



Staying in the club: Exploring criteria governing metacommunity membership for obligate symbionts under host–symbiont feedback



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ABSTRACT

Metacommunity membership is influenced by habitat availability and trophic requirements. However, for multitrophic horizontally transmitted symbiont communities that are closely associated with hosts, symbiont–host interactions may affect membership criteria in novel ways. For example, failure of beneficial services from symbionts could influence the host, and in turn, the entire community. Understanding such host–symbiont feedback effects on symbiont community membership, symbiont community structure, and function is important for understanding if host–symbiont communities are fundamentally different from more traditional ecological communities.

We investigate the membership criteria for a multitrophic insect symbiont community that colonizes host inflorescences at specific developmental stages termed colonization windows. The inflorescences serve as microcosm habitats. Symbionts exhibit a range of interactions from mutualism to parasitism. Hosts exhibit feedback by aborting inflorescences not pollinated by mutualistic symbionts. Habitats are consequently lost for all other symbiont species in such host-derived organs whose development is mutualist-dependent. Using empirical measurements to characterize inflorescence development, we simulate symbiont dispersal colonization across hosts. We vary host densities and lengths of symbiont colonization windows, and track the persistence of each symbiont species in the metacommunity based on its trophic requirements and resource availability within the microcosm.

Since the persistence of the microcosm habitat is dictated by pollination performed by the mutualist, the mutualist fared better than all other symbionts. The length of symbiont colonization windows was positively related with colonization success and symbiont persistence. The cumulative length of the colonization windows of prey dictated predator success; diet breadth or prey colonization success did not influence predator persistence. Predators also had a greater host–plant density requirement than prey for persistence in the community. These results offer valuable insights into host densities required for maintaining symbionts, and have implications for multitrophic symbiont community stability.

Special constraints can govern symbiont community membership, function and structure and symbiont persistence when host–symbiont feedback impacts host microcosm development.

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1. Introduction

Metacommunities can consist of distinct habitats that occur discretely in space and time (Leibold et al., 2004) with community members residing on and dispersing across habitats. Local and global processes in metacommunities govern species persistence and overall community membership. Within local communities, competition and predation can influence persistence (Holt and Bonsall, 2017), while prey availability can affect predator member-

ship (predator persistence) (Holt, 2009). By predator membership, we mean the ability of predators to persist in a community. By metacommunity membership, we denote the ability of any symbiont to persist in a metacommunity. Additionally, global processes such as the ability to successfully disperse across habitats can impact local community membership as well as metacommunity membership (Leibold et al., 2004).

In symbiotic metacommunities, each host may be likened to a habitat (which may be a microcosm) and the symbionts it harbors likened to species residing within that habitat. For symbionts in obligate host–symbiont structured communities, symbiont-mediated effects on host fitness can feed back onto the persistence of the symbiont metacommunity itself (Miller et al., 2018). Often, symbionts

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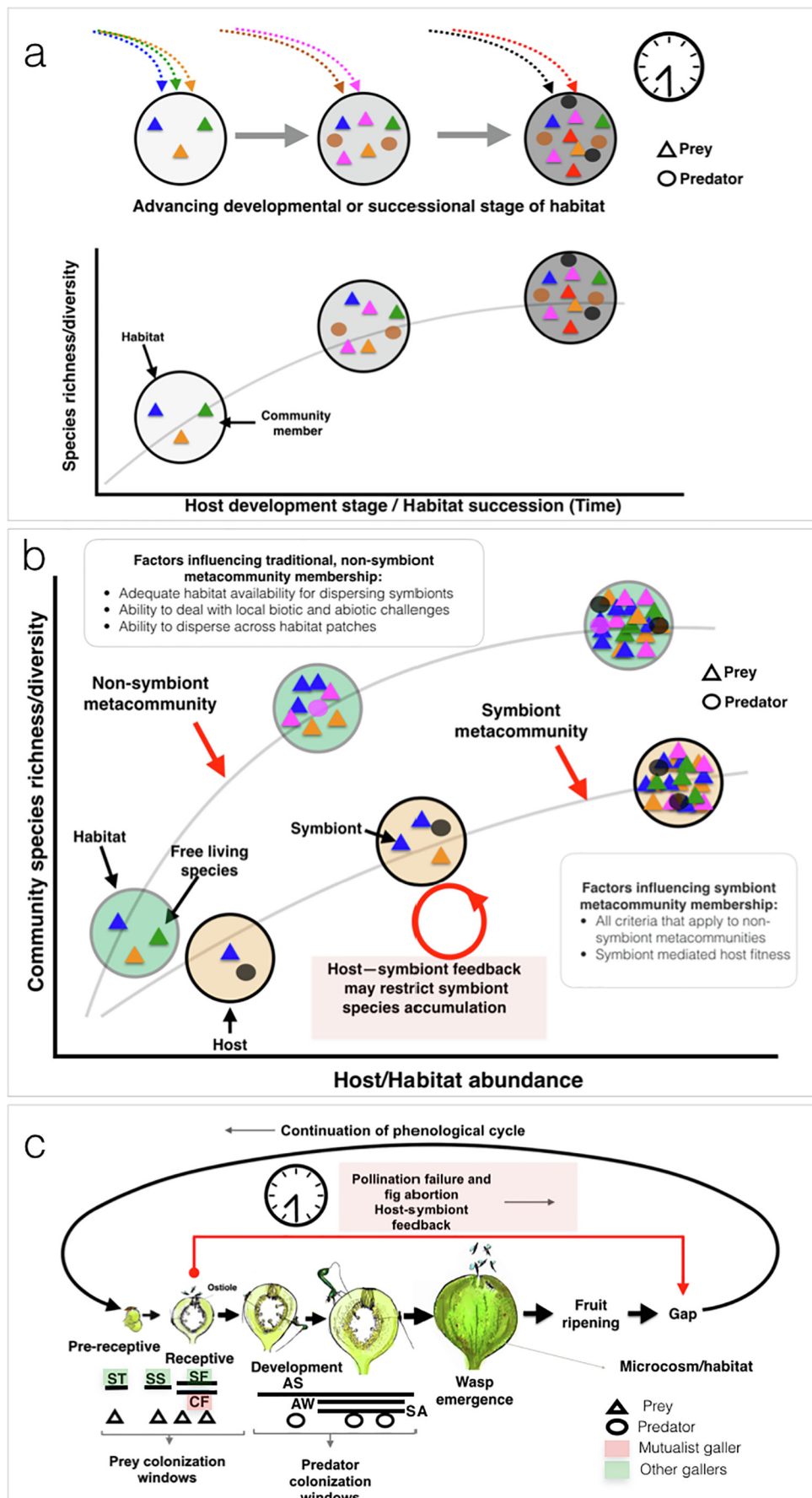


