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Divvying up an incubator: How parasitic and mutualistic fig wasps use space within their nursery microcosm

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Abstract Differential occupancy of space can lead to species coexistence. The fig–fig wasp pollination system hosts species-specific pollinating and parasitic wasps that develop within galls in a nursery comprising a closed inflorescence, the syconium. This microcosm affords excellent opportunities for investigating spatial partitioning since it harbours a closed community in which all wasp species are dependent on securing safe sites inside the syconium for their developing offspring while differing in life history, egg deposition strategies and oviposition times relative to nursery development. We determined ontogenetic changes in oviposition sites available to the seven-member fig wasp community of *Ficus racemosa* comprising pollinators, gallers and parasitoids. We used species distribution models (SDMs) for the first time at a microcosm scale to predict patterns of spatial occurrence of nursery occupants. SDMs gave high true-positive and low false-positive site occupancy rates for most occupants indicating species specificity in oviposition sites. The nursery microcosm itself changed with syconium development and sequential egg-laying by different wasp species. The number of sites occupied by offspring of the different wasp species was negatively related to the risk of syconium abortion by the plant host following oviposition. Since unpollinated syconia are usually aborted, parasitic wasps ovipositing into nurseries at the same time as the pollinator targeted many sites, suggesting response to lower risk of syconium abortion owing to reduced risk of pollination failure compared to those species ovipositing before pollination. Wasp life history and oviposition time relative to nursery development contributed to the coexistence of nursery occupants.

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Introduction

Species coexistence in an ecological community can be attributed to partitioning of limited resources along various niche axes such as space (Lachaise et al. 1982; Albrecht and Gotelli 2001), time (Kronfeld-Schor and Dayan 2003; Ranganathan et al. 2010), diet (Schoener 1968) and chemistry (Gallet et al. 2007; Ibanez et al. 2009). Space is often an important niche axis (Schoener 1974). Besides direct resource competition, differential usage of space can result from apparent competition (indirect competition because of shared natural enemies); shared natural enemies are important in shaping the structure of resource

utilisation in a community and therefore coexistence (van Veen et al. 2006; Bailey et al. 2009). In insect communities in which species share the same resources as well as have common natural enemies, both direct resource competition as well as apparent competition can influence community structure (Jones et al. 2009) where community structure not only includes the number of species, but also the relative abundance of each species and the interactions between community members. In hymenopteran communities, natural enemies such as parasitoids can be important in influencing resource utilisation and thereby community structure and species coexistence of their hosts by imposing selection pressure on enemy-free space (Jeffries and Lawton 1984; Holt and Lawton 1993).

In nursery pollination systems in which pollinators breed within the floral resources that they service, temporal partitioning of oviposition between mutualistic and parasitic community members has been well investigated (Kerdelhué and Rasplus 1996; Després and Jaeger 1999; Elias et al. 2008; Ranganathan et al. 2010). However, investigations of spatial utilisation of resources in such systems are rare (Pellmyr and Leebens-Mack 2000; Pompanon et al. 2006; Dunn et al. 2008; Al-Beidh et al. 2012) despite their rich potential to address fundamental questions in community and evolutionary ecology. Patterns of space utilisation between pollinator offspring, parasite offspring and developing seeds in the nursery can indicate whether parasites of pollination mutualisms compete directly with each other as well as with the mutualists, i.e. pollinators and seeds. In such multitrophic systems, taxa such as parasitoids at higher trophic levels can affect the stability of the mutualism by forcing taxa such as gallers at lower levels to use certain resource types (Dunn et al. 2008). The spatial features of the nursery can therefore suggest the existence of enemy-free zones, which are sites providing greater safety for developing offspring against attack from natural enemies such as parasitoids (Dunn et al. 2008; Al-Beidh et al. 2012).

The fig–fig wasp mutualism is both a classic example of a nursery pollination system and an ecological microcosm. It therefore provides an excellent model in community ecology for answering questions about space utilisation and partitioning (Kerdelhué et al. 2000; Jousselin et al. 2008). In the fig–fig wasp mutualism, offspring of pollinating fig wasps develop in individual flowers at the expense of seeds within a modified globular and enclosed inflorescence called a syconium, which functions as an independent unit (Jandér et al. 2012). Parasites or nonpollinating fig wasps (NPFWs) in this mutualism could be gallers (wasps that induce abnormal proliferations of plant tissue termed galls on which their offspring feed), kleptoparasites (wasps unable to induce a gall but their offspring consume gall tissue, eventually causing the death of galler offspring) or parasitoids (wasps that feed on living or dead developmental stages of gallers and kleptoparasites) and have the potential to affect space partitioning in the syconium because, along with fig seeds and fig pollinators, they also develop within the same syconium, each occupying a single modified flower (Cook and Rasplus 2003; Herre et al. 2008). The community of fig wasps associated with a single fig species can comprise up to 36 species (Cruaud et al. 2011), each species depositing eggs into the syconium at different times during its development; however, oviposition timings may overlap between species (Compton et al. 1994; Ranganathan et al. 2010). Fig flowers are dimorphic; some are pedicellate with short styles (Fig. 1), whereas others are sessile bearing long styles (Fig. 2); pedicel length can also vary among pedicellate flowers. The stratified arrangement within the syconium due to floral dimorphism (especially in monoecious figs) (Janzen 1979; Bronstein 1992; Ganeshaiah et al. 1999) can also influence the accessibility of flowers for oviposition and hence their utilisation. Flower accessibility is modulated by ovipositor length in wasps that oviposit from within the fig syconium or from the syconium exterior (Compton and Nefdt 1988; Bronstein 1991; Nefdt and Compton 1996; Al-Beidh et al. 2012; however, see Elias et al. 2012). Consequently, variation in flower accessibility resulting from constraints of ovipositor length can aid in niche partitioning in such communities. Most importantly, fig wasp larvae are immobile and do not exhibit host-seeking behaviour (Eggleton and Belshaw 1993; Brodeur and Boivin 2004) because of which ovipositing wasps must seek precise oviposition sites with their ovipositors. Thus, an understanding of the quantity and distribution of flowers accessible to an ovipositing wasp is important for a better understanding of space utilisation by the wasps within the syconium nursery.

In nursery pollination systems, enemy-free space can also be created by modifications of flowers. In the fig nursery, early-arriving parasites (e.g. early gallers) may alter the oviposition resources available for later-arriving ones as has been found in other host–parasite systems (Gallet et al. 2007; Ibanez et al. 2009), resulting in a dynamic resource landscape. Despite their fundamental importance for nursery suitability, alterations to the fig nursery during syconium development, and their consequences for spatial resource partitioning within the syconium microcosm, have not been investigated in nursery pollination systems. Similarly, community members may be constrained in their use of the nursery based on life history parameters, which include body size (and therefore requirements for development), egg maturation as well as longevity. Such parameters have not been considered before in nursery partitioning.

