable without stringent filters allowing unrelated non-pollinating gall-inducing fig wasps to enter. However, cheater sister species of pollinators may even be able to breach a stringent ostiolar filter (Zhao J. B. et al., 2014). Ostiolar features may select for smaller wasps, since larger individuals may be excluded by the ostiolar passage (Liu et al., 2013). Spontaneously re-opening ostioles may contribute to greater fitness for foundress pollinator females by allowing oviposition in multiple syconia (Suleman et al., 2013) and those females that lay eggs in multiple syconia may be less prone to the consequences of LMC. In some dioecious figs, foundresses

are more likely to re-emerge from older syconia, suggesting that syconium quality affects re-emergence (Raja et al., 2014).

Type of Stigma and Pollination

Synstigmas occur in 67% of figs, more often in monoecious and actively pollinated species (Teixeira et al., 2018, 2021). Stigmas of long-styled flowers in dioecious and monoecious species have greater pollen capture area compared to short-styled flowers (Jousselin et al., 2004; Teixeira et al., 2018). However, synstigmas preclude precise targeted pollination (Jousselin and Kjellberg, 2001) since pollen tubes can grow through synstigmatic tissue to enter styles distant from pollen deposition (**Figure 2**). Since wasps develop more successfully in pollinated flowers, how pollen tube growth in a synstigma network can be ensured in a flower in which a pollinator has deposited an egg is as yet unknown. Similarly, with a synstigma, it would be difficult if not impossible, to sanction cheater wasps that do not pollinate but only oviposit in the syconium, if the syconium has been also entered by cooperative non-cheater pollinators. These anatomical features may explain the nature of the sanctions described in figs against cheater pollinators (Dunn, 2020).

Actively pollinated figs usually have smaller pollen–ovule ratios compared to those with passive pollination since there is much less pollen wastage and more precise pollen deposition (Pellmyr et al., 2020; but see Deng et al., 2016). Pollinator traits for active pollination (pro-thoracic pockets, coxal combs for pollen removal from the pockets) appear labile and track pollen–ovule ratios of associated fig species (Cook et al., 2004). It is also interesting that although two carpels are initiated in each flower, only one carpel forms an ovule; consequently, the stigmatic surface is equivalent to that required by two carpels and two ovules, when in fact, the flower is uniovulate. The asymmetry between stigmatic surface and ovule number likely results from selection to increase pollen–ovule ratio in this highly specialized mutualism (Leite et al., 2020).

Length of Reproductive Quiescent Phase and Plant Connectivity

In many fig species, although plants flower aseasonally, plants become reproductively quiescent between flowering episodes and enter a "gap phase" (Krishnan and Borges, 2014). With a prolonged gap phase, at any given time there could be very few plants within a population that could accept pollen-carrying dispersing wasps; consequently, wasps may have to travel far to find suitable pollen-receptive trees. Wasp dispersal ability is, therefore, likely greater for those species with longer gap phases compared to those with shorter gap phases, all else being equal. Further, gallers with narrow time windows during which the syconium is suitable for oviposition are more likely to require a larger population of plants within which at least some syconia are in the right stage for oviposition (Venkateswaran and Borges, 2021).

Factors such as syconium development time, flowering synchrony, gap phase duration, and related traits such as wasp flight capabilities, which may be genetic as well as environmentally induced by variables such as syconium size and

time of wasp dispersal (e.g., windy or non-windy conditions), can also affect movement between plants and thereby their connectivity. Connectivity between plants is important in determining foundress number in individual syconia (Duthie and Nason, 2016) which in turn can affect wasp traits and mutualism outcomes (**Figure 3**). Connectivity between plants can also be affected by syconium size and seed dispersal agents (Harrison et al., 2012).

