

Plant connectivity underlies plant-pollinator-exploiter distributions in *Ficus petiolaris* and associated pollinating and non-pollinating fig wasps

A. Bradley Duthie and John D. Nason

A. B. Duthie (aduthie@abdn.ac.uk), School of Biological Sciences, 202 Zoology Building, Univ. of Aberdeen, Aberdeen, AB24 2TZ, UK.
– J. D. Nason, Dept of Ecology, Evolution, and Organismal Biology, 251 Bessey Hall, Iowa State University, Ames, IA 50011, USA.

Mutualism is ubiquitous in nature, and nursery pollination mutualisms provide a system well suited to quantifying the benefits and costs of symbiotic interactions. In nursery pollination mutualisms, pollinators reproduce within the inflorescence they pollinate, with benefits and costs being measured in the numbers of pollinator offspring and seeds produced. This type of mutualism is also typically exploited by seed-consuming non-pollinators that obtain resources from plants without providing pollination services. Theory predicts that the rate at which pollen-bearing 'foundresses' visit a plant will strongly affect the plant's production of pollinator offspring, non-pollinator offspring, and seeds. Spatially aggregated plants are predicted to have high rates of foundress visitation, increasing pollinator and seed production, and decreasing non-pollinator production; very high foundress visitation may also decrease seed production indirectly through the production of pollinators. Working with a nursery mutualism comprised of the Sonoran Desert rock fig, *Ficus petiolaris*, and host-specific pollinating and non-pollinating fig wasps, we use linear models to evaluate four hypotheses linking species interactions to benefits and costs: 1) foundress density increases with host-tree connectivity, 2) pollinator production increases with foundress density, and 3) non-pollinator production and 4) seed production decrease with pollinator production. We also directly test how tree connectivity affects non-pollinator production. We find strong support for our four hypotheses, and we conclude that tree connectivity is a key driver of foundress visitation, thereby strongly affecting spatial distributions in the *F. petiolaris* community. We also find that foundress visitation decreases at the northernmost edge of the *F. petiolaris* range. Finally, we find species-specific effects of tree connectivity on non-pollinators to be strongly correlated with previously estimated non-pollinator dispersal abilities. We conclude that plant connectivity is highly important for predicting plant-pollinator-exploiter dynamics, and discuss the implications of our results for species coexistence and adaptation.

Mutualisms are defined by interactions between species that are reciprocally beneficial. Mutualisms are ubiquitous in nature (Bronstein 2001a) and underlie much of the world's agricultural production and biodiversity (Tylianakis et al. 2008, Bascompte 2009), so understanding their dynamics is of practical as well as ecological and evolutionary significance (Thompson 2005). In addition to conferring fitness benefits to symbionts, the ecology and evolution of mutualism includes diverse costs (Bronstein 2001a). The costs and benefits involved in mutualistic interactions are often difficult to quantify (Bronstein 2001a). Much has been learned, however, from plants associated with species-specific pollinators whose larvae consume seeds within host fruits, because in such systems costs and benefits are easily measured in terms of the numbers of seeds and pollinators that plants produce (Bronstein 2001a). The fitness gain accrued by the production of seeds and pollinators is different for each mutualist. For mutualisms in which pollinators collect pollen in the natal host before dispersing to pollinate and lay eggs in new hosts, plants benefit from the production of both

seeds and new pollinators, which represent plant female and male fitness, respectively, while pollinators do not directly benefit from the production of seeds. Because asymmetry in fitness interest is expected for all mutualisms (Afkhani et al. 2014), insights gained from studies of plants and their seed-eating pollinators are broadly applicable to mutualism more generally.

Empirical studies of plants with seed-eating pollinators, such as figs and their pollinating wasps (Weiblen 2002), observe that the number of pollinator offspring and seeds produced by plants within a population often vary greatly (Addicott 1986, Holland and Fleming 1999, Després et al. 2007). For example, in a study including 23 Florida strangling figs *Ficus aurea*, Bronstein (2001a) found pollinator production within fig syconia (enclosed inflorescences) to range between 0–229, and seed production to range between 0–150. Such variation among figs within a population is common, with high variation in pollinator and seed production reported for species worldwide (Bronstein and Hossaert-McKey 1996, Cook and Power 1996, Wang et al.