Fig. 1. a. The developmental stage or the successional stage of a habitat can restrict community membership, i.e. certain members may only be able to colonize a habitat at particular time durations when new, suitable niches are made available. For example, predators may only occupy a community after the colonization of prey. Such subsequent and conditional colonization may generally influence average local species richness, though not always in a positive manner. b. A hypothetical comparison between a traditional and a symbiont metacommunity. All else being equal, if symbiont metacommunities have more membership-limiting criteria governed by host-symbiont feedback, they may support fewer species with increasing host abundance and will exhibit species accumulation trajectories that are markedly different from those of traditional metacommunities. c. Ontogeny of the syconium in a typical fig with typical phenological developmental stages referred to as phases. Since trees usually bear all their inflorescences in the same phase, the phenology of a single inflorescence or microcosm represents the fruiting phenology of a tree. Microcosm-habitat developmental states: Pre-receptive = phase prior to pollen receipt; receptive = phase of pollen receipt; development = phase when wasps and seeds mature. Details of symbiont species are provided for the model cluster fig *Ficus racemosa*. The timing of arrival (oviposition window or colonization window) of each wasp symbiont during syconium development is indicated by colored bars under the different stages of development of the inflorescence. Symbiont functional classifications and abbreviations are the following. Mutualist galler (herbivore): CF = *Ceratostolen fusciceps*. Gallers (herbivores): SS = *Sycophaga stratheni*, ST = *Sycophaga testacea*, SF = *Sycophaga fusca*. Parasitoids (predators): AS = *Apocrypta species 2*, AW = *Apocrypta westwoodi*, SA = *Sycophaga agraisensis*.

may be mutualists and may assist in host survival or may be parasites of the mutualism (that exhibit a negative association with the host or the mutualistic symbiont, or both) (Kiers et al., 2003). When the partnership between host and symbionts may be necessary for the development or persistence of the host, or the host organs in which the symbiont community assembles, the survival of both parties becomes paramount for community membership of all symbionts. For instance, symbiotic mutualistic bacteria within hosts are key players for the normal development and health of hosts, and both parties (host and symbionts) gain by this association. The development of the light organ of the Hawaiian squid is dependent on the colonization of the correct bacterial symbiont species. Further, this association is crucial for the survival of the squid as the downwelling light emitted by the symbiotic bacteria in the ventral light organ precludes the casting of a shadow and prevents predator detection and attack from below (McFall-Ngai, 1994). In general, symbionts can be important for the development, survival and maintenance of host organs (Douglas, 2010). Therefore, when host-symbiont feedback dictates the ontogeny of hosts (or of specific host organs), incorporating these feedback processes into symbiont community membership is vital. Such investigations are extremely nascent (Miller et al., 2018).

Hosts must be sufficiently abundant in space and time to enable successful dispersal and colonization by symbionts (Arneberg et al., 1998; Venkateswaran et al., 2017, 2018). But host numbers themselves may be mediated by symbiont effects on the hosts. In cases where host-symbiont interactions are characterized by obligate mutualistic interactions, the survival of host and mutualistic symbionts is a pre-requisite for the persistence of the entire symbiont metacommunity; e.g. in human microbiomes the core microbiome may be considered indispensable for human health and survival (Bäckhed et al., 2012), potentially making its persistence critical for other “non-core” microbial symbionts.

Since the colonization of hosts and emigration from hosts may occur only during specific periods of host development (McFall-Ngai, 1994; Kitching, 2001; Srivastava et al., 2004; O'Neill, 2016; Borges, 2017), host ontogeny can heavily influence symbiont community membership. Further, the accumulation and release of symbionts may not only be contingent on the host's own development but also on the number of other hosts in the population that release symbionts (Fig. 1a). This leads to two logical insights. First, when hosts develop asynchronously with each other in ecological timescales, they can facilitate the transfer of symbionts across them. Second, smaller time windows for colonization during host development should decrease host availability and symbiont colonization success (Venkateswaran et al., 2017; Appendix S1).

Even though the stable functioning and persistence of host and symbiont metacommunities are of considerable theoretical interest (Mihaljevic, 2012), membership criteria involving temporal aspects of colonization, inter-symbiont interactions, and host-symbiont feedback have received little attention. Symbiont species accumulation and resulting symbiont biodiversity patterns may be markedly different owing to such host-symbiont feedback effects (Fig. 1b).

In symbiont communities, such as gut-associated microbes and hosts, hosts usually out-live symbionts. In order to study feedback effects on symbionts, the long-term performance of hosts can be monitored. Alternatively, when hosts produce short-lived organs whose development depends on an assemblage of symbionts and whose ontogeny is fundamentally linked to host fitness and also demonstrates feedback effects, then investigation of such organs that serve as habitat microcosms are powerful model systems to address issues pertaining to host and symbiont feedback. Such short-lived organs are abundant in plants, e.g. leaves that harbor unique phyllosphere assemblages that influence leaf health, function and longevity, or flowers that harbor unique insect communities affecting plant fitness (Janzen, 1979; Leveau, 2019).

We investigate a multitrophic symbiont community of fig wasps that assembles in the inflorescences of a host plant, and that exhibits many features of host-symbiont communities as described above.

1.1. Fig microcosms and associated symbiont communities, natural history and membership constraints

Figs and their fig wasp symbionts represent a model plant-insect symbiont community. Multitrophic fig wasp communities that occupy and develop within enclosed fig inflorescences are species-poor, consisting of no more than 30 species (Compton and Hawkins, 1992), but are characterized by rich interactions between symbionts and the host (Compton and Hawkins, 1992; Ghara and Borges, 2010; Ghara et al., 2014). Such symbiont insect communities consist of obligate pollinating mutualists, competitors, and predators (parasitoids). Each symbiont confers a net positive, negative or neutral benefit on the host (Ghara and Borges, 2010; Segar et al., 2013; Krishnan and Borges, 2014; Krishnan et al., 2015; Venkateswaran et al., 2017, 2018). From here on, we refer to the host plant as “host”, parasitoid wasps as “predators”, and the wasp species utilized by parasitoids to complete their development as “prey” species.

Each of the 800 + fig (*Ficus*) species produces many inflorescences (also called syconia; closed urn-shaped structures, singular = syconium), each of which is a host organ that represents an ephemeral microcosm (Cook and Lopez-Vaamonde, 2001). Wasps disperse from the natal inflorescence to another after development to adulthood (Fig. 1c) (Janzen, 1979). Pollinating wasps induce galls within the inflorescence tissue, within which their offspring develop; because they are the sole pollinators for the plant, they are considered the only obligate mutualist of the host. Competing wasp symbionts also induce galls (herbivorous gallers) in the inflorescence, compete for oviposition space and exploit flowers that could have supported seeds or pollinator wasp offspring and thereby negatively impact the host. Both pollinators and competing gallers feed directly from plant tissue within their galls. Late-arriving parasitoids feed on developing gall offspring and show variable but species-specific diet breadths (Ghara and Borges, 2010). Parasitoids that feed on the pollinator could be detrimental to the mutualism, but parasitoids that feed on the non-pollinating gallers may benefit the host and the mutualism

by reducing the numbers of the detrimental galling wasps. We refer to this service as an indirect mutualism. A few fig wasp communities also include seed-eating wasps that are detrimental to the host (Pereira et al. 2007), but they are not considered in this investigation.

After development within syconia, adult wasps leave their natal trees owing to phenological characteristics that preclude their recolonization (see Appendix S1) and colonize other trees by ovipositing into inflorescences; the next generation of wasps develops within the inflorescence and disperses to colonize another tree to continue its life-cycle. However, each wasp has a specific time window, called the colonization or oviposition window (OW), during the development of the inflorescence, when the inflorescence bears suitable oviposition sites (Fig. 1c). Therefore, wasps released at times when trees bear no syconia that are in the right developmental window would miss out on the opportunity to oviposit. When the mutualist wasp misses the oviposition window, this also represents a lack of pollination (mutualistic) services which is also detrimental for the host plant. Interestingly, many fig species often abort un-pollinated inflorescences since abortions may serve to avoid the cost of bearing expensive floral tissue when pollinators are absent. Under-pollinated inflorescences may often also be aborted owing to cheater pollinators who do not provide pollination services; such abortions may be viewed as a host-sanction strategy (Jandér and Herre, 2010). However we do not address cheater wasps in this study. Figs also usually exhibit within-tree reproductive synchrony coupled with population-level reproductive asynchrony. Therefore, in the absence of local availability of pollinators, a tree will abort all its inflorescences (Bronstein et al., 1990; Kameyama et al., 1999). For more details on the natural history, trophic associations, symbiont influences on the mutualism, and resource occurrence in fig wasp communities, see Appendix S1 and Fig. S1.