THE GALL-INDUCING PROCESS IN FIG WASPS: MANY LACUNAE IN KNOWLEDGE

Although many insects engage in gall induction (Espírito-Santo and Fernandes, 2007), the galling process is still poorly understood (Hearn et al., 2019; Takeda et al., 2019; Harris and Pitzschke, 2020; Raman, 2021). Shared signaling mechanisms and hormones between plants and insects can explain the hijack of plant development machinery in gall formation (Guiguet et al., 2016; Schultz et al., 2019; Dodueva et al., 2020). Gall-inducing insects target reactive tissue sites capable of differentiation, e.g., plant meristems (Weis et al., 1988; Ferreira et al., 2019). Furthermore, since galls are fixed structures housing developing insects, their locations are important (Weis et al., 1988) in terms of factors such as access to assured resources, protection, and development on relatively long-lived plant tissues. While gall-inducing insects may stimulate plant development by effector proteins (Giron et al., 2016), gallers themselves produce hormones such as auxin and cytokinin at levels many-fold higher than those in ungalled plants (Yamaguchi et al., 2012; Andreas et al., 2020) creating hotspots of tissue growth. Since auxin and cytokinins predominantly control meristem activity (Lee et al., 2019), whether their local abundance promotes de-differentiation and neoplastic activity resulting in new meristematic sites at ectopic locations (Carneiro et al., 2017) is worth investigating. Gall-inducing adults probably also introduce compounds such as cellulases and ectoapyrase with their ovipositors or their mouthparts, compounds which are likely important in the gall-inducing process (De Lillo and Monfreda, 2004; Cambier et al., 2019).

Gall-induction in figs has received scant attention. For a pollinator or a gall-inducing exploiter, the ability to gall is fundamental to interacting with a fig species (Ghana et al., 2015b). Pollinator galls perform better when larvae develop in pollinated compared to non-pollinated flowers (Jousselin et al., 2003). According to the unbeatable seed hypothesis (West and Herre, 1994), flowers closer to the outer syconium wall in monoecious figs are more likely to become seeds; such seed flowers are presumably metabolically different and unlikely to be galled. While this hypothesis has received some experimental support (Wang et al., 2013), it has never been decisively proved. However, genes involved in carbohydrate and flavonoid metabolism are up-regulated in gall flowers compared to seed flowers (Martinson et al., 2015), suggesting metabolic differences. Flavonoids are negative regulators and modulators of auxin

transport (Brown et al., 2001; Peer and Murphy, 2007); up-regulation of chalcone synthase and related flavonoid synthesis genes suggests that, by preventing transport of auxin out of gall flowers, auxin build-up occurs enabling gall formation. Vascular bundles present at the base of each uniovulate flower (Galil et al., 1970) supply nutrients to the galls from the host plant. In fig wasps, poison sac size and egg load are positively related (Martinson et al., 2014), suggesting an increased requirement for gall-inducing effector production with egg load.

Ovule dimorphism may explain the ability to induce galls in flowers as has been reported in dioecious *Ficus asperifolia* (Verkerke, 1987). The inner ovule integument in gall flowers does not completely surround the nucellus on the raphal side and the insect egg is deposited between the inner integument and the nucellus; consequently, the hatched larva gets easy access to the nourishing nucellus (Verkerke, 1987). However, in seed flowers, the inner ovule integument is complete on the raphal side. Periclinal (parallel) divisions of the raphal cells facilitate easier penetration of the ovipositor between raphal cell layers and those of the inner integument to reach this suitable oviposition site (Verkerke, 1987). In dioecious *Ficus carica*, seed flowers have a wetter stigma and obturator tissue whose secretions facilitate pollen tube growth through the style toward the micropyle (Beck and Lord, 1988) as occurs in other angiosperms (Losada and Herrero, 2017). However, gall flowers lack an obturator and have limited transmitting tissue secretions (Beck and Lord, 1988). A funnel-shaped opening in the style of gall flowers caused by the incomplete fusion of carpellary lobes and a cuticle lining the style in gall flowers likely facilitate style penetration by the ovipositor (Beck and Lord, 1988). In monoecious *Ficus citrifolia*, actively pollinating *Pegoscapus* wasps also oviposit between the nucellus and the inner integument of the ovary (Jansen-González et al., 2012). After mouth part sclerotization, the early instar larva feeds on hypertrophied nucellar tissue; later, after pollination, the endosperm proliferates and forms a syncytial nutritive tissue. Lack of pollination negatively affects larval development with an increased number of empty "galls" (bladders) signifying failed development (Jansen-González et al., 2012).