We therefore asked the following questions using a relatively speciose community of fig wasps associated with a widely distributed Asian fig *Ficus racemosa*: (1) What
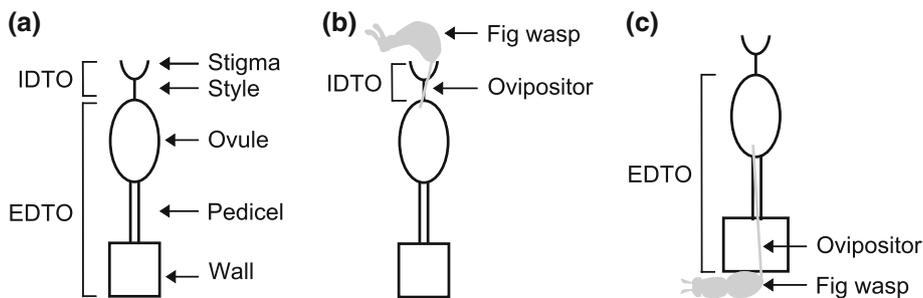
Fig. 1 **a** Schematic diagram of a flower on the syconium wall. The pollinators use the style for oviposition (IDTO), and the nonpollinating fig wasps insert their ovipositor into the flower after piercing through the wall (wall + flower length = EDTO). **b** Schematic representation of a pollinating fig wasp ovipositing through the style. **c** Schema of a nonpollinating fig wasp inserting its ovipositor through the wall

Fig. 2 Floral development stages with progressive syconium development. **a** Pre-A phase; **b** A phase; **c** B phase; **d** C phase. *Fp* Floral primordium, *S* sessile (flowers without pedicel) present towards the outer wall, *P* pedicellate (flowers with pedicel) present towards the inner cavity, *Sty* style; *Sti* stigma. In the C phase, the stigma and style are not very distinct because they usually get damaged due to oviposition activity by wasps
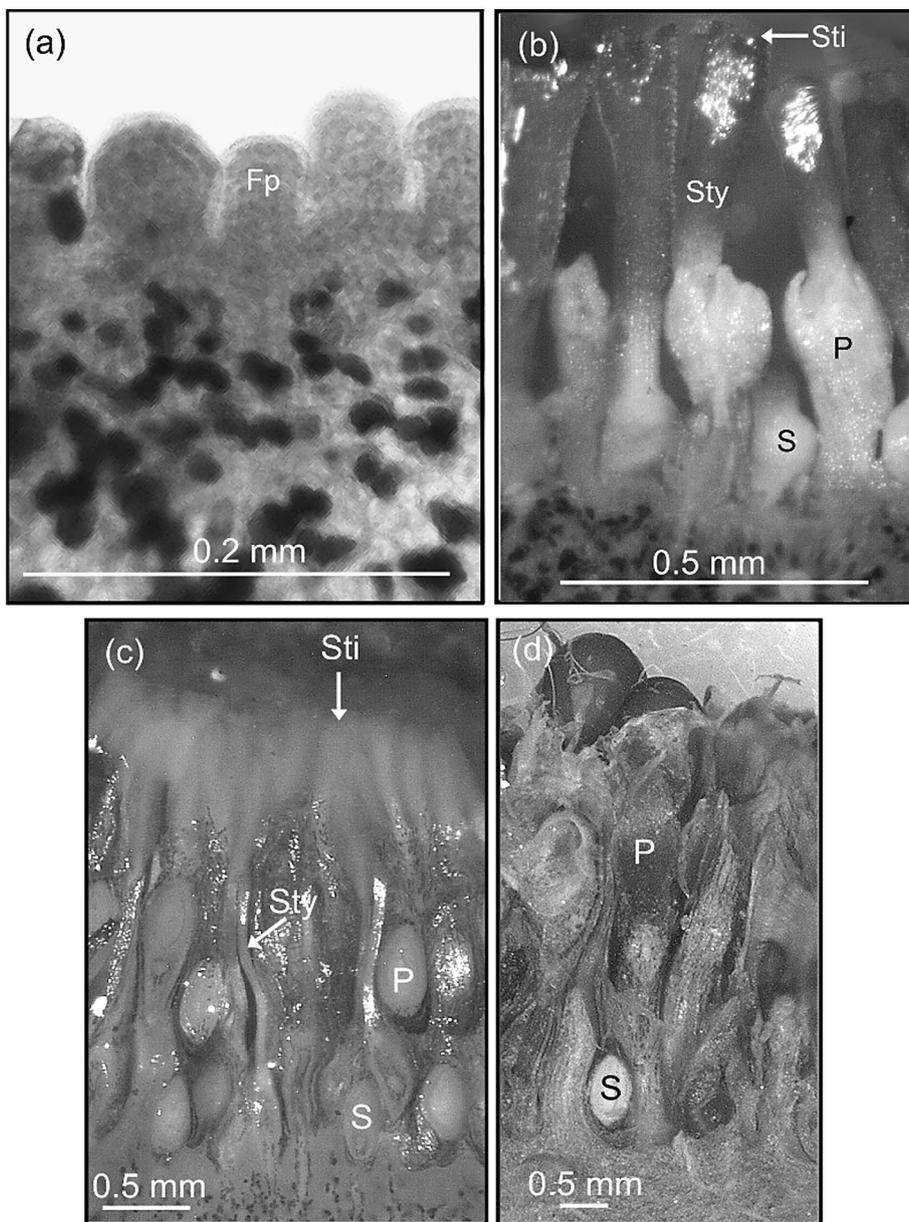
resources are available and accessible to gallers and parasitoids within a syconium at the time of their oviposition? (2) Do flower occupants, i.e. seeds and wasp species, vary in their spatial occupancy of nursery sites within syconia? (3) Is the spatial distribution of the parasites and mutualists within the syconium predictable? We addressed the last question by employing species distribution models (SDMs), which are conventionally used to examine and predict species distributions on much larger spatial scales (Elith and Leathwick 2009). We overlaid previously measured species life history parameters (from Ghara and Borges 2010) on nursery occupancy to achieve better understanding of the use of such a microcosm. Since the members of fig wasp communities are usually highly species specific (Weiblen 2002), and since they depend solely on the fig syconium for their development, this nursery pollination system constitutes a closed system that affords a unique opportunity for such investigations.

