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How to be a fig nematode

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ABSTRACT

Fig (Moraceae: *Ficus*) species host vast communities of organisms that are bound together by complicated ecological networks that have influenced community structure and dynamics over evolutionary timescales. Much attention has been paid to the mutualism between figs and their specialized pollinating fig wasps, as well as with often antagonistic non-pollinating fig wasps. Equally ubiquitous to fig systems, but much less understood are the multitude of nematode groups that have independently evolved obligate associations with pollinating fig wasps and proliferate inside fig syconia. In this review we describe what is currently known (and unknown) about these numerous and increasingly studied nematode taxa and how they interact with the fig systems they inhabit. We identify the groups that are currently understood to associate with fig pollinators and outline their known species distributions and evolutionary history, where possible. Special attention is paid to the life history of these nematode groups, especially which features of nematode biology are generalizable across groups and what idiosyncratic peculiarities exist within individual genera. We outline key biological features including host choice, dispersal, disembarkation, diet, mating, and proliferation within figs. We address biological conundrums that have been raised following observational work such as, why do nematodes sometimes infect the wrong host? What adaptations were required for nematodes to successfully adapt and coexist with figs and their pollinators for millions of years? How do nematodes overcome the constraints of low mating group size? Finally, we outline key considerations, gaps in the knowledge, and limitations to expand this field forward towards promising areas of future research. Through better understanding of fig nematodes, we stand to not only know more about *Ficus* communities, but also more about the evolution and maintenance of interspecific interactions, development, adaptation, and co-evolution in general.

1. Introduction

All organisms are members of complex biological communities that are characterized by near-constant inter- and intraspecific interactions. These interactions can range in ecology from obligately mutualistic to intensely antagonistic and have undoubtedly shaped the evolution of individual species as well as the community. Therefore, a greater understanding of such interactions grants the opportunity to better understand community development and maintenance. A fascinating model system employed to study the evolution and maintenance of mutualisms and communities is the fig-fig wasp mutualism (Galil and Eisikowitch, 1968; Janzen, 1979; Cook and Rasplus, 2003; Weiblen, 2002). The obligate association between *Ficus* trees (Moraceae) and their agaonid pollinator wasp is ancient, dating back likely more than 75 million years (Rasplus et al., 2021). Fig communities have since become pantropical, with likely more than 750 unique species-pairs worldwide (Berg, 1989; Cruaud et al., 2012). Aside from the obligate association between the plant and their pollinator wasp, each fig community harbors a variety of additional species that range in ecology from secondarily mutualistic, commensal, or strongly antagonistic to their fig and wasp hosts. Much attention has been paid to non-pollinating fig wasps (NPFWs), who are ubiquitously associated with fig communities and generally utilize resources provided by the fig-fig wasp mutualism without offering any resources in return (Bouček, 1993; Borges, 2015). Through the examination of antagonistic impacts on the fig-pollinator fitness and stability we can better understand community modulation and the evolution of mutualisms in general.

Equally ubiquitous to fig communities, yet vastly understudied are the nematodes obligately and otherwise associated with fig wasp pollinators that proliferate inside fig syconia. There are over one hundred

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known nematode species associated with figs (Fig. 1). As many fig species have apparently not been examined for nematode occupancy or have no currently identified nematode taxa (Fig. 2), it is unclear how many fig and fig wasp species are associated with nematodes (and how many fig nematode species exist). However, the pace of fig nematode species discovery is accelerating despite relatively limited sampling across host *Ficus* groups (Figs. 1, **2**). Following, it is hoped that many more species will be described in the coming years, especially in geographic locations and *Ficus* subgenera that have been historically understudied. Consistent with this, it is reasonable to suspect that nematode diversity may scale with fig and fig wasp diversity. And although research in this field is rapidly expanding, with new taxa being described at a rate exceeding general nematode description (Fig. 1), our understanding of their role within fig communities, and even basic aspects of nematode biology and life history remain in its relative infancy. In this review we seek to describe our current knowledge of fig syconium-associated nematodes, identify (many) gaps in our understanding, and highlight future exciting avenues of research to help us better characterize this abundant and likely ecologically relevant member of fig communities.

1.1. Evolutionary history and species distribution

The association between pollinating fig wasps and their obligate nematodes is ancient. Dominican amber fossils aged 20–40 million years old (Poinar, 2015) identify a clear association between a female agaonid pollinator wasp and infective-consumptive juvenile nematodes (likely diplogastrid) classified as *Syconema dominicana* (Fig. 3) (Poinar, 2011). Given this age, it is likely that nematodes were already associated with figs and pollinating fig wasps at the onset of initial radiations out of southeast Asia (see (Cruaud et al., 2012)), which may help to describe their current pantropical distributions (Berg, 1989; Machado et al., 2005). Currently, fig nematode species can be observed in every continent containing fig communities (notably apart from South America). Although not yet sampled, Pharmacosycea and Urostigma figs that have defined associations with fig nematodes (Davies et al., 2017a, 2017b) in Central America also extend into northern South America and can be expected to have nematode associations with species that have already been described and/or currently undescribed taxa. The abundance and known distribution of such nematode groups is undoubtedly going to expand as sampling efforts increase (Fig. 1). Interestingly, fig pollinators often serve as hosts to multiple nematode species at the same time, often from divergent groups (Kruger et al., 2021; Jauharlina et al., 2015). It is known that the evolution of the parasitic lifestyle evolved multiple times independently across the Phylum Nematoda (Blaxter and Koutsovoulos, 2015; Blaxter et al., 1998). Thus, the phylogenetic distance between these extant nematode groups (Fig. 4) also suggests multiple independent origins of nematode association with fig wasps across fig community evolutionary history. Rates of pollinator wasp host switching are much higher than previously expected (Satler et al., 2019, 2023), suggesting that an evolutionary history of repeated interactions with divergent nematode groups was likely and presumably harbored significant ecological influence on nematode species persistence through competition or other interactions. The role of co-habitation between these nematode groups and the possibility of niche partitioning is an appealing area of future research that has not yet been explored.

1.2. Known nematode taxonomy

Extant nematode associates of figs and their wasps are numerous and diverse. Currently there are more than 16 recognized genera spread across 4 families and 2 Suborders of the Order Rhabditida that maintain an obligate association with fig wasp pollinators (although 6 of these genera are taxonomically disputed; Fig. 4, Table 1). The first described nematode associate of fig wasps was in 1864 with *Schistonchus caprifici* (Suborder Tylenchina: Family Aphelenchoididae), a plant parasite (specifically of fig florets) associated with the *Blastophaga psenes* pollinator wasp of the domesticated fig species *Ficus carica* (Gasparrini, 1864). In the following decades, *Schistonchus* species have become the most frequently described nematode group of fig pollinators, mostly (and most currently) associated with fig communities in Southeast Asia. However, due to polyphyly and potentially cryptic differences in life history within the group it has been recently broken into three separate genera: *Schistonchus*, *Ficophagus*, and *Martininema* (Davies et al., 2015).