Membership criteria refer to factors that allow species to persist in a community without going extinct. We investigate membership criteria of symbionts by simulating the phenological resource landscape for a model fig species *Ficus racemosa* and its associated wasp community of seven fig wasp species (Ghara and Borges, 2010) and also for other hypothetical fig wasp communities. We assess how symbiont persistence (membership) varies with increasing number of hosts. All wasp symbionts are indicated in Fig. 1c and are hereafter capitalized and italicized in the main text.

Overall, we examine how metacommunity membership of multitrophic symbiont fig wasps associated with a single host plant species is influenced by host-symbiont feedback by simulating hypothetical and natural fig wasp communities using relevant empirically measured community parameters. We vary three important parameters: 1) host abundance (increasing number of trees), 2) lengths of the colonization window (equivalent to the oviposition window) for herbivorous and predatory symbionts, and 3) prey availability for predators. We discuss implications for symbiont community composition and persistence in such ephemeral host-derived microcosms. We simulate symbiont persistence in time, by measuring their colonization opportunities (i.e. how often they are released) and colonization success (i.e. how often they are successful at finding and colonizing a new host when released).

2. Methods

2.1. Estimating lengths of phenological phases from field data

We used the fruiting phenology census from an earlier study on *Ficus racemosa* (Krishnan and Borges, 2014) to inform our simulations and to derive biologically relevant parameters for hypothetical fig wasp communities. From here onwards the phenological

phase is referred to simply as the phase. For more details, see Appendix S1. In all, we analyzed the developmental progression for 13,846 inflorescences, observed over multiple fruiting cycles spanning two years across 14 individual trees and recorded the lengths of 41,122 complete phases (~10 fruiting cycles). Such sampling provides a fair estimate of the phenological cycle and the intrinsic variance in fruiting phenology, typical of a fig species (Bronstein et al., 1990; Kameyama et al., 1999). Using these values, i.e. the length of all phases, we calculated the length of each phase and its associated natural variance (Fig. S2) and incorporated the value of the phase lengths in the simulations described below.

2.2. Agent-based simulation framework for host developmental progression and microcosm colonization

We used a framework that simulates the ontogeny of multiple asynchronous hosts with symbionts dispersing across hosts. Within these simulations we investigate how the timing of colonization during host ontogeny, prey requirements by predatory symbionts, and the role of the mutualistic symbiont in ensuring habitat persistence (through host-symbiont feedback) affect symbiont community success. All these effects are tested for different host abundances.

The simulation framework we adopted is similar to Bronstein et al. (1990) and Kameyama et al. (1999) in that it incorporates trees that randomly initiate their phases to generate the colonization landscapes and to assess colonization success and persistence, but also incorporates other essential features (details of the code in Appendix S1 and S2). While the earlier simulation studies investigated only the performance of the mutualist without mutualist-host feedback, our simulations include an entire multitrophic symbiont fig wasp community with host-symbiont feedback effects and predator-prey dependencies.

Our models do not deal with predator-prey interactions and their population dynamics. More precisely, we consider only one side of the predator-prey interaction: the predator needs the prey to survive. But we do not consider the effect of the predator on the prey. As in Bronstein et al. (1990) and Kameyama et al. (1999), we do not investigate population dynamics of the trees since multiple fig wasp generations can occur within a single host tree generation. Also, as in earlier studies, we do not address the population dynamics of wasps; our simulations keep track of symbiont species harbored by any individual host at every time step. We also do not explicitly test spatial distribution of trees; rather, we test symbiont community performance with increasing host abundance either by increasing the number of hosts or by increasing the lengths of the colonization window for symbionts.

Fig phenology was simulated by parametrizing the length and the variance of each phase of the inflorescence from the natural dataset (see above). Each of the six phenological phase lengths (PR: pre-receptive (~10 days), R: receptive (~4 days), D: development (~27 days), E: wasp emergence (~2 days), FR: fruit ripening (~2 days), G: gap (~25 days); Fig. 1c, Table S1) were parametrized based on a phenological census of *F. racemosa* trees. Overdispersion (with distributions spilling into negative ranges) was prevalent for short phases, especially where variances were greater than the mean. Hence, we adopted a zero-truncated Poisson structure to select positive, non-zero integers from a discrete distribution. The lengths of each of these six phases with their underlying natural distributions were used in our simulations for all host trees. In this way, unique sequences were generated at each fruiting cycle for every tree. To determine when symbionts could colonize hosts, symbiont colonization windows were restricted to fractions of the lengths of each phase. These phase values were used for all model simulations described below. The specific rules for the progression of phenology were as follows.

At the beginning of the simulations, every tree began at a random point in its generated developmental sequence, i.e. each tree starts at a randomly-picked flowering stage in the whole sequence. After a complete developmental cycle, a new and unique sequence was generated. If a tree was not colonized by a mutualist, the tree skipped the intervening D (development), E (wasp emergence) and FR (fruit-ripening) phases and entered the G (gap) phase. In this way abortions occurred only in the absence of pollinator services (Fig. 1c).

We incorporated stochasticity in all our models by two means: all trees started at random points in their development, and we generated each phase with a mean and a variance. Therefore, at every developmental cycle, no two trees had the same total length of development since variation was incorporated at each developmental stage.

We allowed symbionts to emerge and colonize trees. Symbionts emerging from any tree could colonize any other tree in our models as long as the tree served as a suitable oviposition resource; this feature makes our models spatially implicit. All symbionts were introduced by being allowed to emerge, disperse and colonize trees in the first round of release of each tree, after which the persistence of each symbiont species was contingent on its subsequent successful colonization. On each day, the trees that were releasing wasps and trees that were suitable for wasp colonization were noted. Additionally, the presence or absence of symbionts was recorded in each tree for each day. Each symbiont species successfully colonized a host provided that the timing of emigration of the symbiont matched the occurrence of a host at a suitable phase on the same day. In this way, a tree acted as a suitable oviposition resource when its phase corresponded with the timing of the OW of a particular symbiont (when it was suitable for colonization). For parasitoids (predators), an additional pre-requisite for colonization was that the tree needed to harbor the parasitoid-specific prey (galler species). Some parasitoids can utilize multiple prey species while others have fewer prey species. Therefore, parasitoids vary in their specialization of resource use (see Appendix S1).