Materials and methods

Study system and study site

The syconium nursery in a typical monoecious fig has five development stages (Galil and Eisikowitch 1968): A—prepollination phase; B—pollination or female flower phase; C—interfloral or wasp development phase; D—wasp dispersal or male flower phase; and E—seed dispersal phase. Pollinators enter the fig syconium through an opening called the ostiole during B phase (which closes soon after they enter), while parasites usually oviposit into the syconium from the exterior between A and C phases (Ghara and Borges 2010; Ranganathan et al. 2010). Irrespective of the syconium stage during which oviposition occurs, offspring of all wasp species synchronise their development to emerge as adults through exit holes made in the syconium by male pollinators during the D phase (Cook and Rasplus 2003; Herre et al. 2008).

We investigated nursery occupancy of the fig wasp community in *Ficus racemosa* Linn. (Section: Sycomorus), a monoecious species distributed from India to Australia, at the Indian Institute of Science campus (12°58′N, 77°35′E), Bangalore, India. The syconia support the development of the obligate pollinator *Ceratosolen fusciceps* Mayr (Agaonidae: Agaoninae) and six species of nonpollinating fig wasps (NPFWs) belonging to two genera: 1) the genus *Apocryptophagus* (Agaonidae: Sycophaginae): the gallers *A. stratheni* Joseph, *A. testacea* Mayr, *A. fusca* Girault and the putative parasitoid *A. agraensis* Joseph, and 2) the genus *Apocrypta* (Agaonidae: Sycoryctinae): the parasitoids *Apocrypta* sp 2 and *Apocrypta westwoodi* Grandi (Ghara and Borges 2010). The wasps arrive in the following sequence and at the following syconial developmental phases for oviposition: *A. stratheni* (pre-A phase), *A. testacea* (A phase), *A. fusca* + *C. fusciceps* (B phase), *Apocrypta* sp 2 (late A, B and C phases) and *A. agraensis* + *Apo. westwoodi* (C phase) (Ghara and Borges 2010; Ranganathan et al. 2010); therefore, more than one species oviposit into syconia at the same developmental phase.

Resource availability and accessibility to wasps at oviposition

Members of the fig wasp community of *F. racemosa* oviposit across the development cycle of the syconium (Ranganathan et al. 2010) during which the flowers are also expected to undergo morphological changes. Therefore, as the wasps oviposit into the changing syconia, the type of resources available as well as accessibility of those resources to the ovipositing wasps might change. To know what resources (type of flowers) are available to each ovipositing wasp and whether their accessibility varies across syconium development, we sectioned syconia at the stage(s) during which each wasp species oviposited. We categorised flowers as floral primordia or sessile and pedicellate flowers.

We quantified flowers accessible to ovipositing wasps based on the distance required by the ovipositor to reach the ovule, which is equivalent to the style length of flowers in B phase syconia for internally ovipositing pollinators (internal distance to ovary or IDTO) (Fig. 1). Style length was measured from the tip of the stigma to the point of insertion into the ovary on flowers from syconia bagged till pollinator receptive phase (number of syconia = 12). Bagging (covering the syconia with muslin bags) was necessary to exclude wasps from ovipositing into syconia to obtain undamaged styles, since oviposition by pollinators might lead to damaged styles. For externally ovipositing NPFWs, we measured the distance to the ovary as the length of the pedicel + ovary + syconium wall thickness at the time of oviposition (external distance to ovary or EDTO) (Fig. 1). We examined unbagged syconia collected while wasps were ovipositing (n = 9 syconia for pre-A and A phases; n = 10 for B and C phases). We used these measures and the mean ovipositor lengths for each species from Ghara and Borges (2010) to quantify the proportion of flowers accessible to each of the wasp species (proportion of flowers shorter than mean ovipositor length as in Nefdt and Compton 1996). Although this is likely to be an overestimation since ovipositors often traverse looping paths within the syconium (Ghara et al. 2011), this measure of distance to ovary (DTO) (Fig. 1) is the best available approximation of access to oviposition sites within the nursery.

Spatial resource utilisation

To quantify the flowers used by each species, we collected syconia ($n = 128$) in D (wasp dispersal) phase haphazardly from 8 trees and allowed wasps to emerge naturally from them. Wasps that remained unemerged within their galls were dissected out and counted. We determined the total number of seeds and of wasps (males and females) of each species in every syconium, and from this, we calculated the percentage of syconia containing a particular wasp species. We also determined per cent flower occupancy across and within syconia ($n = 74,110$ gall occupants from 128 syconia).

Whether species co-occur within syconia was tested by examining the association between the presence of pairs of various flower occupants (seed–wasp and wasp–wasp) by the probability based odds-ratio test, which uses a contingency design and also provides confidence intervals (Bland and Altman 2000). Based on presence–absence (binary) information, associations between a pair of flower occupants could range from positive to negative. A positive association between any occupants indicates co-occurrence, a negative association indicates absence of co-occurrence, and neutral association indicates random association.

To test whether the flower occupants vary in their spatial occupancy of nursery sites within syconia, we collected syconia ($n = 19$ from 5 trees) in which wasps had completed their development but had not emerged from their galls, and measured their diameter. We sliced each of these syconia into eight longitudinal sections (ostiole to base), measured pedicel length and flower length, and identified the gall occupant for every flower in alternate sections in each syconium. The flower lengths recorded here include pedicel and gall lengths. Since the sample size for galls containing *Apo. westwoodi* was very low in these sections, we sampled opportunistically for this species in other syconium sections. We excluded bladders (empty galls), shrunken flowers and incompletely developed wasps from this analysis. We compared the distribution of each wasp species and seeds between sessile and pedicellate flowers. In pedicellate flowers, gall occupants would be developing closer to the syconium lumen and further away from the syconium wall compared to those occurring in sessile flowers. To determine whether species differ in their occupancy of flowers with different pedicel lengths, we performed a generalised linear mixed model (GLMM) using pedicel length as a response variable and gall occupant as an explanatory variable with syconium volume (calculated from the diameter of the syconium, assuming it to be a sphere) as a covariate and tree identity as a random effect (pedicel length $\sim$ gall occupant + syconium volume + tree ID). We performed a similar analysis with flower length as a response variable with syconium volume

as a covariate, tree identity as random effect and gall occupant as predictor variable (flower length $\sim$ gall occupant + syconium volume + tree ID). The response variables for both analyses were square-root transformed to normalise the error structure. To test for the effect of tree identity on the response variable, we compared models with and without the random effect using an ANOVA (package nlme 3.1-113 in R package i386 3.0.2). We used stepwise model selection, and the Akaike information criterion (AIC) values so obtained were compared to evaluate the effects of gall occupant and syconium volume on pedicel length and flower length. To identify which pairs of flower occupants differ in occupancy with respect to pedicel or flower length, we performed post hoc Tukey tests with adjusted Bonferroni corrections (Herberich et al. 2010; packages lme4 1.0-5 and Multcomp 1.2-12).