In 1973, Martin (Martin et al., 1973) was the first to describe nematode associates of undomesticated fig species in Africa, and found a variety of hugely abundant nematode species from divergent families, often inhabiting the same fig community. One of these identified groups was that of the Family Diplogastridae (Suborder Rhabditina) that was later characterized by Poinar as *Parasitodiplogaster sycophilon* (Poinar, 1979) (and later redescribed (Wöhr et al., 2014)), a parasite of pollinating fig wasps. Following this description, *Parasitodiplogaster* species have been identified as pantropical associates of fig communities (with multiple species groups) in all appropriate continents except Europe and

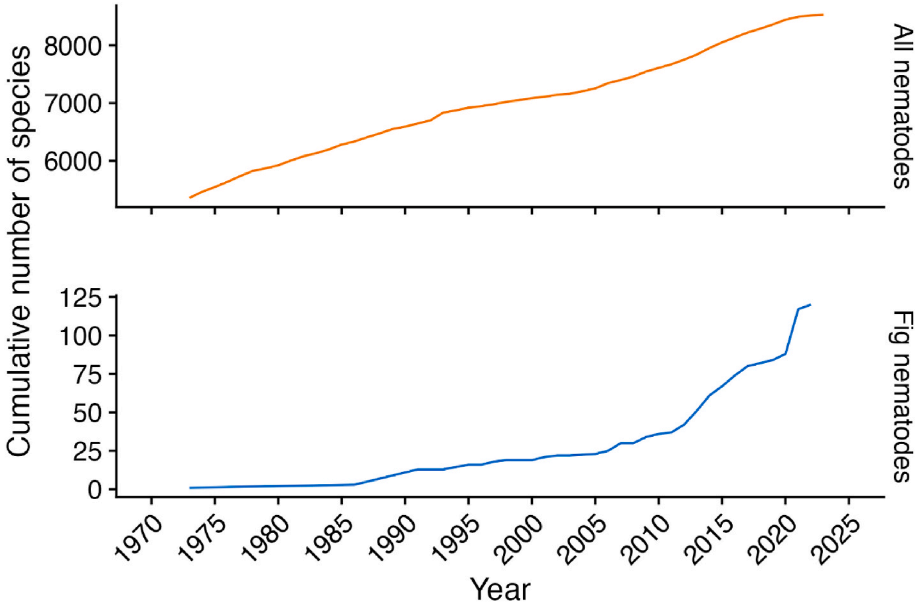

Fig. 1. The pace of fig-associated nematode species discovery. Plotted are the cumulative number of nematode species discovered per year— including all nematodes described (upper panel) and fig-associated nematodes specifically (lower panel). For all nematodes, data were retrieved from Nemys, the world database of nematodes (Nemys, 2022). For fig nematodes, all formally described species are included. Additionally, reported but undescribed species with molecular data suggestive of good species status are included. The current rate of species discovery suggests that more fig-associated nematode species remain to be discovered.

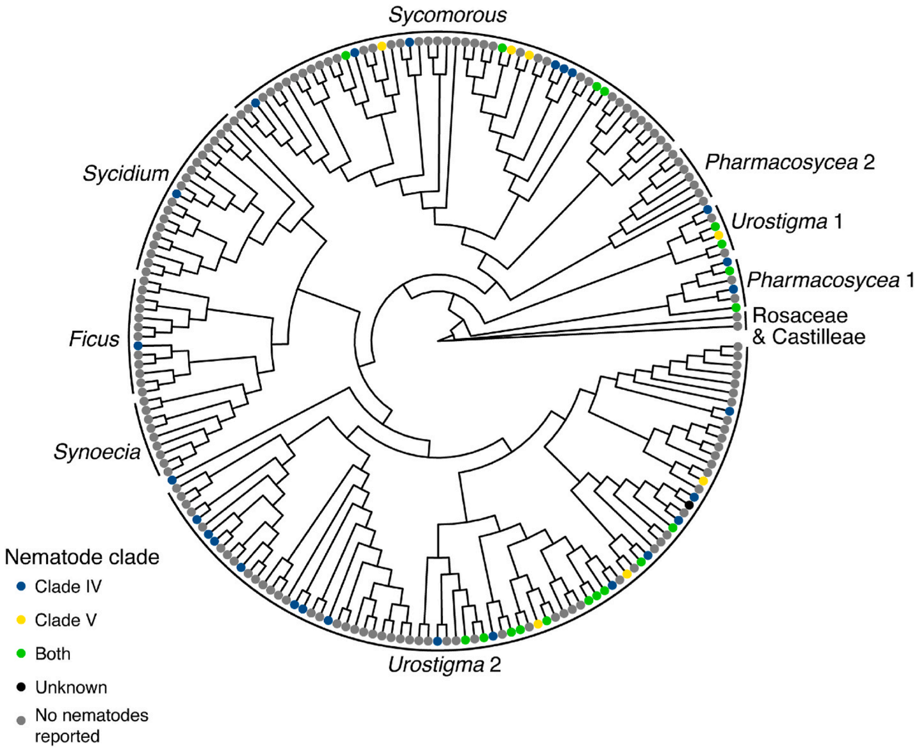

Fig. 2. Nematode fig-association across *Ficus* phylogeny. *Ficus* species are colored by the presence of Clade IV nematodes (*Bursaphelenchus*, *Ficophagus*, *Ficotylus*, *Martininema*, or *Schistonchus*), Clade V nematodes (*Acrostichus*, *Caenorhabditis*, *Parasitodiplogaster*, *Teratodiplogaster*, or *Pristionchus*) or both; in rare cases, nematode taxonomic information is not reported. Most *Ficus* species have no reported nematode species associated with their figs. The cladogram is based on the maximum clade credibility tree reported in Zeng et al, 2019) (Zhang et al., 2018). At least 70 *Ficus* species were found to have fig-associated nematodes in a literature search (Supplemental Table sheet 1); 14 of these species were not included in the Zeng et al, 2019 phylogeny (Supplemental Table sheet 2). Clades *Ficus*, *Pharmacosycea*, and *Urostigma* were found to be polyphyletic in Zeng et al, 2019); *Urostigma* and *Pharmacosycea* separations here presented as "1" and "2" respectively. Nodes were not scrutinized for bootstrap support.

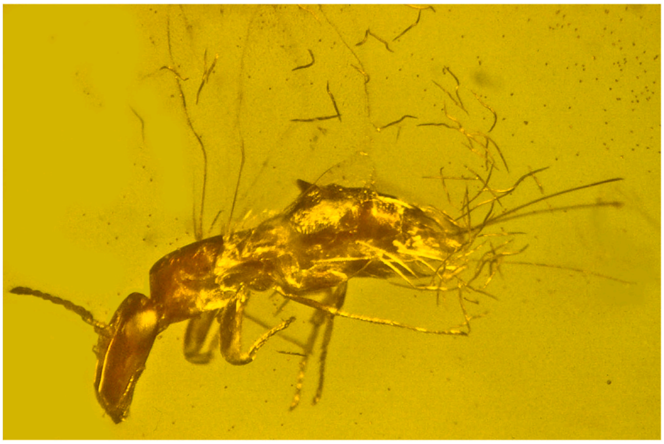

Fig. 3. Dominican amber fossil showing third and fourth larval stage (L3-L4) *Syconema dominicana* (Diplogastridae) nematodes associated with a female agaonid pollinating fig wasp. Such fossils provide convincing evidence of the ancient association between fig wasps and nematodes (at least 20–30 million years old). Photo courtesy of George Poinar.