2005, Cardona et al. 2013). To comprehensively understand mutualism, it is necessary to also understand the causes of this high variation in the distribution of mutualists, but such causes remain unclear for plants with seed-eating pollinators.

The rate at which seed-eating, pollen-bearing mutualists (hereafter 'foundresses') visit host plants is a key parameter that theory predicts will causally affect the production of pollinator offspring and seeds (Morris et al. 2003, Bronstein et al. 2003, Wilson et al. 2003, Duthie and Falcy 2013). Higher foundress visitation rates may lead to more effective pollination (Després et al. 2007), potentially increasing seed production. But increasingly high foundress visitation will also incur increased seed predation from pollinator larvae (Herre 1989, Shapiro and Addicott 2003). Higher foundress visitation is therefore expected to increase total pollinator production on a plant. As pollinator (and therefore foundress) density increases further in a population, plant seed production decreases, resulting in lowered plant density and an eventual decrease in pollinator population growth that ultimately leads to stable populations or dampened oscillations of species abundances over time in ecological models (Morris et al. 2003, Wilson et al. 2003).

Given the density-dependent regulation predicted by ecological models, the high variation observed among plants in seed and pollinator production may suggest that density-dependent mechanisms are weak in regulating plant and seed-eating pollinator interactions (Addicott 1986). Alternatively, spatial variation in foundress visitation may lead to variation in pollinator and seed production with populations still regulated strongly by density-dependent mechanisms. In a spatially-explicit model of plants and seed-eating pollinators, Duthie and Falcy (2013) varied the aggregation of plants by varying plant habitat autocorrelation. Their model demonstrates that when the spatial distribution of plants is aggregated and the dispersal of pollinators is limited, the mean number of foundress visits a plant receives will be strongly influenced by the plant's location. Where plants are closely aggregated, foundress visitation will increase thereby increasing pollinator production at the potential cost of seeds. In contrast, areas where plants are more spatially isolated will be visited less frequently by foundresses, which may decrease pollinator production but also decrease the probability of pollen transfer.

Mutualisms are almost universally exploited by individuals that obtain resources or services without incurring the costs associated with providing resources or services in return (Bronstein 2001b, Ferrière et al. 2002). The most abundant and diverse of these exploiters are specialist species obligately associated with their mutualist hosts. In plant–pollinator mutualisms, exploiters often feed on a subset of developing seeds, but do not pollinate plants. Obligately exploiting species are especially diverse in the interactions between figs and their pollinating wasps. While most of the 750+ described species of figs are each pollinated by a single host-specific wasp species, they are additionally associated with a phylogenetically diverse community of non-pollinator wasp species that oviposit within fig syconia. Non-pollinator wasps are typically host-fig-specific (Weiblen 2002), and each species of fig typically includes 2–30 non-pollinating species (Compton and Hawkins 1992). Many of these non-pollinating species

gall and develop within fig ovules like pollinators, though some are parasitoids, cleptoparasites, or inquiline predators of other pollinating or non-pollinating fig wasps. How non-pollinating exploiter fig wasps, and exploiters more generally, affect the dynamics of mutualism remains unclear (Bronstein 2001b, Borges 2015).

Theoretical studies of plants and their seed-eating pollinators have modelled the ecological (Bronstein et al. 2003, Morris et al. 2003, Wilson et al. 2003, Duthie and Falcy 2013) and evolutionary (Ferrière et al. 2002, Jones et al. 2009) consequences of exploitation. Exploiters in these models are competitively inferior to pollinators because they rely on already pollinated flowers that have not already been used for pollinator oviposition (and would otherwise develop into seeds). Duthie and Falcy (2013) predict that exploiters will be most abundant where plants are isolated, and least abundant where plants are especially aggregated. They predict this pattern of exploiter distribution to be caused by pollinators pre-empting plant flowers where connectivity between plants is high (i.e. less movement is required among plants), leaving the flowers of isolated plants less frequently visited as sites of pollinator oviposition and therefore more often available as sites of exploiter oviposition.