Each simulation was run with discrete tree population sizes ranging from 10 to 100 in increments of 10 for 1800 days (5 years); a previous investigation on fig tree–pollinating wasp stability incorporating the same agent-based framework revealed that a 5-year period satisfactorily predicted long-term (1000 year) outcomes (Anstett et al., 1997). Colonization success was measured by two metrics: a) The total number of colonization opportunities (CO), i.e. the total number of times a symbiont was released from any tree during a simulation. If a symbiont is released from a tree, it represents an opportunity for dispersal and colonization of suitable trees in the simulation and hence represents the colonization opportunity for the symbiont. b) The proportion colonization success (PCS) for each wasp symbiont species, i.e. the ratio of the number of times wasps were successfully able to colonize a resource to the total number of times they were released in the simulation (CO). These two metrics are important because they provide unique measures of performance of each symbiont. PCS indicates the probability that a symbiont will successfully colonize a resource in the landscape when released by a host. However, the frequency of symbiont release could still be very low and curtailed by other factors. CO, on the other hand, also captures the frequency of the release of the symbiont. Therefore, these metrics are distinct and are useful when considered together.

Thirty iterations were conducted for each host density tested. We do not account for space in our model and use the term tree abundance to indicate the number of potentially accessible hosts (host density).

Assumptions of our models

- 1) All wasp species live only for a single day and they can colonize trees only when their release coincides with the availability of a suitable plant host on the same day. Though wasps can live more than a day when provided with ad libitum water and sugar supply (Ghara and Borges, 2010), studies also suggest that wasps during flight are susceptible to extreme exhaustion resulting in reduced lifespans of less than a day (Jevanandam et al., 2013; Venkateswaran et al., 2017). Extrinsic mortality can also be high due to predation pressure, desiccation, and high temperatures (Ranganathan and Borges, 2009; Ghara and Borges, 2010; Jevanandam et al., 2013), further reducing the longevity of wasps.
- 2) When no colonization by the mutualist occurs during the receptive phase (pollination failure), all inflorescences in the tree are aborted due to the lack of pollination and the tree enters the gap phase after which the tree initiates another cycle (Fig. 1c), making habitat resources unavailable for symbionts on the tree for that cycle.
- 3) Successful parasitoid (i.e. predator) colonization has no effect on subsequent prey (galler) release, i.e. even if parasitoids manage to colonize a tree, prey will be released from that tree. We do not account for predator–prey dynamics (negative feedback of predators on their prey), i.e. this is intentionally not a population dynamics model at this stage of our investigations. Although such negative predatory effects on prey can also influence symbiont membership, their inclusion demands a separate investigation which is beyond the scope of this study.
- 4) We use phenological parameters from 14 trees observed over a two-year cycle and assume that this variation captures the natural variation of a larger host–plant population.

2.3. Features of the simulation model variants

“Dummy” models are often used to investigate the change of a single or few parameters on simulation outcomes. We used four dummy models (and a dummy model variant) to understand the functioning of the natural fig wasp community of *F. racemosa* (Fig. 2). All parameter values used in each dummy model and in the real model are listed in Table 1. All effects are compared as a function of host abundance (Appendix S1). In the dummy models, we consider the performance of representative wasp species as functions of their OWs and diets. All four dummy models contain the mutualists as well as the condition that the lack of mutualist colonization (pollination) leads to syconia abortion. Sensitivity analyses were conducted to ensure that parameter changes had a robust effect on all colonization success output values despite the inherent stochasticity present in the models (Appendix S1).

In Model 1, we vary the position of the OW of two theoretical wasp gallers (Fig. 2). As both OW positions are within the pre-receptive window, and there is no inflorescence abortion within the pre-receptive window, we expect OW position to have no effect on CO (Fig. 2, Fig. 3). In Model 2, we vary the length of the OWs (Fig. 2). Since a tree is colonized by a wasp if and only if there is another tree releasing this wasp species within its OW, therefore, the likelihood of colonization should increase with OW length (Fig. 2). We also note from our preliminary analyses (results not shown) that if the OW of two species completely overlap, then the trees holding them after colonization are also identical. This is because in our simulations, if release and colonization events coincide, then colonization happens with probability 1; PCS will then have the value of 1 while CO can take any whole number value. Hence there is no difference in the colonization events between such species.

In addition to the oviposition requirements for parasitoids, they also require the presence of their prey within the syconium. In

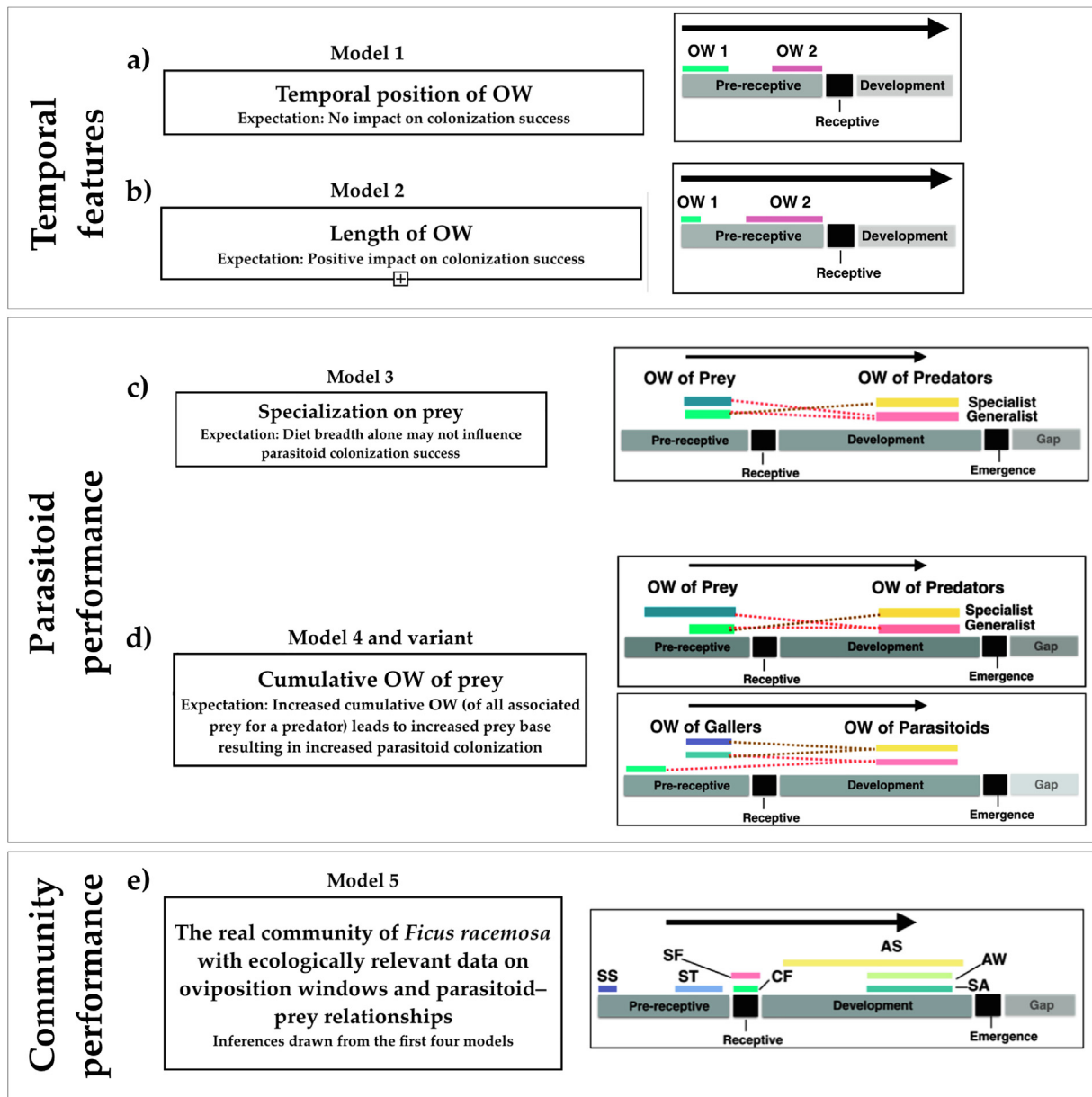


Fig. 2. Description of the models. a) The influence of colonization success when OWs occur at different times of development of the microcosm. b) The influence of colonization success when colonization windows (oviposition windows) are of different lengths. c) The influence of the number of prey species (prey specialization) on colonization success of two hypothetical parasitoid (predator) species. d) The influence of prey colonization success on colonization success of parasitoids (also see Appendix S1 for variant of Model 4). Models 3 and 4 are applicable to parasitoids in the community. e) The colonization success of members of the natural *F. racemosa* wasp community (species abbreviations are as indicated in Fig. 1c). For parameter details see Table 1.