South America and has since had a sister taxon described as *Teratodiplogaster* (Kanzaki et al., 2009). In addition, other diplogastrid genera are associated with fig pollinators, notably *Pristionchus* and *Acrostichus*, and more infrequently with *Rhabditolaimus* (Kruger et al., 2021; Gupta et al., 2021). In addition, there are a number of taxonomically disputed genera within Diplogastridae that may represent unique genera or may be congeneric to extant *Parasitodiplogaster, Teratodiplogaster*, or *Pristionchus* species groups upon further investigation. These genera include *Canalodiplogaster*, *Prodelphodiplogaster*, *Sigmodiplogaster* (all proposed in (Bajaj and Tomar, 2015)), *Ceratosolenus* (Anand, 2005, 2006), *Mononchoides* (Jauharlina et al., 2015), *Parasitocylindrocorpus* (Kruger et al., 2021; Martin et al., 1973; Lingaiah et al., 2012), and *Virenodiplogaster* (Bajaj, 2016). Far from being simple wasp-parasites, recent research has highlighted the ecologically complex and dynamic roles that Diplogastrids may play in the fig systems in which they interact (see Section 2). Our understanding of these roles and the basic biology of many of these species remains limited, offering the possibility of exciting future research efforts.

Aside from Aphelenchoididae and Diplogastridae, Martin also described the presence of plant-parasitic nematodes from the Family Cylindrocoporidae (Martin et al., 1973) (now identified as a Diplogastrid (Kruger et al., 2021; Susoy, 2012)). More recently, other divergent plant or fungal associated nematode groups have been described, including *Ficotylus* (Tylenchina: Anguinidae) (Kanzaki et al., 2022) and *Bursaphelenchus* (Tylenchina: Aphelenchoididae) (Kanzaki et al., 2022). The ecologies and evolutionary histories of these groups remain virtually unknown at present (Giblin-Davis et al., 2014) and may enter the synconium through another invertebrate other than the pollinating wasp. Excitingly, recently bacterivorous nematodes of the genus *Caenorhabditis* (Rhabditina: Rhabditidae) have been identified, including the closest known relative to the universal model organism *Caenorhabditis elegans* (Kanzaki et al., 2018).

Unsurprisingly, fig communities also harbor nematodes that are not strictly associated with pollinating fig wasps and are not confined to syconia, but likely coexist on the same trees as the nematodes described above (Kruger et al., 2021; Jauharlina et al., 2015). While these groups will remain outside of the scope of this current review, they include important, widely studied, and agriculturally relevant nematodes such as root-knot nematodes (Tylenchina: Heteroderidae: *Meloidogyne*) (Abrantes, 2008; Lima-Medina et al., 2013; Peraza-Padilla et al., 2013; Santos et al., 2020; Maqbool et al., 1987), cyst nematodes (Tylenchina: Heteroderidae: *Heterodera*) (Maqbool et al., 1987; Krnjaic, 1975; Sun et al., 2017), and dagger nematodes (Dorylaimina: Longidoridae: *Xiphinema*) (Wyss et al., 1980; Coiro et al., 1987; Aumann, 1997). Other lesser studied nematodes have also been described such as foliar (Tylenchina: Aphelenchoididae: *Aphelenchoides*) (Maeseneer, 1964; Marlatt, 1970) or spiral nematodes (Tylenchina: Hoplolaimidae: *Helicotylenchus*) (Santos et al., 2020). In addition, dead and dying wood of *Ficus* trees are important food and habitat resources for bark and wood

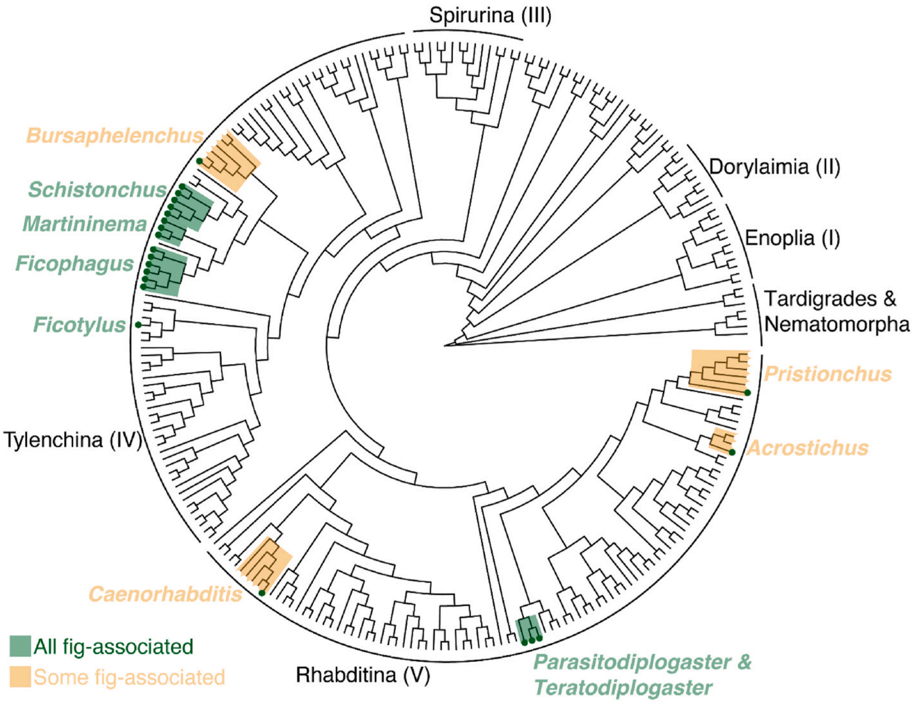

Fig. 4. Nematodes have evolved to thrive in figs at least eight times independently. Clades highlighted in green are from genera where all members of the genus are fig-associated (*Schistonchus*, *Martininema*, *Ficophagus*, *Parasitodiplogaster*, *Teratodiplogaster*; the genus *Ficotylus* has reported two species— *F. congestae* is associated with fig interiors (Davies et al., 2009) whereas *F. laselvae* is associated with the exterior bracts of figs (Giblin-Davis et al., 2014)). Clades highlighted in yellow are members of genera where most known species are not fig-associated (*Bursaphelenchus*, *Caenorhabditis*, *Pristionchus*, and *Acrostichus*). Genera whose taxonomic status (or fig-association status) are in dispute are not labeled here. The cladogram is based on maximum likelihood trees inferred in (Ahmed et al., 2022). Their Rhabditina (file "Ahmed_Rhabditina_IQTREE_Fullname_output.treefile") and Tylenchina (file "Ahmed_Tylenchina_IQTREE_Fullname_output.treefile") trees were merged with their Nematoda tree (file "Ahmed_nematoda_IQTREE_PMFS_Fullname_output.treefile"), and duplicate species were removed. Fig-associated groups were added to this backbone tree following these reported phylogenetic relationships (Susoy et al., 2016): (Rhabditina, including diplogastrids) (Kanzaki et al., 2014a), (aphelenchids) (Giblin-Davis et al., 2014), (*Ficotylus*) (Kanzaki et al., 2018), (*Caenorhabditis*), and (Susoy et al., 2016) (*Pristionchus*). Fig-associated clades were pruned to include a maximum of five species for the purposes of illustration (*Caenorhabditis* and *Pristionchus* have many sequenced genomes compared to other nematode groups, and these were pruned as to not suggest that most nematode diversity is in these groups). Clades are labeled I–V following (Blaxter et al., 1998). All labeled clades are strongly supported by the previously cited phylogenetic analyses and suggest at least eight independent shifts to the fig environment. Unlabeled internal nodes were not scrutinized for bootstrap support.

insects and their associated nematodes, all of whom likely perform ecologically relevant, yet currently underappreciated roles related to nutrient-cycling within fig communities. Notably, *Ficotylus laselvae* is associated with exterior fig bracts (Giblin-Davis et al., 2014), although the only other member of the genus thrives in syconia (Davies et al., 2009). Despite their reduced attention here, one cannot undermine the ecological importance of non-syconia associated nematode in nature or on the cultivation of domesticated figs (Sarkosh et al., 2022), and a wealth of future research focused on these groups should be happily warranted.