Modelling species distribution in the nursery

Species distribution models (SDMs) are numerical tools used to gain ecological and evolutionary insights into the distribution of species, and to predict the occurrence of species across landscapes (Elith and Leathwick 2009). These models are based on a consistent relationship between the distribution of a species and its physical environment and have hitherto been used on large landscapes. Such models use true presences and true absences of a species at a location to provide reliable predictions about species distribution (Elith and Leathwick 2009). For example, Raxworthy et al. (2003) predicted the distribution of reptile species across Madagascar using information about their occurrence in specific habitats. Model performance can be evaluated using a relatively small set of statistics such as area under the receiver operating characteristic curve (AUC), as well as model sensitivity (true-positive rate, i.e. ratio of actual positives to total number of positives) and specificity ($1 -$ false-positive rate, where false-positive rate is the ratio of negatives incorrectly classify as positives to the total number of negatives) (Fawcett 2006). A good model should be able to predict the presence of a species when the species is truly present and declare a species absent when it is truly missing.

The fig system is appropriate for SDM analysis because one flower usually accommodates only one individual occupant, either seed or wasp; moreover flowers and their occupants can be easily quantified. We built predictive models for each type of flower occupant including seeds within individual syconia using a generalised linear model (GLM) framework with flower length as a predictor for gall occupant and syconium volume as a covariate (gall occupant (0/1) $\sim$ (flower length + syconium volume)). Since the data had many absences compared to presences (many more zeroes than ones and therefore zero-inflated), we used

a bagging generalised linear model (GLM) method which combines traditional GLM with bootstrap aggregation and has better predictive ability and performance with zero-inflated data sets (Osawa et al. 2011). Tree identity was not added as a random effect in this analysis because of constraints of application of the bagging method to GLMM (Takeshi Osawa, pers. comm.). We coded the flower occupant as 1 if it was present and 0 if it was absent except for seeds for which the coding was reversed to make the presence of seeds zero-inflated (i.e. 0 if seed was present, and 1 if seed was absent). The code reversal for seeds enabled us to use the same R code provided by Takeshi Osawa for all analyses (Takeshi Osawa, pers. comm.). We built the models after partitioning all data into training (70 %) and test (30 %) sets. Since the number of zeroes (i.e. absences) was many times greater than the number of ones (i.e. presences), and we needed to ensure that both the training and test sets had adequate presence data, we constituted these sets by separating the presence and absence data into two subsets; we then randomly split the presence and absence data between the training and test sets. This two-step procedure ensured the availability of nonzero (i.e. ones or presences) data in the test data set since sample sizes (i.e. presence values) for some gall occupant species were very low. We first ran the bagging GLM analysis on the training data set. We sampled the absence data (i.e. zeroes) with replacement to draw out samples equal to the total number of presences (i.e. ones) for each wasp species. After sampling, we merged the presence and absence data into a single data set and performed a binomial GLM analysis with a logit link function. We repeated this process 5,000 times resulting in 5,000 GLM outputs, which we used to calculate average values and standard errors of slope and intercept coefficients. We used these average values on the test data to make predictions about the presence or absence of a gall occupant. We calculated AUC values, specificity and sensitivity as indices of model performance using the package Epi in R. We performed all statistical analyses using the software package R (version 2.14.1).

Flower length can be a good predictor of the spatial position (nearer the syconium wall or away from the wall) of a species of gall occupant only if flower length is independent of gall size within a species. Therefore, for several syconia, we examined the relationship between gall size and total flower length for each wasp species (Online Resource 1). We used gall width as a measure of gall size. We haphazardly selected five syconia for each type of gall occupant; however, for A. testacea, only three syconia were used. The data on gall size and flower length were subjected to a Shapiro–Wilk's test for normality. Since the data were not normally distributed, a nonparametric Kendall's correlation analysis was performed for each species

of flower occupant separately for each syconium. In general, we did not find a significant correlation between gall width and total flower length (Online Resource 1). Therefore, the SDMs were performed with total flower length as a predictive variable.

Results

Resource availability and accessibility to wasps at oviposition

In pre-A stage syconia, all floral primordia were morphologically similar (Fig. 2a). In A phase syconia, flowers differentiated into sessile and pedicellate types, but the synstigma (combined stigma of all flowers lining the fig syconial lumen) was not yet formed, and hence, the syconium space was not tightly packed (Fig. 2b). Consequently, wasps ovipositing before pollination (A. stratheni and A. testacea) had less spatial constraints compared to those ovipositing in the B phase or later. Apocryptophagus stratheni deposited eggs inside the syconium lumen and not specifically into a flower (Online Resource 2a and 2b), and their offspring developed inside very large galls, which can sometimes fill the syconium cavity (Online Resource 2c). In B and post-B phases, the flowers were differentiated into sessile and pedicellate types, with the stigma of all flowers conjoined to form a synstigma, and the styles appeared more slender than in earlier phases since the flowers were tightly packed (Fig. 2c).

Based on the distance to ovary (DTO) measurements and assumptions on the reach of ovipositors, the internally ovipositing pollinator C. fusciceps could access only 75 % of the flowers, i.e. reach the ovary of the flower by its ovipositor passing down the style (Table 1). However, all externally ovipositing gallers and the putative parasitoid A. agraensis could access almost all flowers for oviposition (Table 1). The late-arriving parasitoid Apo. westwoodi could reach 94 % of flowers. For the parasitoid Apocrypta sp 2, the percentage of flowers accessible for oviposition decreased with syconium development from 100 % in A phase to less than 60 % in C phase (Table 1).