Models 3 and 4, we consider the CO of parasitoids, and their dependence on the prey species. In Model 3, we compare the CO of two parasitoids – one that feeds on two prey types (generalist), and the other that feeds on only one prey type (specialist), such that the OWs of the two prey coincide (Fig. 2, Fig. 3), as do that of the predators. A priori, we may expect that the generalist parasitoid does better, as it has more prey options. However, we also note that because the prey OWs coincide, all the trees holding one prey type also hold the other in our simulations. Hence there may be no difference in the success of these two parasitoids. In Model 4, we again compare the CO of generalist and specialist parasitoids, but now the OWs of the two prey are not the same because they are of different lengths and have different positioning (Fig. 2). We now expect the generalist parasitoid to do better for two potential reasons: 1) feeding on a prey that has greater persistence (with lar-

ger OW) may itself enable the predator to perform better since larger windows increase the number of trees harboring the prey and will aid predator colonization, or 2) an increased number of trees holding all relevant prey because of decreased overlap of prey OWs can also allow for better predator performance. Both of these factors could lead to an increased prey base and requires to be tested independently.

We use a variant of Model 4 to disentangle the role of better performance of prey because of increased OW vs. the role of an increased non-overlapping cumulative oviposition window. Here, we address how the extent of overlap of prey OWs dictates parasitoid success while keeping the colonization success of all prey constant. Unlike Model 4, in the Model 4 variant, we incorporate two predators and three prey (Fig. 2). Each predator specializes on two prey (with one shared prey species). All prey species have

Table 1

The positions and lengths of oviposition windows (OWs) of the different wasp symbionts and the number of hosts (for parasitoids) in each model. The abbreviations indicate the developmental stage of the inflorescence: PR = pre-receptive phase, R = receptive phase, D = developmental phase. Wasp abbreviations for Model 5 are the same as in Fig. 1c.

	Symbionts	Number of prey species	OW positioning	OW length (discretized)
Model 1 (Influence of OW position)	Hypothetical galler 1	Nil	0.2 to 0.5 of PR	~3 days
	Hypothetical galler 2	Nil	0.6 to 0.9 of PR	~3 days
Model 2 (Influence of OW length)	Hypothetical galler 1	Nil	0.0 to 0.1 of PR	~1 day
	Hypothetical galler 2	Nil	0.6 to 0.9 of PR	~3days
Model 3 (Influence of parasitoid specialization)	Hypothetical galler 1	Nil	0.6 to 0.9 of PR	~3days
	Hypothetical galler 2	Nil	0.6 to 0.9 of PR	~3days
	Hypothetical galler3	Nil	0.6 to 0.9 of PR	~3days
	Hypothetical parasitoid 1	2	0.5 to 0.8 of D	~8 days
	Hypothetical parasitoid 2	3	0.5 to 0.8 of D	~8 days
Model 4 (Influence of galler performance on parasitoids)	Hypothetical galler 1	Nil	0.6 to 0.9 of PR	~3days
	Hypothetical galler 2	Nil	0.6 to 0.9 of PR	~3days
	Hypothetical galler3	Nil	0.3 to 0.9 of PR	~3days
	Hypothetical parasitoid 1	2	0.5 to 0.8 of D	~8 days
	Hypothetical parasitoid 2	3	0.5 to 0.8 of D	~8 days
Model 5 (Parametrized values of the natural <i>F. racemosa</i> wasp community)	<i>Ceratosolen fusciceps</i> (CF)	Nil	R	~4 days
	<i>Sycophaga agrimensis</i> (SA)	1	0.5 to 0.8 of D	~8 days
	<i>S. stratheni</i> (SS)	Nil	0.0 to 0.1 of PR	~1 day
	<i>S. testacea</i> (ST)	Nil	0.6 to 0.9 of PR	~3 days
	<i>S. fusca</i> (SF)	Nil	R	~4 days
	<i>Apocrypta</i> species 1 (AS)	3	0.2 to 0.9 of D	~19 days
	<i>Apocrypta westwoodi</i> (AW)	2	0.5 to 0.8 of D	~8 days

equal OW lengths (Fig. 2d). For one of the predators, the two prey have completely overlapping OWs while for the other predator, the two prey have completely non-overlapping OWs. We expect that the predator with prey having overlapping OWs would perform worse—the trees holding each prey species would be the same, all else being equal.

Lastly, we simulated the real model with parameter values and species associations of the fig *F. racemosa* and its wasp community (Model 5 = the natural wasp community) (Fig. 2e). This model was run to obtain a priori expectations for how a natural wasp community may function to guide future studies. Results of this model were interpreted by referring to the results of the previous models.

All simulations were run using R 3.3.1 (R Core Team, 2017). The code for all model variants can be found in Appendix S2.

2.4. The influence of tree abundance on extinction probabilities and symbiont persistence

To understand the influence of host availability on persistence of the symbiont community, we also calculated the extinction probability of each symbiont in the natural community for the duration of our simulations, i.e. the number of times a species went extinct in the 30 iterations for differing tree abundances (from Model 5). We investigated extinction probability as a function of tree abundance. All calculations and simulations were conducted using the software package R.

3. Results

3.1. Influence of host–symbiont feedback (microcosm persistence) on community structure

Our results show that host densities and symbiont colonization windows affect species persistence or extinction. The length of each phase and associated variances estimated from the natural

data set are presented in Fig. S2. Higher tree abundance resulted in successful colonization of CF (pollinator), which allowed microcosms to persist (Fig. S4). With only few trees, abortions were common (Fig. S4a) which decreased with increasing tree abundance (30 trees, Fig. S4b; 100 trees, Fig. S4c). We describe our results using the metrics CO (colonization opportunities, i.e. the number of times symbionts were released) and PCS (proportion colonization success, i.e. the proportion of times they were successful at colonizing a host when released).

3.2. Model results

3.2.1. Models 1 and 2

Symbiont oviposition window (OW) temporal sequence (Model 1) did not affect either the proportion colonization success (PCS) or colonization opportunities (CO) (Fig. 3a, b; Table S2) unlike the length of the OW (Model 2) (Fig. 3c, d; Table S2). Longer durations of resources aided in colonization of symbionts as expected. Colonization was inferred using PCS and CO; there were no significant differences between PCS or CO for the two galler species in Model 1 while there were significant differences in PCS and CO in all tree abundance regimes in Model 2. PCS, more than CO, increased with increasing tree abundance in all simulations for all symbionts (Fig. 3c, d; Table S2; Table S3a, b). These results were confirmed by our sensitivity analysis showing that our models were robust despite the stochasticity (Appendix S1).