2. How to be a fig nematode: life history and association with fig communities

Although nematodes are environmentally ubiquitous and display immense species diversity, most extant species are tremendously mobility limited without the assistance of a vector (Borges, 2022) (though notable exceptions exist, as in (Ptatscheck et al., 2018)). This is undoubtedly true for fig nematodes, all of which described here are reliant upon pollinating wasp females as a phoretic vessel to a new fig environment for energetic resources and reproductive capability. As an additional generalized constraint, and like most other extant nematodes (Denver et al., 2011), all of the nematodes described here are gonochoristic organisms with separate male and female sexes (see Table 1) required for successful reproduction (Van Goor et al., 2021a). Within their lifetimes, all fig-syconia nematodes must be capable of contacting their wasp host, using them to disperse to a receptive fig, exit the host, consume energetic resources, possibly compete with hetero-specifics/generics, congregate and mate with conspecifics, and lay eggs within the fig environment before dying a short while later (Fig. 5). Even more drastically, they must be capable of synchronizing all these life history events with the development of their pollinating wasp host to ensure successful dispersal from a mature fig to ensure their own reproductive success. Failure to fine-tune and master any of these key events over evolutionary time would have certainly resulted in extirpation and extinction. However, the subsequent success of multiple divergent extant nematode groups accomplishing these intensely specialized behaviors represents interesting examples of parallel co-evolution. In this section we will describe what is known about these life history adaptations, peculiarities that exist between the different groups, and what remains unknown.

2.1. Birth, host choice, and dispersal (embryo – L3and/or dauer)

Despite multiple constraints that could have limited their evolutionary success as a group, fig nematodes are abundant in many fig communities, present in 40–50% (Gulcu et al., 2008; Van Goor et al., 2022) and sometimes as much as 80% (Van Goor et al., 2018) of sampled figs at particular localities. Before dying, inseminated adult female nematodes deposit embryos/eggs throughout the fig environment, often in close spatial proximity to developing pollinating females with which they are synchronized for timely departure (Giblin-Davis et al., 1995) (Fig. 5, fig stages B–C). Eggs/embryos molt directly into L2s (at least in the case of *Parasitodiplogaster* (Ramírez-Benavides and Salazar-Figueroa, 2015)), who move throughout the fig environment, before molting again into infective juveniles (Giblin-Davis et al., 2006) (dispersal phase, see (Fielenbach and Antebi, 2008); Fig. 5, fig stage D). The food source facilitating the molt between L2-L3 is currently unclear for many groups but may be explained by a more omnivorous diet than previously assumed (see Section 2.2). In the dauer form there is the development of an ensheathed cuticular layer and/or a buccal plug that provides additional environmental resistance but prohibits the ability to consume food sources (Bartholomaeus et al., 2009). Dauer formation is a facultative state of diapause that is routinely employed in most diplogastrids

Table 1
The currently recognized extant groups of nematodes associated with pollinator fig wasps that proliferate inside of fig syconia. All fig-syconium associated nematodes are currently identified within the Order Rhabditida. Presented here are the Infraorder and Families, as well as the genera of these known groups, followed by their (often presumptive) sexual mode and diet. Citations are provided to indicate the sampling location of individual species by continent. Following taxonomic revision made by Davies ((Davies et al., 2015)) North American species previously referred to as *Schistonchus* are now identified as *Ficophagus*.

						Collection	Locality		
Family (Suborder)	Genus	Sexual Mode	Diet	Asia	Oceania	Africa	Europe	North America	South America
Anguinidae (Tylenchina)	*Ficotylus*	Gonochoristic	Plant Unknown		(Davies et al., 2009)			(Giblin-Davis et al., 2014)	
Aphelenchoididae (Tylenchina)	*Bursaphelenchus*	Gonochoristic	Plant	(Kanzaki et al., 2014a)		(Kruger et al., 2021; Kanzaki et al., 2022)			
	Ficophagus	Gonochoristic Possible ESD	Plant	(Davies et al., 2015; Gupta et al., 2021; Jauharlina et al., 2022; Shi et al., 2019; Zeng et al., 2019, 2020; Zhang et al., 2019; Zhao et al., 2022; Waghmare et al., 2022; Sriwati et al., 2017)	(Davies et al., 2015, 2020a; Lloyd and Davies, 1997)	(Kruger et al., 2021; Davies et al., 2015; Martin et al., 1973; Vovlas et al., 1998)		(Davies et al., 2017a; Davies et al., 2017b; Davies et al., 2015; Giblin-Davis et al., 1995; Center et al., 1999; Giblin-Davis et al., 2023; Ramírez-B et al., 2011; Decrappeo and Giblin-Davis, 2001)	
	Martininema	Gonochoristic	Plant	(Davies et al., 2015; Gupta et al., 2021; Jauharlina et al., 2022; Shi et al., 2019; Sriwati et al., 2017; Zhao et al., 2020)					
	Schistonchus	Gonochoristic	Plant	(Jauharlina et al., 2015; Davies et al., 2015; Gupta et al., 2021; Reddy and Rao, 1986; Krishnan et al., 2010; Kolaei et al., 2016; Kanzaki et al., 2023; Bajaj and Tomar, 2014; Zeng et al., 2007, 2010, 2011, 2013a, 2013b, 2013c; Anand, 2002; Fard and Zare, 2020; Rajeshwarianand, 2002)	(Bartholomaeus et al., 2009, 2012; Lloyd and Davies, 1997; Davies et al., 2010, 2013a, 2013b, 2020b; Zhao et al., 2015)	(Kruger et al., 2021; Martin et al., 1973; Vovlas et al., 1998)	(Gasparrini, 1864; Gulcu et al., 2008; Vovlas et al., 1992; De Luca et al., 2010; Fursov, 2009)		
Diplogastridae (Rhabditina)	*Acrostichus*	Gonochoristic	Unknown	(Susoy et al., 2016)		(Kruger et al., 2021)			
	Parasitodiplogaster	Gonochoristic Possible ESD	Wasp Fungus Nematode	(Jauharlina et al., 2015; Bajaj and Tomar, 2015; Zeng et al., 2018)	(Bartholomaeus et al., 2009)	(Kruger et al., 2021; Martin et al., 1973; Poinar, 1979; Wöhr et al., 2014, 2015; Jauharlina et al., 2012; Kanzaki et al., 2012)		(Van Goor et al., 2018; Giblin-Davis et al., 1995, 2006; Ramírez-Benavides and Salazar-Figueroa, 2015; Herre, 1995; Kanzaki et al., 2010, 2013, 2014b, 2016; Poinar and Herre, 1991; Kanzaki and Giblin-Davis, 2010)	
	Pristionchus	Gonochoristic	Wasp Fungus Bacteria Nematode	(Gupta et al., 2021; Susoy et al., 2016)		(Kruger et al., 2021; Susoy et al., 2016)			
	Teratodiplogaster	Gonochoristic	Wasp Fungus	(Jauharlina et al., 2015; Gupta et al., 2021; Bajaj and Tomar, 2015; Kanzaki et al., 2014; Yousuf, 2012)	(Kanzaki et al., 2009)	(Kruger et al., 2021; Kanzaki et al., 2012)			
Rhabditidae (Rhabditina)	*Caenorhabditis*	Gonochoristic	Bacteria	(Kanzaki et al., 2018; Jauharlina et al., 2022)					