Spatial resource utilisation

The syconium nursery did not usually accommodate all eight possible occupants, including seeds, simultaneously. On average, a nursery housed five types of flower occupants including seeds. The earliest arriving NPFW galler species A. stratheni did not occur in any of the sampled syconia. Only 20 % of syconia contained all wasp species (except A. stratheni) and seeds. The galler Apocryptophagus fusca was the sole occupant in only one of 128 syconia

Table 1 Nursery sites accessible to fig wasps for oviposition during syconium ontogeny

Syconium phase	Wasp species	Wasp biology[a]	Accessibility[b] (%)	Distance to ovary (mm) Mean ± SD (range) [n flowers, n syconia][c]
Pre-A	A. stratheni	Large size, pro-ovigenic, produces large galls	100	0.94 ± 0.17 (0.66–1.13) [160, 9]
A	A. testacea	Large size, pro-ovigenic, produces large galls	100	1.86 ± 0.17 (1.47–2.37) [135, 9]
A	Apocrypta sp 2	Parasitoid, synovigenic	100	1.86 ± 0.17 (1.47–2.37) [135, 9]
B	C. fusciceps	Small size, pro-ovigenic, pollinator	75	1.68 ± 0.50 (0.85–2.87) [167, 12] (IDTO)
B	A. fusca	Small size, pro-ovigenic, galler	100	3.64 ± 1.01 (1.54–6.09) [138, 10]
B	Apocrypta sp 2	Parasitoid, synovigenic	95	3.64 ± 1.01 (1.54–6.09) [138, 10]
C	A. agraensis	Parasitoid, pro-ovigenic	99	5.23 ± 1.74 (2.25–10.57) [150, 10]
C	Apocrypta sp 2	Parasitoid, synovigenic	54	5.23 ± 1.74 (2.25–10.57) [150, 10]
C	Apo. westwoodi	Parasitoid, synovigenic	94	5.23 ± 1.74 (2.25–10.57) [150, 10]

[a] Life history parameters from Ghara and Borges (2010)

[b] Accessibility measured as IDTO = Internal distance to site for oviposition for the pollinator and as EDTO = External distance to site for oviposition for all other wasp species

[c] Distance to ovary = EDTO except for the pollinator where it is IDTO, n flowers = number of flowers sampled, and n syconia = number of syconia sampled for the flowers

sampled. In seven of 128 syconia, there were two types of flower occupants, the galler *A. fusca* and either seed or the parasitoid *Apocrypta* sp 2. Only one in 128 syconia contained only wasp species without containing seeds; in this syconium, the pollinators were the most abundant at 85.5 %. All associations between pairs of wasp species or wasps and seeds were either neutral or positive, but not negative (Fig. 3). There were significant associations between pollinators and seeds and between the following galler–parasitoid pairs: pollinator—*A. agraensis*, pollinator—*Apocrypta* sp 2 and *A. testacea*–*Apo. westwoodi* (Fig. 3). Seeds, the galler *A. fusca* and the parasitoid *Apocrypta* sp 2, occurred in the most syconia (Table 2), followed by the pollinator *C. fusciceps,* which occurred in 81 % of sampled syconia. *Apocryptophagus agraensis* was the least common wasp across syconia.

Flower occupancy of different wasp species and of seeds across syconia was quite similar to that observed within syconia (Table 2) with seeds occupying 60 % of the flowers. Within a syconium, pollinators were most abundant among the wasp species and occupied nearly a quarter of the flowers. The second galler species (*A. testacea*) to arrive in the syconium development sequence and both late-arriving parasitoid species (*Apocrypta* sp 2 and *Apo. westwoodi*) were the lowest in abundance. However, the coefficients of variation (CV) values for all NPFWs were very high indicating that their numbers were highly variable. Only seed occurrence had a low CV showing that the numbers of seeds remain more or less constant between syconia.

Wasps mostly occupied pedicellate flowers while seeds were found in larger numbers in sessile flowers (wasps: $V = 105$, $P = 0.0012$, $n = 14$ syconia; seeds: $V = 0$, $P = 0.0012$, $n = 14$ syconia; Wilcoxon matched-pairs signed-ranks test). The pollinators *C. fusciceps, A. testacea* and *A. agraensis* were more frequent in pedicellate flowers (*C. fusciceps*: $V = 86$, $P = 0.0024$, $n = 13$ syconia; *A. testacea*; $V = 52$, $P = 0.013$, $n = 11$ and *A. agraensis*: $V = 54$, $P = 0.008$, $n = 10$). *Apocryptophagus fusca, Apocrypta* sp 2 and *Apo. westwoodi* were equally distributed between sessile and pedicellate flowers (*Apocryptophagus fusca:* $V = 37.5$, $P = 0.72$, $n = 11$ syconia; *Apocrypta* sp 2: $V = 20$, $P = 0.062$, $n = 6$ and *Apo. westwoodi* $V = 5$, $P = 0.42$, $n = 4$).

In the analyses investigating seed and wasp occupancy of pedicellate flowers, the models incorporating tree ID as a random effect were found to be better than those without tree ID (Online resource 3). Seeds and wasp species differed in their occupancy of pedicellate flowers (Fig. 4), and syconium volume had a significant effect on pedicel length (Online resource 3). Seeds occupied flowers with the shortest pedicel lengths (Fig. 4). Gall occupants differed in their flower occupancy when total flower length was used as a parameter (Online resource 3, Fig. 5a); here also, flower length increased with syconium volume (Online resource 3). Once again, seeds occupied the shortest flowers and were present mostly in flowers towards the outside of the syconium. The galler *A. testacea*, as well as the parasitoid *Apo. westwoodi*, occupied flowers of distinctly different lengths with *Apo. westwoodi* occupying the
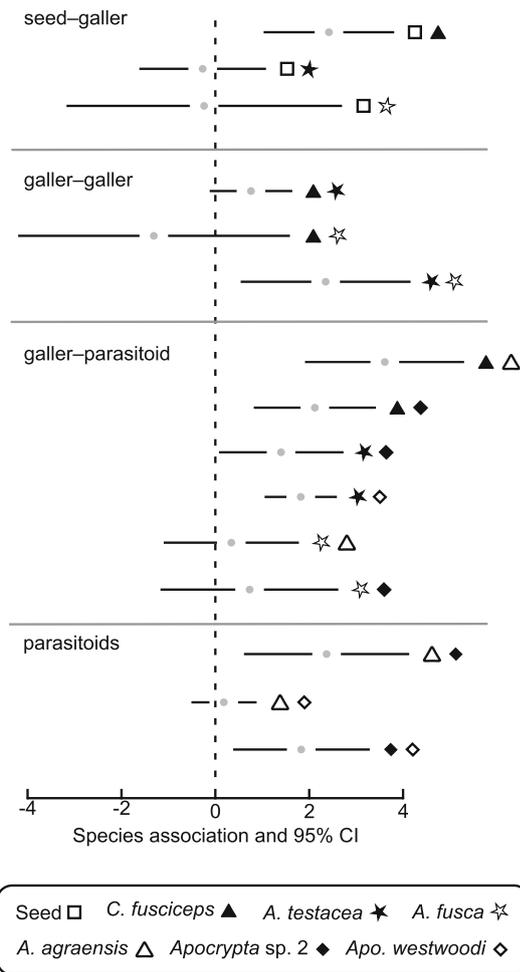
Fig. 3 Associations between wasp species and wasp–seed pairs. Association (*grey circle*) and 95 % CIs are plotted. Any association overlapping the central line is a nonsignificant or neutral association. Associations to the right are positive, whereas those to the left are negative associations
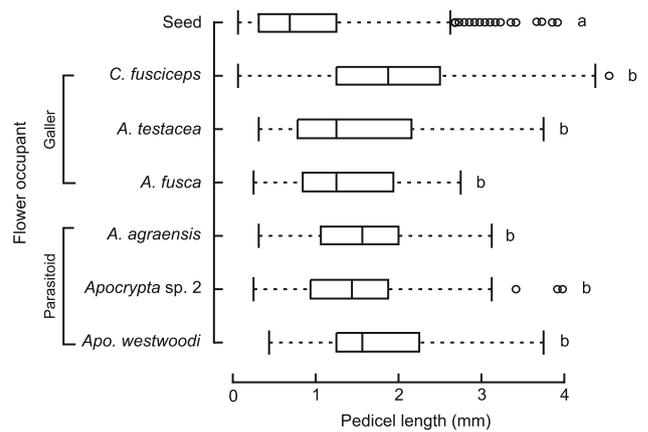