3.2.2. Models 3 and 4

As expected initially (Fig. 2), more prey types did not necessarily increase predator performance. The results of Model 3 indicated that predator diet breadth alone did not affect colonization in our simulations (Fig. 3e, f; Table S2).

The increased CO for parasitoids through increased galler OW length in the results of Model 4 (Fig. 3g, h) were as expected (see both PCS and CO of galler and parasitoids). We tested the effect

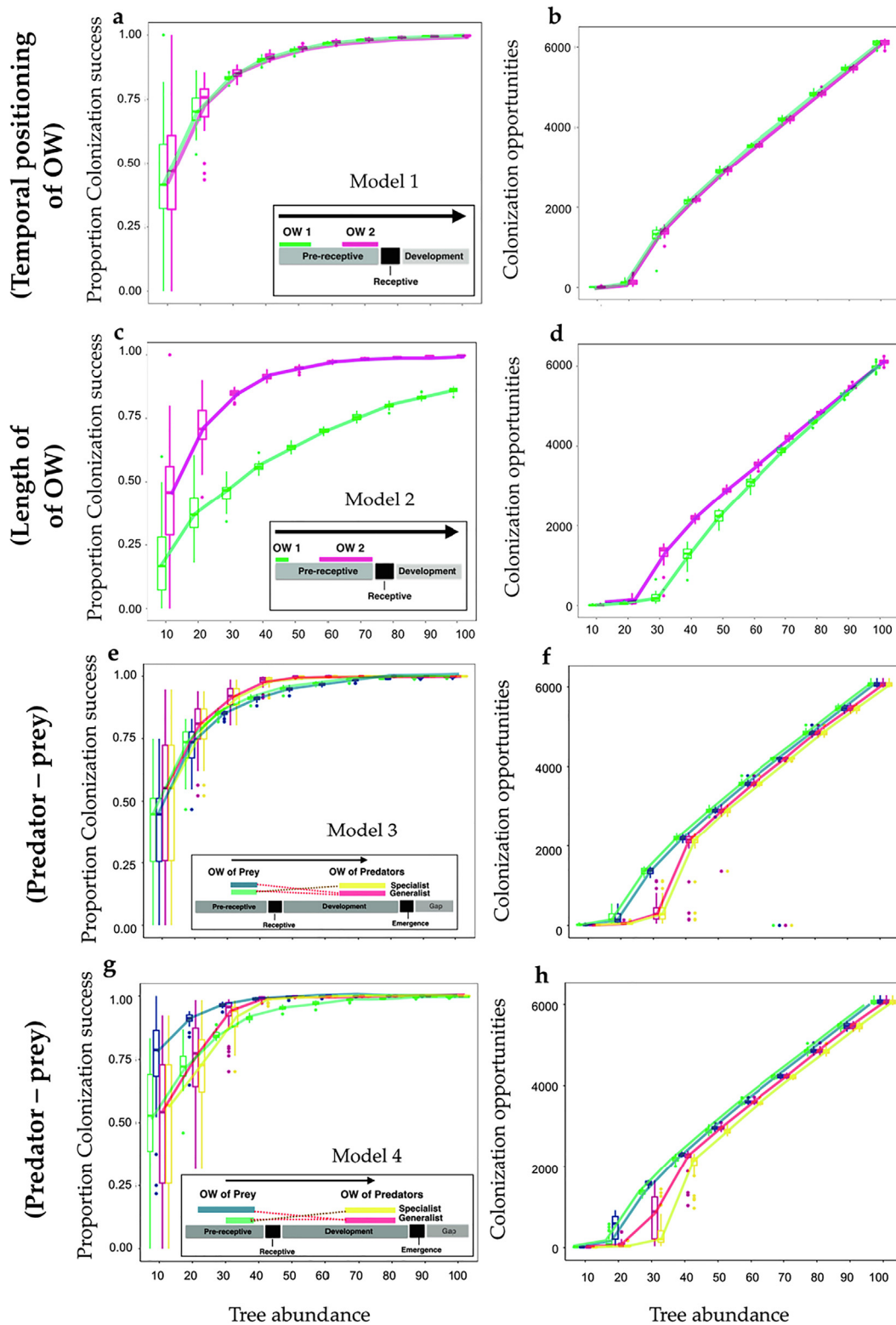


Fig. 3. The colonization success (PCS and CO) of predator and prey as a function of tree abundance. The length and positioning of the oviposition windows of each wasp species over inflorescence development are indicated in the in-laid schematics. a) Model 1: Two hypothetical galler wasps that have the same OW length but that differ in their colonization sequence. The sequence does not affect colonization success. b) Model 2: Two hypothetical galler wasps that have differing OW lengths. Longer OWs enhance colonization success. c) Model 3: Two hypothetical parasitoids (i.e. predators), one specializing on two hypothetical galler prey species (broad diet breadth) and another specializing on one prey types (narrow diet breadth). d) Model 4: The same as Model 3 except that the galler that is exclusively preyed upon by the generalist predator has a longer oviposition window than the other two gallers; this indicates that the subset of trees with more prey in general enhances parasitoid colonization rates (also see the variant of Model 4 in Fig. S3). All models incorporate mutualist–host feedback; the performance of the mutualist is not shown in these models.

of staggering prey OWs without increasing their lengths on predators through the variant of Model 4 (Model 4b, Fig. S3). This model revealed that, for parasitoids with the same number of galler prey species, those feeding on galls with staggered OWs had greater colonization success (Model 4b, Fig. S3). This result was again confirmed by our sensitivity analysis (see Appendix S1).

These results collectively indicated that the cumulative length of non-overlapping OWs of prey types was positively related to parasitoid colonization. A high cumulative OW length could be achieved by either a single prey type with long OW or multiple prey types with non-overlapping windows that add up. This cumulative length of prey OWs was necessary and sufficient to explain how all prey species attacked by a predator positively influenced the predator. Diet breadth and prey colonization success alone were not satisfactory at explaining the colonization performance of predators. Drawing from this, we also infer that predators that are highly specialized on a single prey with a large oviposition window may fare better than generalist predators that have multiple prey but with a short cumulative oviposition window.

3.2.3. Model 5 (the natural *F. racemosa* symbiont community)

Here we describe the performance of each wasp of the *F. racemosa* wasp community. These results provide a priori expectations

for future empirical investigations. We compare and contrast CO and PCS to draw how they each influence performance of wasp symbionts. The galler with the smallest oviposition window (*Sycophaga stratheni*, SS) had the lowest PCS and CO at all tree regimes because the number of trees providing oviposition resources would be fewer by virtue of the small time period available for oviposition (Fig. 4a, b; Table 1). The mutualist pollinator (*Ceratosolen fusciceps*, CF) had the highest CO (Fig. 4b). At low tree abundance, mutualist populations became extinct leading to the extinction of all other wasp species (Fig. S5a–e). The parasitoids/predators *Apocrypta westwoodi* (AW) and *Sycophaga agragensis* (SA) had the same OW lengths (~8 days) and they showed no difference in their PCS with respect to each other at all tree regimes despite specializing on different prey types (Table 1, Fig. 4a); this result was consistent with that of Model 3. However, SA had a higher CO than AW since it parasitized the mutualist that was more successful than any of AW's prey (Fig. 4b), a result that was consistent with Model 4. *Sycophaga testacea* (ST) had an OW between that of SS and the other five wasp species; its PCS curve showed a faster increase with increasing tree abundance as compared to SS but not when compared to the other wasp species (Fig. 4a). *Apocrypta* species 2 (AS) with the highest OW (~19 days, Table 1) showed the steepest rise in PCS with tree abundance (Figure a). AS also