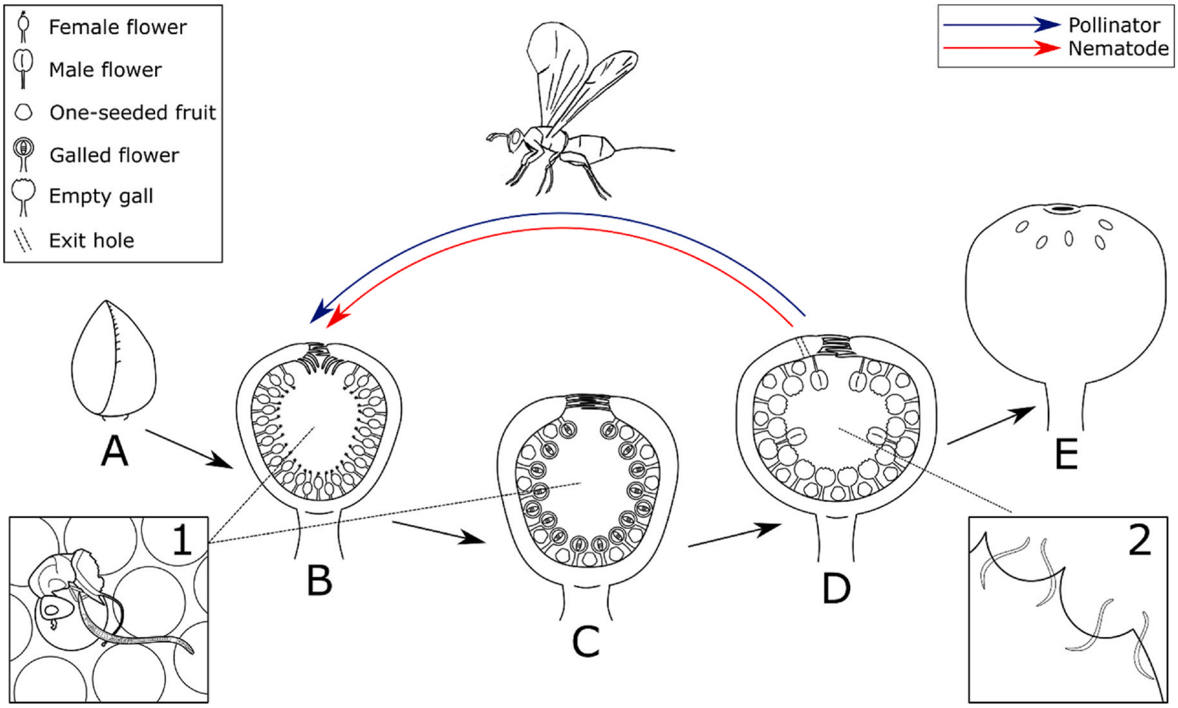

Fig. 5. Generalized lifecycle for fig nematodes that use pollinating fig wasps as vectors to proliferate inside of fig syconia. Over the phenology of monoecious fig species female pollinating fig wasps laden with fig nematodes enter through the ostiole of wasp-receptive figs (Phase B here, Phase A indicates the pre-receptive phase) to pollinating female flowers and lay her eggs before dying within. Nematodes molt into a consumptive phase (L4) before exiting the pollinator to reproduce in large aggregates (Image 1). Over the B and C phases nematode eggs will develop in close spatial proximity to developing wasp larvae and seeds. At late C phase and into early D phase (depending on genus) nematode eggs will molt into young juveniles (L2), before molting again into infective juvenile dispersal phase (dauer, L3s, or other). They will then perform nictation behavior (Image 2) to contact a fig wasp host as they are exiting the fig to start the cycle anew, before the fig becomes mature and falls from the fig tree (E phase). Some nematode species (Aphelenchoidids and others) may associate with their hosts at a variety of alternative life phases (ranging from embryos to L2s and beyond), highlighting some of the vast differences in life histories present between these groups that have coevolved with fig wasps. Figure courtesy of Finn Piatscheck.

but may not be required for other fig nematode associates, such as aphelenchoids (Giblin-Davis et al., 2003). Interestingly, aphelenchoid nematodes may associate with their wasp hosts at a variety of times outside of L3/dauer phases, with *Schistonchus* nematodes described in association with wasps in the L2 phase in *F. racemosa* (Reddy and Rao, 1986), and *Schistonchus* embryos, juveniles, and adults observed in association with the haemocoel of *F. carica* wasps in Europe (Vovlas et al., 1992). This is in contrast to other aphelenchoid nematodes such as *Ficophagus* in the US, wherein mated entomogenous females (L4) may colonize hosts alongside L3 dauers (Giblin-Davis et al., 1995), suggesting a multitude of mechanisms through which infection can take place outside of dauer formation for many fig nematode taxa. Microscopic and genomic work (such as that conducted in (Susoy et al., 2016)) could help parse apart the operative phases in which different fig nematodes disperse with their hosts and how variant this dispersal phase may be, which will impact our knowledge of the infectious dynamics of these nematodes and likely many others.

Interestingly, it appears as if dispersal-phase nematodes (dauers, L3s, and beyond) choose different locations within the figs to encounter their hosts, mostly depending on the nematode group. Diplogastrid nematode dauers appear to centralize on top of developing wasp galls, whereas dispersal-phase aphelenchoids position themselves on top of male flowers (JVG personal observation for *Parasitodiplogaster* and *Ficophagus* nematodes in monoecious Urostigma figs in Panama). Once at this “infective staging ground” these dispersal-phase nematodes locate wasps hosts using volatile and/or CO2 cues (Gupta et al., 2021) and perform nictation behavior (Campbell and Gaugler, 1993; Ogawa et al., 2015) to contact them. Once contacted, nematodes typically enter into the haemocoel or the internal body structure of the wasp, often centralizing within the abdomen or thorax (Van Goor et al., 2018; Giblin-Davis et al., 1995). Alternatively, *Caenorhabditis* nematodes (as well as other groups) may not enter the body cavity and may remain on the external portion or in cracks of the exoskeleton during dispersal (Woodruff and Phillips, 2018).