Fig. 4 Occupants in flowers of different pedicel lengths (*box-and-whiskers plots*). *Vertical lines* indicate medians, and circles denote outliers. *Different alphabets* denote significant differences between groups by post hoc Tukey tests

longest flowers (Fig. 5a). There was greater overlap in spatial occupancy of galls between wasp species when pedicel length alone was considered (Fig. 4) instead of total flower length (Fig. 5a). This suggests that some gall occupants modify total flower length during the course of development rather than influencing pedicel length. Since gall occupancy is a function of both oviposition preference as well as survival from enemies such as parasitoids, the presence of parasitoid offspring in flowers with the longest total lengths (i.e. the flowers furthest away from the syconium wall) suggests the absence of true enemy-free space in this microcosm.

Modelling species distribution in the nursery

Total flower length was used to predict the distribution of gall occupants within syconia. The high true-positive rate (sensitivity) and low false-positive rate (high specificity values) for all gall occupants (Fig. 5b) indicated that the SDM model could predict the presence or absence of the occupant quite accurately based on the spatial features of the nursery, here encapsulated by flower length. In general, AUC and sensitivity (true-positive) values were closely related for all species. The highest sensitivity and specificity (1 − false-positive rate) were shown for *A. testacea*, an early-arriving galler whose offspring develops within very large galls. The next highest sensitivity was demonstrated for the pollinator and the two *Apocrypta* parasitoid species. With the exception of *A. fusca*, a galler that parasitises the flowers at the same time as the pollinator, the specificity values of all gall occupants were lower than their sensitivity values (Fig. 5b). The sensitivity of the model when all NPFWs were pooled together was also high (AUC value = 0.92, sensitivity = 0.90, specificity = 0.81). Therefore, flower length

Table 2 The distribution of flower occupants within and between syconia

Flower occupant	Per cent syconia containing the occupant	Per cent flower occupancy across syconia (pooled)	Per cent flower occupancy within syconia Mean ± SD (CV)
Seed	93	60.10	56.79 ± 29.15 (0.51)
C. fusciceps	81	23.29	17.14 ± 22.08 (1.29)
A. testacea	61	1.05	1.52 ± 3.54 (2.32)
A. fusca	95	5.12	8.27 ± 14.17 (1.71)
A. agraensis	51	2.02	1.88 ± 3.87 (2.06)
Apocrypta sp 2	92	7.53	12.91 ± 15.74 (1.22)
Apo. westwoodi	58	0.90	1.49 ± 2.31 (1.56)

CV coefficient of variation; $n = 128$ syconia

Fig. 5 **a** Occupants in flowers of different total lengths (*box-and-whiskers plots*). The flower length includes the gall length and pedicel length. *Vertical lines* indicate medians and circles denote outliers. Different alphabets denote significant differences between groups by post hoc Tukey tests. **b** True-positive (sensitivity) and false-positive rates (per cent values) of species occupancy of flowers of different lengths by the predictive species distribution model (SDM) analyses. AUC per cent values are provided below the bars for each species. Sensitivity = (1 − false-positive rate). For seeds, the predicted values are for seed absence
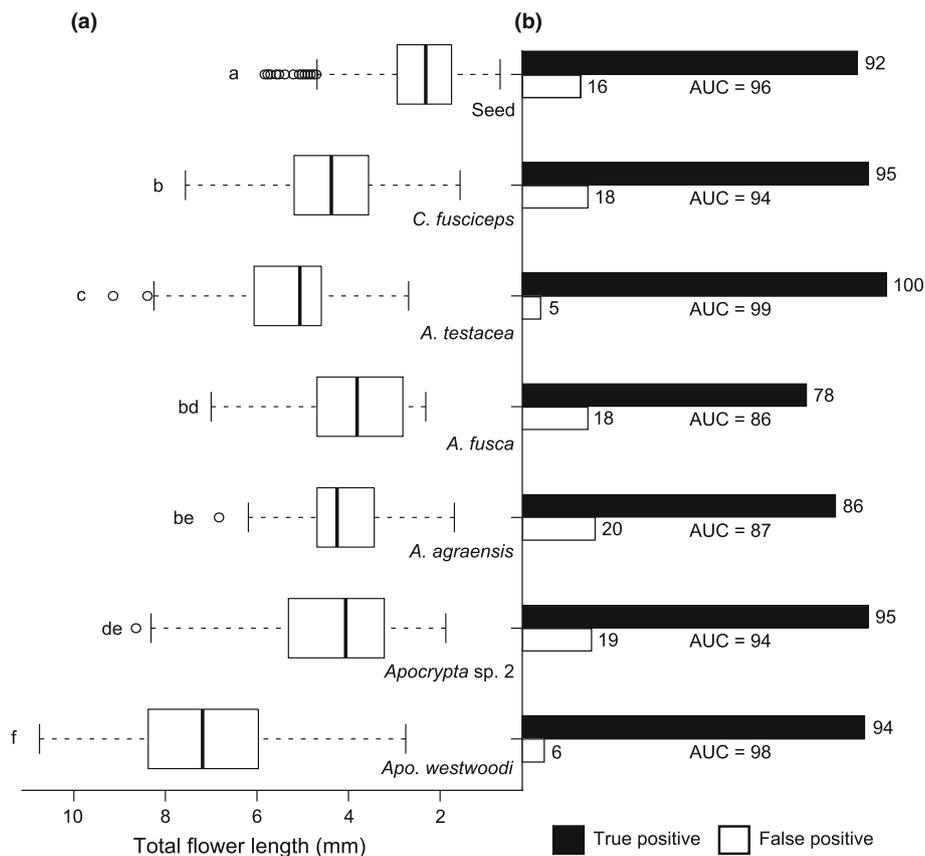
appears to be a good predictor for the location of developing and surviving offspring for most wasp species in the syconium nursery.