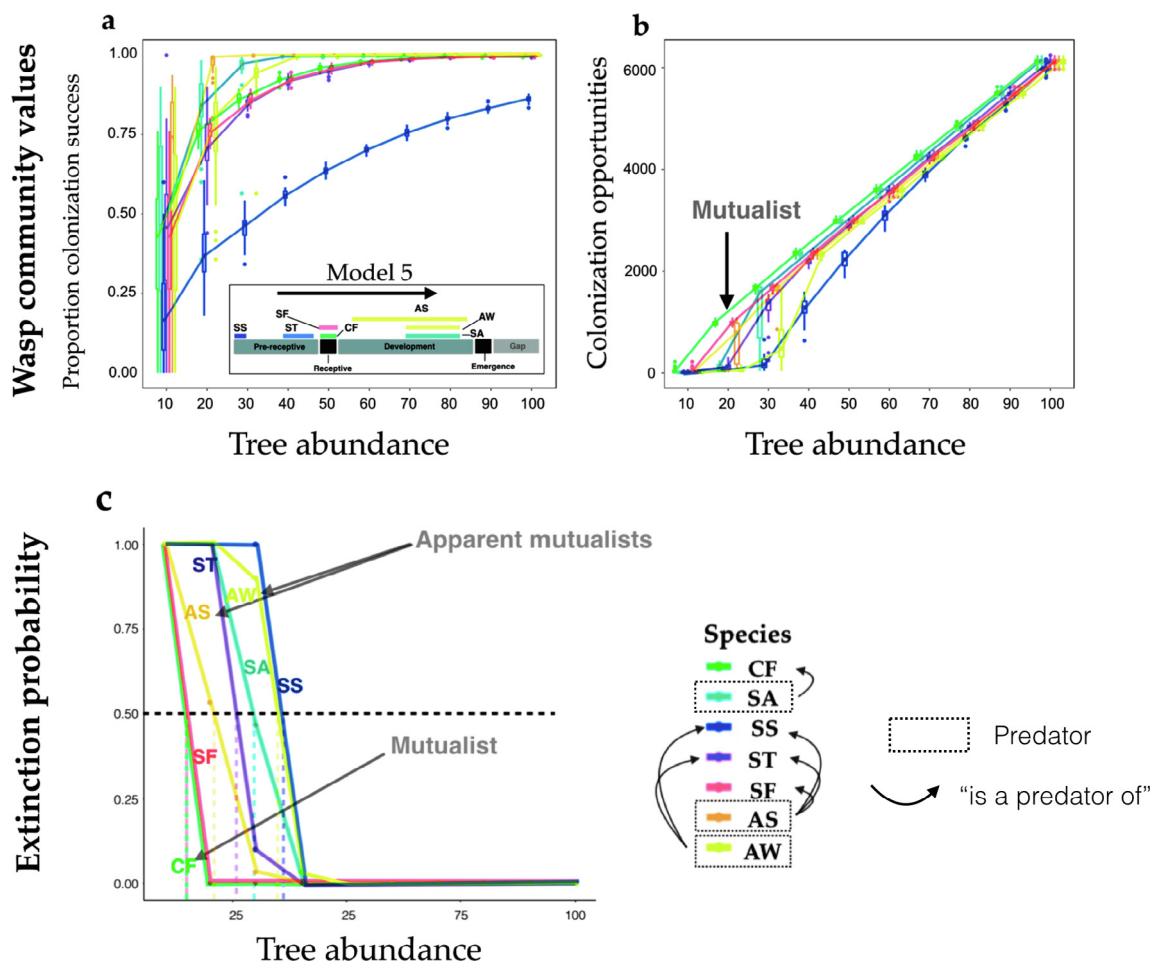


Fig. 4. The colonization success (PCS (a) and CO (b)) for the natural fig wasp community of *Ficus racemosa* as a function of tree abundance. Both proportion colonization success (PCS) and colonization opportunities (CO) values suggest that species with larger oviposition windows are more successful at colonizing hosts and parasitoid performance is based on prey (galler) availability, consistent with the previous models. However, the pollinators (CF) outperform all other wasps at all tree abundance as indicated by their COs. c) The probabilities of extinction with increasing tree abundance for each species in the natural community of *F. racemosa*. The horizontal dotted line represents a 50% extinction probability. Vertical colored (dotted) lines indicate the tree abundance required to sustain the wasp species for five years with a 50% extinction probability. Predators (parasitoids) are indicated within dotted boxes and arrows indicate their galler prey. Species abbreviations are as in Fig. 2. Predators (i.e. parasitoids) are indicated within dotted boxes and arrows indicate their galler prey.

parasitized the most successful galler (*Sycophaga fusca*, *SF*) and, consistent with the results of Model 4, showed the highest CO compared to the other parasitoids (Fig. 4b).

In all models, the variability in PCS and CO for wasp species was lowest at high tree abundance (Fig. 4a, b) reflecting the decreased variability and an increased guarantee of resource occurrence with increasing tree abundance in the simulations. When OW values were the same (as for *Apocrypta westwoodi* and *Sycophaga agraeensis*; *Sycophaga fusca* and *Ceratosolen fusciceps*), PCS values at all regimes were the same (statistically non-significant) while CO values were different (Table S4a, b), consistent with the results of Model 4.

3.3. The influence of tree abundance on extinction probabilities of species in the natural *F. racemosa* symbiont community

The persistence of the mutualist was the highest at all host densities with no other symbiont species having higher survival probabilities. The minimum host requirements for persistence were highly dependent on the length of the colonization window; species with smaller OWs required more trees for persistence (Fig. 4c). For parasitoids, the minimum tree abundance required was never less than their most successful prey in the simulations. Parasitoids, despite having larger OWs than the gallers (such as *Apocrypta* species 2), were more likely to face lower absolute colonization success than gallers, due to their additional dependency on presence of galler prey within inflorescences. For instance, though the OWs of parasitoids *Sycophaga agraeensis* (*SA*) and *Apocrypta westwoodi* (*AW*) were of identical duration, the extinction probability of *AW* was greater than *SA* (as seen in tree regimes of 25 to 50, Fig. 4c). The parasitoid *SA* is dependent on *Ceratosolen fusciceps* (*CF*), which is the mutualist, and *CF* performs better than any other wasp in any tree regime including *Sycophaga testacea* (*ST*), a galler prey species for *AW*. Therefore, the observed differences in extinction probabilities between the parasitoids *SA* and *AW* in the model indicated that they were contingent on the success of their specific galler prey. These results provide a preliminary framework for future theoretical and empirical investigations.

4. Discussion

Symbiont communities can be influenced by host development and host–symbiont feedback. In our investigations, such feedback ensured that no symbiont out-performed the mutualist (as inferred through the colonization opportunity (CO) measure, Fig. 4b). Typically host–symbiont feedback effects are addressed with respect to responses between host and symbiont numbers (Mihaljevic, 2012). In fig symbiont metacommunities, symbiont wasps and host plants drastically differ in lifespan. Many inflorescence abortions may occur within the host's lifespan without host mortality. Immediate host–symbiont feedback without host demise may be highly beneficial for metacommunity persistence since non-mutualist numbers may be immediately controlled relative to the pollinating mutualist performance, without reduction in host numbers. With respect to host symbiont communities structured around a core mutualism, this predisposes the mutualist symbionts to greater stability and persistence at any host density, thereby increasing the persistence of the entire metacommunity. In the absence of feedback through abortions after mutualism failure, such stability will cease to exist.