Here we test the predictions of Duthie and Falcy (2013) using a natural community that includes a fig, its species-specific pollinator, and a guild of host-fig-specific non-pollinators. Using the spatial locations of *Ficus petiolaris* trees from six populations in Baja California, as well as counts of foundresses, pollinator offspring, seeds, and non-pollinator offspring from mature fig syconia, we test four specific hypotheses linking tree connectivities to their production of wasps and seeds: 1) the mean number of foundresses entering the syconia of a fig tree will increase with fig tree connectivity, 2) the mean number of pollinator offspring produced per syconium will increase with the mean number of foundresses per syconium on a tree, 3) and the mean number of seeds and 4) the mean number of non-pollinator offspring produced per syconium will decrease with the mean number of pollinator offspring produced per syconium on a tree.

Material and methods

Study species and site

The monoecious Sonoran Desert rock fig, *Ficus petiolaris* (family Moraceae, subgenus *Urostigma*, section *Americana*), is endemic to the Sonoran Desert of Baja California and adjacent mainland Mexico. Like all figs, *F. petiolaris* trees produce enclosed inflorescences (syconia) containing numerous uni-sexual female and male flowers. In *F. petiolaris*, the number of uni-ovulate female flowers ranges from 150–700, depending on syconium size (Duthie and Nason unpubl.). These flowers line the inner cavity and possess styles of varying length that point towards the syconium's hollow interior. Male flowers are fewer and mature weeks later, precluding self-pollination within syconia. Although most fig species produce syconia in synchronous bouts (hereafter 'crops') that can be separated by periods of several months to years (Windsor et al. 1989), nearly half of *F. petiolaris*

trees produce syconia with at least some degree of within-crown asynchrony (Gates and Nason 2012). Asynchronous reproduction allows for greater overlap in phenology and outcrossing among trees when population densities are low, as is common in *F. petiolaris* (Gates and Nason 2012). Here we sample only from trees located in Baja California, where *F. petiolaris* is the sole wild species of fig.

Ficus petiolaris is pollinated by a single and unnamed specialist species of *Pegoscapus* wasp (superfamily Chalcidoidea, family Agaonidae). Upon arrival to 'female phase' trees with receptive syconia, foundresses enter syconia through a small bract-lined ostiole, then actively pollinate female flowers while ovipositing through styles into a subset of fig ovules (Duthie pers. obs.; Supplementary material Appendix 2 video). After pollination and oviposition, syconia enter into 'interphase', a period in which seeds and ovules galled by wasp larvae develop over several weeks. After development is complete, syconia enter into 'male phase' at which time emerging males compete for access to female pollinators. After mating, females collect pollen from mature male flowers within syconia, then exit syconia through holes chewed by males to disperse to new trees bearing receptive female phase syconia.

The community of non-pollinating chalcidoid fig wasps associated with *F. petiolaris* in Baja California includes seven species, all of which oviposit into fig syconia externally by inserting their ovipositors through syconia walls. Each species of non-pollinator is regularly found in all fig populations, often developing within the same syconium (Duthie et al. 2015a). The community includes three species of *Idarnes* (family Sycophagidae) and two species of *Heterandrium* (family Pteromalidae), all of which gall fig ovules within the same syconia as pollinators, and likely compete with pollinators and each other for limiting ovule resources (Duthie et al. 2015a). The community also includes a species of *Aepocerus* (family Pteromalidae), which oviposits early in the female phase of syconium development and produces especially large galls that protrude into the centre of syconia and appear to originate from the tissue of the syconium wall. The use of apparently different syconium resources and the early oviposition of *Aepocerus* make it unlikely to be a competitor of galling wasps, but its use of space within syconia might make its interaction amensal by crowding out other species. *Aepocerus* is host to a specialist parasitoid of the genus *Physothorax* (family Torymidae).