Discussion

The nursery in the fig–fig wasp pollination mutualism is a microcosm that changes as the syconium develops. The pattern of nursery occupancy by the mutualists (plant seeds and pollinator offspring) in this pollination mutualism has been attributed to several factors, most of which involve the resolution of conflict between the mutualists. Correspondingly, several hypotheses have been posited for the locations of developing mutualists in the nursery. According to the short ovipositor hypothesis (Galil 1977; Janzen 1979), pollinator ovipositors are unable to reach the ovaries of all flowers, and seeds therefore develop in the unreachable flowers. This hypothesis has been refuted by other studies (Bronstein 1988; Ganeshaiah et al. 1995; Nefdt and Compton 1996) as well as by the results of our present study. The ovipositors of the pollinator *C. fusciceps* can access 75 % of the flowers in an *F. racemosa* syconium (Table 1), which is much higher than the observed mean percentage of flowers occupied by pollinator offspring

(17 %; Table 2). The unbeatable seeds hypothesis suggests that some flowers are biochemically or developmentally destined to become seeds and cannot be galled to serve as hosts for developing pollinator larvae (West and Herre 1994; Wang et al. 2012). This hypothesis has never been directly tested, and our study also did not examine it specifically. Another hypothesis posits that the total number of pollinators that enter a syconium may collectively have insufficient eggs to saturate all the flowers of a syconium, which would leave many such flowers to develop into seeds if pollinated (Nefdt and Compton 1996). This hypothesis has been refuted in some fig species (Anstett et al. 1996), but an egg limitation may occur in other fig species with very large syconia with few pollinators per syconium (Nefdt and Compton 1996). We have not examined this hypothesis in our present study. Pollinators may also prefer to oviposit into flowers closer to the syconium cavity to allow galls containing developing larvae more space to grow (Anstett 2001).

The above hypotheses for the locations of seeds and pollinators in the syconium nursery were formulated to highlight conflict resolution only between the mutualistic partners—the figs and the pollinating wasps. However, all fig–fig wasp mutualisms examined to date have parasitic wasps associated with them, whose offspring either

compete with the mutualists for space or prey upon the mutualists (seeds and pollinators) or on each other (Cook and Rasplus 2003; Herre et al. 2008). Therefore, space utilisation in this nursery also depends on competition between parasites (gallers and parasitoids) and mutualists. The final location and frequency of developing offspring found in D phase syconia would depend on the oviposition preferences for specific locations, competition for space in the nursery as well as survival from enemy attack (Dunn et al. 2008; Al-Beidh et al. 2012).

Our results have shown that oviposition in the nursery can also be influenced by the biology and life history strategies of the wasps that differ in fecundity and longevity traits as well as in development time (Ghara and Borges 2010). In *Ficus racemosa*, each species has a different nursery utilisation strategy and different oviposition constraints. *Apocryptophagus stratheni* is a rare species, the largest of the gallers, with a short lifespan of 1 day and the longest developmental time within the fig wasp community of *F. racemosa* (Ghara and Borges 2010). Being pro-ovigenic, i.e. eclosing with a full complement of mature eggs (Ghara and Borges 2010), and having to lay its eggs within a day, its likely strategy is to deposit eggs into the pre-A phase syconium lumen since the available flowers are ill-defined (flower primordium stage). At such a stage, there are no other heterospecific competitors and it appears that *A. stratheni* utilises a unique niche. Galls produced by this species may arise from the syconium wall; they are very large and consequently reduce the space available for seeds and other wasps within the syconium. Since *A. stratheni* deposits eggs into the syconium before it has been pollinated, individuals run the risk of losing the nursery itself, should pollinators fail to arrive, as unpollinated syconia are usually aborted by the tree. This must constrain individual *A. stratheni* wasps to lay only few eggs in each syconium and to distribute eggs between several syconia as a bet-hedging strategy. Even though several individuals must oviposit into the same syconia in order to ensure mates for their offspring that can only mate within the syconium (M Ghara and RM Borges, pers. observation) because of apterous males, the number of eggs laid overall by this species into each syconium will be low based on the strategies of individual wasps. For the first time, we have also shown that gallers that arrive very early, even before differentiation of floral primordia into sessile and pedicellate flowers, can lay their eggs into the syconium lumen and trigger gall formation possibly from tissues lining the fig wall. This novel finding should stimulate more investigation into the biology of the very early-arriving large gall formers in the fig system.

The second parasitic galler *A. testacea* arrives after *A. stratheni* when flowers have begun to differentiate into pedicellate or sessile and long- and short-styled forms (Fig. 2). This pro-ovigenic wasp is also short-lived (maximum lifespan of 6 days; Ghara and Borges 2010) and produces large galls, although smaller than those of *A. stratheni*, which also protrude into the syconium lumen. Since it oviposits before pollination, like *A. stratheni*, it also runs the risk of having its nursery aborted if pollination fails. This probably constrains the number of eggs individuals deposit into each syconium as a bet-hedging manoeuvre. This may explain why although 61 % of syconia contain *A. testacea* offspring, only 1.5 % of galls are occupied by *A. testacea* in a syconium. However, syconia occupied by *A. testacea* galls leave less room for other galls owing to their large size.

The third parasitic pro-ovigenic galler *A. fusca* is longer-lived than the earlier mentioned gallers (maximum lifespan of 18 days; Ghara and Borges 2010), and arriving for oviposition concurrently with the pollinator runs a limited risk of nursery abortion. Consequently, it occurs in 95 % of syconia where it occupies 8.3 % of flowers, which is many orders of magnitude higher than the occupancy of the earlier gallers (Table 2). The galls produced by this species are the same length as those of the pollinators (Fig. 5), do not protrude into the syconium lumen, and therefore could be very likely competing with the pollinator for oviposition resources.