The impact of such short-term effects without host demise and long-term effects, including an influence on host numbers, on the persistence and maintenance of symbiont metacommunities requires more attention. Such investigations may even be performed in fig wasp systems in which parasitic galler wasps are able

to hijack the host microcosm development and allow it to persist even in the absence of pollination (Krishnan and Borges, 2014; pers. observ. as observed in *F. racemosa*). Here, symbionts other than the pollinators may regulate host–symbiont feedback and fig wasp symbiont community structure. There has been no rigorous work quantifying the effect of non-pollinating wasps in driving fig development in the absence of pollination.

Mutualisms are often context dependent (Hoeksema and Bruna, 2015), and overexploitation of the host by mutualists without offering adequate services to the host may turn into parasitism. Mutualism stability may therefore be conferred by parasites or predators of the mutualists such as by parasitoids of the pollinator when pollinators over-exploit resources (Dunn et al., 2008). However, to prevent overexploitation by competitors or by the predators of the mutualist, certain guilds of parasitoids (predators) may help confer stability by preying on non-mutualist species that directly compete with the mutualist (Yadav and Borges, 2017). Such parasitoids, therefore, could act as apparent mutualists, and may also be very important for the stability of such mutualisms (Krishnan et al., 2015). Because our model reveals that such parasitoids that may serve as apparent mutualists require a higher abundance of trees for their persistence than the mutualist, rethinking the minimum host abundance to account for the stability of beneficial symbionts in higher trophic levels is crucial and perhaps has valuable conservation implications (Shanahan et al., 2001). This is especially relevant since such apparent mutualists may confer “top-down” stability to the community (Estes et al., 1998). In many symbiont metacommunities, mutualists may be a prerequisite for community establishment and may be more persistent than other symbionts, while apparent mutualists may contribute to community stability. This requires an accurate characterization of trophic associations between symbionts; *F. racemosa* and its wasp community in South India is perhaps the only fig wasp system where predator–prey relationships between gallers and parasitoids of the entire community have been elucidated experimentally (Yadav and Borges, 2017).

Increasing host densities should support greater symbiont colonization and persistence as demonstrated by the results of all our models. However, our results also clearly show that the length of colonization window interacts with the development of fig syconia (host-derived organs) to eventually influence colonization success (as indicated through PCS and CO) and overall symbiont community persistence. We propose that the time period available for colonization of a host is an important determinant for successful symbiont colonization and persistence, and is extremely relevant for symbiont transfer amongst hosts in varied developmental stages. In other words, the distribution of developmental stages of hosts in the host population could influence symbiont transfer and persistence. These findings are particularly interesting owing to their applicability to other similar symbiont metacommunities such as gut microbial symbionts even though feedback effects may not be as immediately manifested as in the case of figs with the termination of their inflorescences in the absence of the symbiont pollinator and pollination. For example, in many mammals, it is well known that certain essential microbes are transferred into the alimentary tract of the offspring during lactation, thereby being acquired only during these early stages of growth and are then harbored for life (Gilbert, 2014). However, other microbial symbionts may be acquired during broader windows at various stages of host growth and through various diets or other sources (McFall-Ngai, 1994; Walter and Ley, 2011). Therefore, such differences in the colonization window lengths of symbionts could make certain symbionts more vulnerable to extinction than others with consequences for the persistence and structure of the symbiont metacommunities.

Our simulation results also showed that certain features of symbiont metacommunities are similar to non-symbiont metacommunities. That colonization success of predators never exceeded that of their best performing galler prey is in accord with the trophic rank hypothesis which postulates that species diversity reduces while moving up the trophic level owing to additional requirements of prey availability for predators (Srivastava et al., 2008; Losos and Ricklefs, 2009). In all our simulations, total prey occurrence increased with increasing cumulative OW lengths of the prey. Therefore, the colonization success of predators correspondingly increased irrespective of actual diet breadth or the success and persistence of single galler prey. As we have shown, when two parasitoid species have different numbers of prey, e.g. one prey species vs. two, and when the prey species have overlapping windows, the parasitoids show no difference in performance indices. In fact, in our models, prey performance with respect to each other, and predator performance with respect to each other are identical. This is an outcome of the simplifications in our model to capture an essential aspect of the persistence dynamics of this complex system. No matter how general a diet breadth, the overlap (or the lack thereof) of the oviposition window of the prey could potentially have a significant influence on predator persistence. Finally, in all our results, increased host abundances led to increased metacommunity persistence. This is in agreement with island biogeography theory; increasing numbers of microcosms/refugia/islands support increased species diversity and abundance (MacArthur and Wilson, 1967; Losos and Ricklefs, 2009).

A few assumptions in our model require consideration for future work. First and most obviously, we did not attempt to capture predator and prey population dynamics, but restricted our examination of this complex system to resource presence or absence for either predator or prey. Our models were also spatially implicit and we assumed that all symbionts had the same dispersal ability. This is in contrast to previous experimental investigations of the *F. racemosa* wasp community which suggest that predators exhibit reduced dispersal capacities compared to their prey (Venkateswaran et al., 2017), and that dispersal traits are likely constrained by symbiont phylogeny. Therefore, increased host abundances than those predicted by our models, may actually be required for the persistence of predators with reduced dispersal kernels (Herrera et al., 2011) and therefore the minimum tree numbers for the persistence of such predators are likely underestimates.

There are also the other important assumptions that require further discussion since they ignore many interesting biological features of fig–fig wasp systems. We assume that all wasp lifespans are limited to a single day while in fact most non-pollinating wasps have much longer lifespans than the pollinator (Ghara and Borges, 2010). Therefore, longer lifespans could reduce the number of hosts required for persistence. Future investigations could address how symbiont longevity influences such communities. Further, we treat each tree as a completely synchronized unit producing all its syconia at the same time. We do not consider the case when trees exhibit within-tree asynchronous inflorescence initiations as has been observed for several fig species (Smith and Bronstein, 1996). Even with within-tree asynchronous fig production, we would expect that individuals with large oviposition windows are more likely to cycle within the same tree and therefore remain persistent, but this needs more detailed investigation.

We are far from understanding the actual distances that different fig wasp species of a single community traverse in space, or the actual amounts of time they have available for dispersal. Should one endeavor to conduct an empirical study to validate these results, we strongly believe that an investigation of these realized dispersal abilities is essential to understand the scale at which to situate an empirical study.

With more limiting factors that affect survival and persistence in terms of community membership-limiting criteria, the number of species that coexist may reduce, both in ecological or in evolutionary time, in a conventional habitat or within a living host offering habitats to symbionts. If symbionts severely influence the fitness of their host and determine host numbers, the feedback that arises through this association could be an important parameter influencing symbiont diversity. Our investigation provides a novel framework and important insights for symbiont metacommunity membership in natural microcosms.

5. Data accessibility

All simulated data and the phenology data will be deposited in a suitable online repository such as Dryad or any other suitable repository upon publication.

Authors contributions

VV conceived the study, VV ran the simulations and analyzed the data, VV and RMB were involved in jointly writing the manuscript and reviewing it and the data for important intellectual content.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtbi.2020.110512>.

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