The non-pollinating galler *Sycophaga sycomori* enters *Ficus sycomorus* syconia through the ostiole and deposits its eggs into the embryo sac via the stylar route (Galil et al., 1970). Here, the proliferating nutritive tissue is nucellus and not endosperm, since even those syconia that are never pollinated (e.g., in Israel where pollinators are absent) result in completely developed syconia and production of parthenocarpic fruit. Similarly, in *F. citrifolia*, larvae of non-pollinating gall-inducing *Idarnes* species feed on hypertrophied nucellar tissue (Jansen-González et al., 2014). Although *Idarnes* oviposits into the syconium from the outside, its ovipositor uses the same route as the pollinators, i.e., insertion down the style (Elias et al., 2012), and the egg is deposited between the inner integument and nucellus (Jansen-González et al., 2014). That two unrelated gall-inducing wasps have converged on the same entry route to the identical egg deposition site in the same fig species, even though one wasp inserts its ovipositor from the exterior of the syconium, suggests ease of navigation via this route and/or abundant sensory cues that enable finding the right location. However, in the monoecious

Ficus curtipes which lacks a synstigma, the *Eupristina* pollinator does not insert its ovipositor down the style, but, most unusually, penetrates the style much below the stigma; this may also occur in other monoecious species that lack a synstigma (Zhang F. P. et al., 2009). If such style-bypassing oviposition behavior can evolve, then why longer style length deters successful oviposition in female trees in gynodioecious figs needs to be addressed. Gall-inducing sycophiles *Camarothorax* and *Otitesella* in monoecious *Ficus ingens* oviposit into ovules through the syconium wall during the late pre-pollen receptive phase since the syconium wall and ovary are not sclerified at this stage, and are easy to penetrate (Baijnath and Naicker, 1989).

Sycophiles ovipositing before the pollen-receptive phase, induce large galls, much larger than pollinator galls, and may also negatively affect the growth of syconia (Zhang and Li, 2020). Such gallers may oviposit directly into the early syconium lumen, even before flower primordia are formed, e.g., *Sycophaga stratheni* in *Ficus racemosa* (Ghara et al., 2014; Yadav and Borges, 2018b); these gallers likely stimulate ectopic meristems within the syconium lumen. Knowledge of specific egg deposition sites will enable a better understanding of the galling process. Gall sizes are usually characteristic of galler species (Compton et al., 2018; Yadav and Borges, 2018b), and may structure the entire community of gallers, inquilines, and parasitoids occupying the syconium (Borges, 2015a; Compton et al., 2018).

Gall location within the syconium may contribute to successful reproduction. In some species, e.g., *Ficus hispida,* pollinators developing in the center of the fig syconium (closer to the lumen) have more mating opportunities, produce more offspring, and also have a more-female biased sex ratio (Peng et al., 2014), suggesting that gall location is important in reproductive success. For unknown reasons, gall failure in dioecious *Ficus hirta* occurred more frequently in peripheral galls, closer to the syconium wall (Yu et al., 2018). In *Ficus hirta*, the pedicels of pollinator male galls elongate to move them closer to the lumen, increasing the likelihood of escape from parasitoid attack (Yu and Compton, 2012). However, the opposite was observed in the monoecious *Ficus racemosa* (Li et al., 2016) suggesting a variety of processes at work in different fig species. In most fig species, male pollinators are vital to prevent fig syconia from becoming tomb blossoms wherein the developed female wasps are unable to leave their nursery owing to the lack of sufficient males that can cut through the syconium wall to release them. Whether special features and adaptations are at work to protect the successful development of male pollinators needs to be a focus of investigation. It appears that unusual behaviors in fig wasp males, that are vital to the survival of wasps in these enclosed brood-sites, are selected for under unusual circumstances. For example, in Israel, non-pollinating *Sycophaga sycomori* males cooperate to release females from the syconium by tunneling through the syconium wall, a behavior normally performed by male pollinators in East Africa (Galil and Eisikowitch, 1968). Such behavior is critical for the success of *S. sycomori* in Israel where the pollinator is absent. While pollinators only develop in male trees in dioecious species, non-pollinating gallers, ovipositing from the exterior, can develop in syconia of male and female trees (Wu et al., 2013);