Of the parasitoids, *Apocrypta* sp 2 is the first to arrive, and it has the longest oviposition window, which stretches from late A through C phases (Ranganathan et al. 2010), during which the reach of its ovipositor declines as the syconium expands (Table 1). This parasitoid is also synovigenic, i.e. maturing its eggs throughout its lifespan of up to 27 days (Ghara and Borges 2010). Since it appears able to exploit different developing stages of potential hosts, it is the most common parasitoid within syconia (13 % of gall occupancy) and also across syconia (92 % of syconia) compared to the other parasitoids (Table 2). The similarity between cuticular hydrocarbons of *A. fusca* and *Apocrypta* sp 2 (Ranganathan 2012) and results of on-going exclusion experiments (P Yadav and RM Borges, unpublished data) suggests that these species constitute a host–parasitoid pair. If this is correct, then *Apocrypta* sp 2 has access to a very common host, since after the pollinators, *A. fusca* is the most common wasp in the syconium nursery (Table 2). *Apocrypta* sp 2 may also prey upon the early gallers *A. stratheni* and *A. testacea* (P Yadav and RM Borges, unpublished data). Its wide prey base therefore could contribute to the high frequency of *Apocrypta* sp 2 in the nursery.

The other two parasitoids, *A. agraensis* and *Apo. westwoodi*, arrive concurrently in the C phase (Ranganathan et al. 2010) and therefore parasitise later developing stages of wasps in the nursery. These two late-arriving parasitoids were least common within and across syconia compared to

the earliest arriving species (Table 2). Of the two, *A. agraensis* is shorter-lived (maximum lifespan of 4 days) and is also pro-ovigenic compared to the much longer-lived (23 days) synovigenic *Apo. westwoodi* (Ghara and Borges 2010). Arriving at the same time for oviposition, one might predict intense competition between these parasitoid species, which may be resolved if one competitor, especially the one constrained by a shorter lifespan and pro-ovigeny, specialises on a more common prey species within the syconium. It is therefore interesting that cuticular hydrocarbon similarity suggests that *A. agraensis* and the commonly occurring pollinator are host–parasitoid pairs (Ranganathan 2012). *Apocrypta westwoodi*, on the other hand, preys upon the large gall producers *A. testacea* and *A. stratheni* (P Yadav and RM Borges, unpublished data), both of which are uncommon in syconia. This may explain the low occupancy of *Apo. westwoodi* within syconia. It is possible that the late-arriving *Apo. westwoodi* is a specialist parasite of late stages of gallers that produce large galls. *Apocrypta westwoodi* occupied galls of the longest flower length (Fig. 5), facilitated by its ovipositor, which has nearly the longest reach into the nursery syconium (Table 1). It therefore appears that such galls, despite their protuberance into the syconium lumen, furthest away from the syconium wall, cannot escape the reach of the long ovipositor of *Apo. westwoodi*, which has the second longest ovipositor in this closed community of wasps (Ghara and Borges 2010).

Contrary to what has been observed in other fig systems (Dunn et al. 2008; Al-Beidh et al. 2012), there does not, therefore, appear to be enemy-free space in this syconium nursery. In this fig microcosm, the survival of host (i.e. prey) species in galls that are easily accessible to parasitoids (i.e. predators) suggests that the different wasp species co-exist in this system by utilising unique developmental stages of the nursery and by employing specific oviposition strategies that follow from their life history and longevity constraints as discussed above. Furthermore, however late may be the arrival of wasps for oviposition in syconium ontogeny, their offspring are constrained to complete development by the time male pollinating wasps cut an exit hole in D phase to release females laden with pollen. This is because usually only male pollinators are able to effect wasp release from the syconia (Cook and Rasplus 2003) as in *F. racemosa*. This special feature of the nursery places additional constraints on nursery suitability for an ovipositing wasp. Taken together, these features contribute to decipherable patterns of resource utilisation of the nursery which is also evident from our ability to use species distribution models (SDMs) successfully to predict the presence of surviving offspring of species within the nursery.

The SDM analyses were able to uncover patterns that could not be found using the conventional pairwise analyses. According to these conventional analyses (i.e. pair-wise tests), flower lengths occupied by *C. fusciceps* and *A. fusca* did not differ; however, SDM analyses showed that the sensitivity (true-positive) rate for flower length occupancy by *C. fusciceps* was 95 compared to 78 for *A. fusca* (Fig. 5b). Thus, the SDM analysis could differentiate between the locations of these two species in the syconium. Similarly, the pairwise comparisons showed that *A. fusca* and *A. agraensis* overlapped significantly in their occupancy of flowers of certain lengths, but there was a much higher sensitivity rate for *A. agraensis* (86) compared to that for *A. fusca* (78) by the SDM analyses (Fig. 5b). The same held true for the overlap found between the locations of wasp offspring of *A. agraensis* and *Apocrypta* sp 2 by the conventional analyses. Therefore, SDMs revealed patterns that were not uncovered using the standard pairwise analyses. On the other hand, the host–parasitoid pair of *A. testacea*–*Apo. westwoodi* showed similar and very high sensitivities and specificities even though the pairwise analyses revealed that the surviving offspring of *Apo. westwoodi* occupied much larger longer flowers than those of its host *A. testacea* (Fig. 5). This emphasises that knowledge of wasp biology helps the interpretation of the SDM results. Therefore, the sensitivity and specificity values of *A. testacea* in the SDM analyses were the highest because it is an early galler producing large galls and has the first choice of oviposition sites. The earliest arriving galler *A. stratheni* was not modelled in this exercise, but had it been, we predict that its sensitivity and specificity values would be the highest of all wasp species in this community. Similarly, since *A. fusca* is probably a host for the common parasitoid *Apocrypta* sp 2, and often occupies the same syconia as the abundantly developing pollinator, it is not surprising that it was more difficult to model its location using SDM analyses. As in other studies of fig syconia (Dunn et al. 2008), we also found that seeds were found in the shortest flowers closest to the nursery wall, and that the locations of seeds and of the mutualistic pollinators could be accurately predicted. We therefore find that the SDM approach can be used successfully to investigate spatial occupancy in the fig microcosm.

Our study has used data on the locations of surviving offspring of the seven-member fig wasp community in the fig nursery and not the locations of egg deposition by all fig wasp species, which is currently not technically feasible given the thousands of potential egg deposition sites within each syconium. Yet, our investigations of the development of the nursery and ensuing modifications to nursery space, coupled with knowledge of the accessibility of oviposition sites, have provided insight into the various forces that could contribute to niche partitioning within the fig nursery microcosm and hence species coexistence in this community of fig wasps.

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