Some fig nematodes have been described as justifiably choosy about their hosts. Because (typically speaking) only a female pollinating fig wasp will enter into a new fig, selection should strongly discourage infecting anything *other* than such a wasp. Logically, *Schistonchus* nematodes associated with *Ficus racemosa* have thus been shown to correctly choose a pollinating fig wasp female over other wasp types, allowing for successful transmission and reproductive events (Krishnan et al., 2010). However, *Parasitodiplogaster* nematodes associated with *Ficus petiolaris* in Mexico and multiple Panamanian fig communities routinely infect NPFWs as well (Van Goor et al., 2021b), even though this is a reproductive dead end for them. This effect may be more widespread than previously believed, as well: *Schistonchus* nematodes of *Ficus carica* (Vovlas and Larizza, 1996) and *Parasitodiplogaster* nematodes of *Ficus laevigata* (Giblin-Davis et al., 1995) have been described associated with NPFWs (at least their ovipositors), but the fitness effects related to this infection have not been defined. Additionally, *Ficophagus*, *Martininema*, and *Caenorhabditis* nematodes have been shown to actively proliferate in female figs of the dioecious *Ficus hispida* even though this is also a reproductive dead end for them (because no pollinating wasp progeny are generated to disperse them) (Jauharlina et al., 2022). A hypothesis capable of explaining this “wrong choice” phenomenon is that these nematode species have evolved to *not* be particularly choosy about hosts – it’s better to make the wrong infection decision than no decision at all.

Nematodes infecting pollinating fig wasps are expected to not harm wasps while in transit to a new fig environment. Damaging or destroying their phoretic vessel would lead to their own certain mortality and failure to reproduce, thus all fig nematodes should have evolved periods of inactivity while in transit. Pollinating female fig wasps have evolved the ability to tolerate moderate levels of *Parasitodiplogaster* nematode infection, up to 10 individuals per host, without limitations to dispersal or reproductive ability (Giblin-Davis et al., 1995; Jauharlina et al., 2012). Overcrowding, or more than 10 individuals within a single host have been implicated in longevity experiments to lead to mechanical damage leading to early mortality or reductions in flight ability for *Parasitodiplogaster* associates of *F. petiolaris* in Mexico (Van Goor et al., 2018), *Ficophagus* and *Martininema* of *F. macrocarpa* and *F. hispida* in China (Shi et al., 2019), and *Schistonchus* and *Teratodiplogaster* associates of *F. racemosa* in India (Gupta and Borges, 2019). The nematodes of *F. racemosa* may utilize information about the numbers of other individuals already inhabiting a wasp host to prevent this overcrowding which may represent a viable mechanism through which nematodes help to ensure their own reproductive successes (Gupta and Borges, 2021). However, interestingly, it appears as if NPFWs are much more sensitive to nematode infection when it occurs. 25% of the most common NPFW (*Idarnes flavicollis* spp.) associated with *F. petiolaris* in Mexico are infected while exiting a *Parasitodiplogaster*-infested fig, and observational work suggests that infection of even a single nematode is greatly correlated with tremendous interruptions to their dispersal ability, and therefore their reproductive potential (Van Goor et al., 2021b). By eliminating antagonistic NPFWs these nematodes can offer an indirect mutualistic service to figs and fig wasps and may present an interesting and previously undefined community modulation. When NPFW abundance gets too high they are more likely to be infected with nematodes, and this nematode infection likely extinguishes their reproductive ability in general. Infectious events with community associates other than pollinating fig wasp females is likely more widespread than previously believed (occurring at least within Urostigma and Pharmacosycea figs (Van Goor et al., 2021b)), but further work is required to fully understand the extent and ecological role of this effect.

2.2. Arrival and diet (dauer or L3 – L4)

After their pollinating fig wasp host has arrived at a wasp-receptive fig and begins the process of pollinating and ovipositing eggs the dispersal-phase nematodes inside of her will begin molting into L4 stage (Giblin-Davis et al., 2006) (Fig. 5, fig stage B). This molting process (and the next molt into adult stages) is likely facilitated by diet and is often characterized by great body form elongation when compared to the dispersal-phase form. This body size elongation/expansion is significantly greater for fig nematodes than closely related nematodes that are not associated with figs, as can be seen in a comparison between the fig nematode *Caenorhabditis inopinata* and its sister species *C. elegans* (Woodruff et al., 2019; Hammerschmith et al., 2022). Is this increase in body form an adaptation to the fig environment? If so, what is the fitness benefit associated with this?

Many fig nematodes will not begin consuming or exiting the wasp host until she has died, which limits the fitness effects enacted upon her unless overcrowding occurs (see Section 2.1). Alternatively, many other nematodes inside the pollinating wasp foundress exit the host *before* she dies, such as while she is pollinating. These minimal fitness impacts have led some to conclude that certain *Parasitodiplogaster* (Van Goor et al., 2018; Ramírez-Benavides and Salazar-Figueroa, 2015; Jauharlina et al., 2012), *Schistonchus* (Vovlas et al., 1992; Gupta and Borges, 2019), *Ficophagus* (Shi et al., 2019), and *Teratodiplogaster* (Gupta and Borges, 2019) species act as commensals or necronemics within fig systems. However, this is likely tied to the population structure of the pollinating wasp host in which they interact and have co-evolved with. When fig species are routinely visited by only a single wasp foundress, the nematodes inside of her (which are highly likely to be full siblings) will have near strict vertical transmission mirroring their host wasp lineages over broad periods of time. However, in fig systems that are routinely characterized by multiple pollinator foundresses there could be the possibility of multiple nematode lineages interacting with each other and for horizontal transmission of offspring and lineages. This is expected to lead to competition for host resources among these nematode lineages, which is then expected to drive the evolution of more virulent nematode species (Anderson et al., 1991). This effect has been demonstrated for *Parasitodiplogaster* species associated with several Panamanian figs (Herre, 1993, 1995) and may showcase nematodes that function ecologically more as “true” parasites or antagonists than commensals. Thus, the ecological role of individual nematode species (even within the same genera) is a complex issue that is tied to the broader community dynamics and evolutionary history of the fig system they inhabit.

Plant-consumptive nematodes have not thus been described having enacted strong fitness consequences on their wasp or fig hosts and are generally considered to be commensals. However, the bulk of the current research on plant-parasitic groups such as *Schistonchus*, *Ficophagus*, and *Martininema* have focused on species descriptions and not on ecological role within fig systems, which is certainly an interesting area of future exploration. Strangely, *Ficus petiolaris* figs infested with *Parasitodiplogaster* nematodes produce significantly more seeds than uninfested figs (Van Goor et al., 2021b); an effect which is still not completely understood. Likewise, it is still unclear how multiple nematode groups inhabiting the same wasp host and fig environment influences the ever-expanding and complicated interaction webs occurring within fig communities. Recent efforts have highlighted an extensive nematode diversity present within the same fig, often interacting with the same pollinating fig wasp species (Kruger et al., 2021; Jauharlina et al., 2015). While it has been speculated that co-habitation can lead to interspecific conflict (Giblin-Davis et al., 1995), there may alternatively be surprising and unforeseen community level-benefits (Bronstein and. Bronstein, 2015), which should be examined carefully in the future.