in such instances, male gallers release females from syconia on female trees (Wu et al., 2013). Similarly, male gall-inducing wasps *Walkerella yashiroi* and *Sycobia hodites*, associated with monoecious *Ficus microcarpa* and *Ficus benjamina* respectively, can release females independent of male pollinators (Wang et al., 2015; Farache et al., 2018b). How such behaviors have evolved is unknown. The large galls of *Idarnes* group *flavicollis* swell and block the ostiolar bracts, even entrapping pollinators at the syconium entrance (da Silva and Pereira, 2018). Since *Idarnes* requires pollinator males for release from syconia, a balance between pollinator and *Idarnes* galls within syconia is likely maintained over evolutionary time, but its mechanism is unknown.

The fig syconium is also host to inquilines, although their biology is barely understood (Cook and Rasplus, 2003). Inquilines are insects that parasitize a gall, starving out the galler larva and feeding on gall contents. In *Ficus curtipes*, the putative inquilines *Diaziella yangi* and *Lipothymus* sp. (Pteromalidae) oviposit into galls initiated by pollinators, but the galls and eclosing adults are larger than pollinators and pollinator galls, suggesting that these are secondary gallers, not strict inquilines, and capable of gall proliferation to some extent (Chen et al., 2013). Inquiline biology should clearly be an active area of research in this system.

A PLETHORA OF UNANSWERED QUESTIONS IN AN IDEAL MODEL SYSTEM

The fig–fig wasp mutualism has attracted the attention of ecologists and evolutionary biologists. Consequently, a diversity of interactions within the syconial microcosms have been uncovered. However, there are many facets that still need investigation. A list of additional important lacunae is presented below; this list is certainly not exhaustive but may serve to inspire new work on this iconic and unusual mutualism between plants and gall-inducing insects.

While sanctions imposed by fig plants on cheating pollinators have been documented (Dunn, 2020), there are no studies on the mechanisms underlying these sanctions. Similarly, there is no research on mechanisms of pollen tube competition and female choice in figs compared to the rich literature on this aspect in other angiosperms (Erbar, 2003; Lora et al., 2019). How mate choice may be exercised in those fig species possessing synstigmas is enigmatic and completely unknown. The synstigma forms a compitum (transmission tract) for pollen tube competition which may also contribute to male reproductive success (Teixeira et al., 2021). We, therefore, need good plant embryology coupled with egg deposition and larval development, and also good insect oviposition behavior observations as in older classic papers (e.g., Johri and Konar, 1955; Galil and Snitzer-Pasternak, 1970; Galil and Eisikowitch, 1974). We need simple but elegant experiments; e.g., Ramya et al. (2011) demonstrated that pollinators use broken-off wing density at the ostiole (resulting from wing remains of foundresses already within the syconium) to make decisions on which syconium to enter. Such cues may determine

foundress distribution across syconia within a plant helping to stabilize the mutualism (Borges, 2015b). We need to determine how syconia delay their development over longer or shorter time scales, from days to weeks to months. We need comparative studies of floral development across *Ficus* and its relatives (Leite et al., 2020).

We need sensory biology of oviposition coupled with the mechanobiology of ovipositor stiffness, steering, and egg-laying processes (Cerkvenik et al., 2019; Polidori and Wurdack, 2019; van Meer et al., 2020). That ovipositors of gallers can sense volatiles was established only for *Sycophaga fusca* in *Ficus racemosa* (Yadav and Borges, 2017) but must occur in other species also. We lack comparative studies of antennae and their sensilla as in cynipid gall wasps (Polidori and Nieves-Aldrey, 2014). We lack connections between life-history and sensory biology (Javoiš et al., 2019). We know nothing about waste management within the syconial microcosm as in aphid galls (Kutsukake et al., 2019) or how waste in a syconial microcosm, where hundreds of wasps develop, may be recycled. We require data on interactions between plant traits and larval trophic levels (Krishnan et al., 2015; Segar et al., 2018) and mode of feeding, since unusual reports of early instar larvae suspended in acellular gall fluid and ingesting a liquid diet (Yadav and Borges, 2018b) need wider validation.