Dauers are incapable of consuming resources (as they are often ensheathed, harbor a buccal plug, and are metabolically inactive) (Bartholomaeus et al., 2009). Some developmental cue triggers dauer exit (see (Butcher et al., 2008; Mylenko et al., 2016)) into the fourth larval stage (L4), but this cue in fig nematodes remains unknown. A possible hypothesis could be that the mechanical damage suffered by the wasp as she enters the syconium through the ostiole, which often greatly damages the abdomen or other body tissues may inform this nematode molt. Alternatively (or additionally), nematodes may perceive volatiles or other chemical cues presented in the receptive fig (florets, etc.) to begin the molting process. Once molted, nematodes will commence consuming different tissues within the fig. Members of the Family Aphelenchoididae (*Schistonchus*, *Ficophagus*, *Martininema*, *Bursaphelenchus*) will generally exit their host unharmed and parasitize developing fig florets, often resulting in mild necrosis to these tissues without limiting plant fitness (Giblin-Davis et al., 1995, 2023; Vovlas et al., 1992; Krishnan et al., 2010; Center et al., 1999). Consistent with the notion that mycophagous nematodes lineages often evolve specialized interactions with Arthropods that frequently result in plant parasitism (Giblin-Davis et al., 2003), *Bursaphelenchus* associates are believed to be obligate plant parasites (Kanzaki et al., 2014a) even though all of their close relatives are fungivores, facultative plant consumers, or predators (Kanzaki et al., 2019; Kanzaki and Giblin-Davis., 2020). Members of the Family Diplogastridae (*Parasitodiplogaster*, *Teratodiplogaster*, *Pristionchus*, *Acrostichus*, etc.) have been classically associated with wasp parasitism and consumption (Poinar, 1979; Giblin-Davis et al., 1995), though their true ecological context may be much more complex (see below). The newly described *Caenorhabditis* species (Family Rhabditidae) associated with figs are almost certainly bacteriovorous like other members of the genus (Woodruff and Phillips, 2018) or may feed on other particulate matter. Finally, the diet and ecology of other known fig nematodes remains unclear, notably for the genus *Ficotylus* (Family Anguinidae) (Giblin-Davis et al., 2014), on top of the myriad of nematode groups that have yet to be described. Metagenomic barcoding of prokaryotic, protist, fungal, plant, other nematode and/or insect sequences on individual nematodes (as in (Susoy et al., 2016)) may be used in the future to disentangle these relationships to help determine the functional diet of these taxa.

Interestingly, several nematodes associated with figs have been suspected, and in some cases documented demonstrating an omnivorous lifestyle. This has been highlighted most thoroughly in the Diplogastridae, specifically in *Pristionchus* associates of figs in Africa and Southeast Asia (Susoy et al., 2016), as well as in *Pristionchus* species not associated with figs (Giblin-Davis et al., 2003). Here, research has showcased vastly different mouthparts for individuals of the same species (polyphenism) that is correlated with the food sources available to the individual nematodes. Further, the abundance and utilization of these different stomal morphs appear at significantly higher levels than has been seen in other nematode taxa, making them an appealing target for current and future research (Susoy et al., 2016; Ragsdale and Sommer, 2015). Specifically, mouth forms are described found within the same population that are associated with the consumption of wasp material, but also forms that presumably could be used to consume bacteria, fungus, or even other nematodes (Susoy, 2016). Other diplogastrids have been described with similar differential mouth forms, for example *Parasitodiplogaster* nematode males associated with *F. maxima* in Panama have been identified with two distinct mouthforms and variable overall body plans within the same fig which may allow for a variety of ecologies, including facultative predation of other nematodes (Kanzaki et al., 2013) (nematode predation polyphenisms also exist in *Pristionchus* species not associated with figs (Woodruff et al., 2019)). This is likely due to the food source that these nematodes are consuming, as it has been documented that *Parasitodiplogaster* nematodes in North America have been seen with fungal spores and hyphae in their mouths, and possibly contain gut endosymbiotic bacteria that assist with the digestion/infection of their hosts (Poinar and Herre, 1991). Finally, there are other mouth and body morphs whose function remains unknown, as in *Pristionchus racemosae*, which has been documented with an "umbrella-head" morph (Jauharlina et al., 2015; Susoy et al., 2016) that may be used for gathering liquid such as bacteria, yeast, or plant tissue exudates. Similar "umbrella-heads" have been observed in *Parasitodiplogaster* (JVG personal observation) and a size-variant "scoop-like" head morph may have similar ecological functions in *Teratodiplogaster* nematodes (NK personal observation). Future metagenomic analysis of intestinal contents in these morphs may be interesting for future study. Thus, the diet of some nematode associates is not fully elucidated to date and is likely to be more dynamic than previously believed, which could result in unexpected consequences (and possibly even benefits) for fig and wasp mutualists. Further, the molecular mechanisms underlying this environmentally informed mouth part development remains completely unknown.

2.3. Mating and proliferation (L4 – reproductive adult)

While consuming energetic resources (wasp, plant, fungi, bacteria, etc.) nematodes will molt into reproductive adults (Fig. 5, fig stages B–C), the final life stage before dying inside the fig. They will generally form large mating aggregates wherein males will mate multiply, and females will exit the aggregate after being inseminated to deposit eggs around the interior of the fig, notably on top of developing wasp galls (Van Goor et al., 2018; Giblin-Davis et al., 1995). The period in which fig nematodes are mating (corresponds to the late B and early C-phase of fig phenology) is the easiest time to sample them, as they are all within close spatial proximity and the fig landscape is relatively "clean" (wasp galls and seeds are still very early in development) and easy to examine.

As far as is currently known, all nematode associates of fig syconia are gonochoristic, with obligate male-female sexes. There are no known instances of self-fertility through hermaphroditism or parthenogenesis in any fig nematode. As such (and as is true for most nematodes), it has been presumed that all nematode associates of figs have genetic sex determination (GSD), with XX females and X0 males, in which sex is determined at the time of birth (Denver et al., 2011; Van Goor et al., 2021a). Following, it is presumed that most nematode associates would be expected to produce 50/50 male/female sex ratios. However, many nematode species here are severely constrained by low founding mating group size (sometimes as low as 2–5 individuals/fig) (Van Goor et al., 2018). Consistent with low mating group size, many nematodes have been described as extremely inbred with low genetic variation (Gulcu et al., 2008; De Luca et al., 2010; Woodruff et al., 2021). In these particular nematode species GSD presents a large problem – if sex is determined genetically it is chance-based which individuals make it into a wasp host and represent a new mating group. One would expect due to chance alone that this "luck of the draw" method would result in many instances of reproductive maladaptation (grossly male biased sex ratios, or conversely insufficient numbers of males for females) or complete reproductive failure (all male or all female broods).