We need observations that capture wasps in the act of a potential host shift (Michaloud et al., 2005). While monoecious figs often have large cross-continental populations serviced by single pollinator species or putative species complexes (Bain et al., 2016), they also share pollinators (Satler et al., 2019). Pollinator sharing is facilitated by matching flowering phenologies (Liu et al., 2015), but it must also be facilitated by the ability to enter syconia and induce galls, compatible development times, and so on. Similarly, dioecious species are likely pollinated by many different parapatric species of fig wasps that show genetic and morphological variation (Yu et al., 2019). We need a better understanding of the mechanisms supporting such variation. Experimental introduction of single foundress females into non-host figs resulted in successful development of more but smaller offspring, or fewer and larger offspring (Yang et al., 2012). The mechanisms underlying such results need to be discovered. While hybridization is frequently reported, we also need to understand why hybridization does not occur, e.g., possible polyploidy in *Ficus tannoensis* (Wachi et al., 2016).

Since syconia could be pollinated by just one foundress bringing in pollen from a single parent, this single source of pollen and of wasp eggs could give rise to traits of kin selection and cooperation between seed embryos (Bawa, 2016) and perhaps even among wasps. Sibling rivalry and parent–offspring conflicts affect brood size patterns in plants (Uma Shaanker et al., 1988) and placental animals (Fowden and Moore, 2012). However, seeds and pollinator galls usually lack obvious size variation, unless "bladders" or empty galls may be considered as possible outcomes of diverted resources resulting from resource conflict. This begs questions about sibling rivalry or lack thereof between pollinators developing in adjacent galls, and also between developing seeds. We, therefore, need genotyping of individual seeds and pollinator brood within syconia to answer these

questions and to couple them with positional and growth effects in the syconium.

It is undoubtedly interesting that the majority of plant-associated arthropods with intrasexually selected weapons are gall-inducers, e.g., Acari, Thysanoptera, Hemiptera, Diptera, and Hymenoptera (Rico-Guevara and Hurme, 2019). Like the microcosm of the syconium, which selects for sexual dimorphism as well as for male intrasexual competition (Nelson and Greeff, 2009b), the microcosm of galls in other plant families could provide similar selection pressures. Research on sexual selection in fig wasps should inform and inspire investigations in other gall-inducing taxa.

The hallmark of the interaction between figs and gall-inducing fig wasps is simultaneous seed and wasp development within jointly constructed brood sites (Borges, 2017). However, this interaction can be perturbed by climate change in various ways. Global warming likely affects insect development (Rebaudo and Rabhi, 2018; Huey and Kingsolver, 2019). Higher temperatures result in smaller syconia and smaller wasps (Krishnan et al., 2014), and higher fig wasp mortality (Jevanandam et al., 2013). We urgently need more data on such aspects. That fig microcosms can become model systems for understanding the impacts of warming on insect diversity cannot be overemphasized.

Since the fig syconium develops into a fruit, effects of pollinators and dispersers on the evolution of syconium traits need to be integrated (Harrison et al., 2012; Leonard and Francis, 2017; Valenta et al., 2017). We, therefore, need crosstalk between pollination biologists, sensory ecologists, plant development biologists, insect physiologists, and evolutionary biologists since the intricacies of the fig microcosm will only be revealed with such collaboration. While there is asymmetry in evolutionary rates and generation times between fig trees and mutualistic fig wasps, which may lead to faster speciation rates in the wasps (Souto-Vilarós et al., 2019), the fig partners appear to have the upper hand, and may win the evolutionary race. Is

this an example of the Red King effect (Borges, 2015b)? It is entirely possible that fig wasps are constantly chasing host figs because diverging too far away from the host would result in local extinctions. We could therefore be witnessing host chases rather than strict co-evolution (sensu Endara et al., 2017). Only good data on traits and trait evolution within a strong phylogenetic framework will provide the answers to such questions.

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The author confirms being the sole contributor of this work and has approved it for publication.

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