A potential mechanism around this constraint has been recently hypothesized for two divergent nematode groups in Panamanian fig communities: *Parasitodiplogaster* and *Ficophagus*. Here, mating groups of these two genera produce strongly precise female-biased sex ratios regardless of mating group size (and sometimes producing mirrored sex ratios within the same fig) (Van Goor et al., 2022). These female-biased sex ratios are expected under Local Mate Competition theory for inbred organisms to maximize fitness through the insemination of the most daughters by the fewest possible sons (Taylor and Bulmer, 1980). These observed sex ratios are produced at levels greatly surpassing binomial expectations underlying GSD. Likewise, these female-biased sex ratios are produced at levels similar to those of their pollinating wasp hosts (Herre, 1985, 1987) but without the benefit of haplodiploid sex determination (de la Filia and Bain, 2015). Instead, it is hypothesized that these divergent groups have independently evolved a form of environmental sex determination (ESD) in which individual nematodes assess the number and sex of other conspecifics involved within an infective/mating group in order to inform their own sex determination, as has been previously described for the nematode Family Mermithidae (Blackmore and Charnov, 1989). The molecular mechanism underlying this potential ESD remains to be known explicitly, but future work may be capable of providing a clearer picture. It would be interesting to investigate the sex determination mechanisms of other fig nematodes to see if evidence of this ESD mechanism is present elsewhere and could be described as an adaptation to the fig environment in general. Curiously, similar female-biased nematode sex ratios have been described in *Ficophagus* nematodes in the USA (Giblin-Davis et al., 1995) and in *Schistonchus* nematodes in Europe (Kolaei et al., 2016). Mated entomogenous females of *Ficophagus* species in the United States have been described infecting pollinator wasps which may help to offset small founding population sizes in these groups (Giblin-Davis et al., 1995). Additionally, non-fig associated *Bursaphelenchus* nematodes have been recently described with stochastic sex determining mechanisms distinct from both chromosomal *and* environmental sex determination (Shinya et al., 2022), though this mechanism has not yet been defined for fig-associates of the genus (though is increasingly possible with single-worm genome sequencing). In *Caenorhabditis inopinata*, the sex determination gene *her-1*, which is conserved throughout nematodes (Streit et al., 1999), appears to be disrupted by a transposable element insertion (Kanzaki et al., 2018). This suggests rapid evolution of sex determination systems in a fig nematode, and this may also be connected to the problems of GSD and low propagule numbers described above. In addition, the recent description of *Schistonchus pumilae* associated with *Ficus pumila* in Japan identifies the presence of flagellated sperm (Kanzaki et al., 2023), which is generally uncommon throughout Nematoda and likely has functionally significant effects on mating groups in this species. If true, these concepts would presumably represent multiple unique evolutionary events with likely different molecular mechanisms in which this ESD or other alternative sex determining mechanisms and mating systems arose, allowing excellent capabilities for comparative work.

After mating and female deposition of eggs throughout the fig the individual nematodes will die. Aside from low initial mating group size, fig nematodes are also often constrained by relatively low egg-loads per inseminated female, sometimes as low as 15 eggs per gonad arm (Ramírez-Benavides and Salazar-Figueroa, 2015; Woodruff et al., 2019). Previous work has assumed that these eggs remain dormant until just before female pollinating fig wasps emerge in order to ensure synchronicity with their phoretic host. However, recent observations show that *Parasitodiplogaster* nematodes consume fig wasp males (that emerge 3–5 days earlier than their female counterparts). This consumption of male fig wasps allows the energetic resources necessary to produce a second, more rapid lifecycle (as has been described in *Steinernema* (Nguyen and Smart, 1992)) within figs. This would allow them to overcome the constraint of small mating group and egg-load size and amplify their local population numbers to ensure that more individuals can infect pollinating wasp hosts a short while later (JVG unpublished). It is therefore likely that other nematode groups that aren't as resource limited (either through the consumption of plant material, fungus, or bacteria) also produce multiple lifecycles per fig. This effect is not yet characterized but should be investigated thoroughly in the future. If this effect is consistent and true, it is likely that nematode rates of evolution greatly surpass that of their wasp hosts (Machado, 1998), which may help to explain their successful adaptations to figs and their pollinating wasps over evolutionary time.

3. Future directions

Our general understanding of the actual diversity of nematodes associated with fig syconia remains in its relative infancy. Most of the research that has been conducted to date has only been on a handful of fig communities, and many others remain uninvestigated. To date, no fig nematodes have been described in the entire continent of South America (Table 1), although they are likely to exist there. Further, no fig nematodes have been described in association with any *Ficus* subgenus Synoecia species, and very few have been described in the subgenera Ficus or Sycidium (Fig. 2). Is this simply because these groups have not been studied carefully enough, or are these fig environments prohibitive for nematode proliferation? Likewise, the ecological and evolutionary research that has been conducted on fig nematodes has been dominated by a select number of nematode groups (notably *Parasitodiplogaster* and broader Diplogastridae, as apparent here). It is undoubtedly true that other fig nematodes interact with their fig environments in meaningful and ecologically relevant ways that we have not yet appreciated. Particularly, members of the Family Aphelenchoididae are due for more thorough ecological understanding. There are certainly nematode groups in which we are still truly unsure of their ecologies or life histories. Even more severe, there are most definitely nematode groups associated with figs that we have not yet described. There is a mountain of descriptive work to be done and relatively few individuals currently involved.

3.1. Limitations

Researching fig nematodes comes with a few important caveats and difficulties that must be overcome to successfully move this field forward. Simply accessing some fig species is notably difficult in that they grow in areas that are challenging to sample and investigate, as in remote areas of the tropics. Even when successfully sampling nematodes, due to their stereotyped body plans it is sometimes difficult to differentiate between taxa and know what is present within a fig without extensive microscopy and/or genomic tools. Thankfully sequencing efforts are becoming increasingly affordable, and already barcoding/sanger sequencing (Nunn, 1992) has been overtaken by more informative whole-genome data (Susoy et al., 2016). However, access to these techniques is not uniformly available and should require extra consideration. Finally, many fig nematodes are difficult or impossible to culture (Giblin-Davis et al., 1995), which makes it very difficult to study these groups outside of their natural context, and limits our experimental and manipulative abilities. Fig systems in general are difficult to control in an experimental setting, which forces individuals to be creative in the work that they do and/or develop better ways of interacting within the model system.

3.2. Bridging ecology, evolution, and development: culturable fig nematodes

Recent work has identified a fig nematode associated with *Ficus septica* to be the closest known relative of the model organism *Caenorhabditis elegans*: *C. inopinata* (Kanzaki et al., 2018). Importantly, *C. inopinata* is culturable, allowing for the potential to combine the evolutionary and ecological research that's been conducted on figs for decades with the expansive molecular toolkit available for *C. elegans* (Woodruff et al., 2019; Woodruff and Teterina, 2020). Members of the diplogastrid genus *Pristionchus* (notably the exemplar *P. pacificus*) have been developed as a satellite model for comparative work on *C. elegans* and other nematodes of interest (Ogawa et al., 2015; Sommer, 2015). Of course, there are *Pristionchus* species that are known to interact with fig communities, and they have already exhibited interesting biology worthy of future investigation (Susoy et al., 2016; Susoy, 2016). Compared to other members of the Aphelenchoididae, *Bursaphelenchus* nematodes have slender bodies amenable to swimming or cruising (Kanzaki et al., 2022; Shinya et al., 2022), which suggests that they may be prime candidates for future culturing efforts. Likewise, some diplogastrid nematode species (such as *Pristionchus*, *Teratodiplogaster*, and some *Parasitodiplogaster*) interact with figs routinely filled with liquid, which could be useful for future possible culture formulation. If these fig nematodes could be cultured, we would have the capacity to embark on some very exciting scientific endeavors. Combining the powers of these two previously parallel fields allows us the capacity to ask more high impact questions that can better help us understand adaptation, development, and interspecific interactions in general, and should be greatly explored in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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