Mapping and sampling of fig trees

Trees of *F. petiolaris* were mapped for six sites along a latitudinal gradient on the Baja California peninsula (site 70, 23°73'76.9"N, 109°82'88.7"W; site 96, 24°03'38.0"N, 110°12'57.0"W; site 112, 27°56'04.3"N, 113°06'71.9"W; site 113, 27°14'85.2"N, 112°43'55.4"W; site 172, 28°29'06.9"N, 113°11'19.7"W; site 158, 29°26'27"N, 114.02°09.0"W). In the summer (dry season) of 2007, 2010 and 2013, a total of 859 mature, male phase syconia from 80 crops were collected. The volume of each collected syconium was measured, then syconia were partially cut open and placed in individual vials overnight (min 12 h) to allow sufficient time for new adult wasps to emerge. Emerged wasps were preserved in 95% ethanol, then shipped to Iowa State

University where counts of pollinators and non-pollinators were obtained for individual syconia. Because foundress *Pegoscapus* wasps die within the syconium in which they pollinate and oviposit (Herre 1989), and foundress corpses (at a minimum their head capsules) remain intact inside syconia through male phase, we were also able to obtain estimates of arriving foundresses for each syconium. For each crop, we quantify foundress visitation rate as the mean number of foundresses collected per syconium; visitation therefore requires that females arrive at trees and enter a syconium. Per syconium foundress counts normally ranged from 1–4 but also included unpollinated, zero-foundress syconia, which are sometimes induced to mature when containing sufficient numbers of developing non-pollinator wasps. These syconia produce non-pollinators but not pollinator offspring or seeds. To estimate seed counts, syconia were dried, and seeds were placed in separate coin envelopes and shipped to Iowa State University. Seed counts were sampled for 120 syconia from 11 trees.

Analyses

For each tree from which syconia were sampled, we defined local tree density as tree connectivity using the distance to the n th nearest neighbour of the focal tree. Advantages of using the n th nearest neighbour (as opposed to simply nearest-neighbour) have long been known to include an increase in accuracy of density determination, and the detection of large-scale heterogeneity (Thompson 1956, Shaw and Wheeler 1985). For ease of interpretation, we define r_n as -1 times the distance to the n th nearest neighbour in km because after multiplying by -1 , r_n increases with tree connectivity. To ensure that our results were not scale dependent, we used four n values: $n = 5, 10, 20$ and 40 . Because our results were robust to different r_n values, we present $n = 20$ in our primary results; other scales are reported in supplemental material (Supplementary material Appendix 1 Table A1–A4).

To determine the relationship between foundresses visitation rate and r_n , we used R (<www.r-project.org>) to fit a linear regression model using mean foundresses per syconium on a crop as a dependent variable and r_n as an independent variable; syconium volume and tree latitude were also included as covariates. To test the effect of fig tree connectivity on pollinator, seed, and non-pollinator production, the same analysis was performed using mean counts of pollinator, seed, and non-pollinators produced per syconium on a crop as dependent variables. In the case of non-pollinators, only galls of fig ovules were used in the analysis, which included all *Idarnes* and *Heterandrium* and excluded *Aepocerus* and *Physothorax* (Duthie et al. 2015a). In all regressions, data points (mean foundresses, wasps or seeds per syconium) were weighted by the number of syconia sampled per crop.

Regressions predicting pollinator, non-pollinator, and seed densities included multiple relevant covariates. When regressing pollinator densities against foundresses per syconium, r_n , syconium volume, and tree latitude were included as covariates. Similarly, when regressing non-pollinator densities against pollinator densities, r_n , syconium volume, tree latitude, and foundresses per syconium were all included as

covariates. Finally, when regressing seed densities against pollinator densities, r_n , syconium volume, tree latitude, foundresses, and non-pollinators were included as covariates. In particular, the number of foundresses has been shown to have a positive effect on pollinator offspring production in other *Ficus* (Herre 1989, West et al. 1996), and models of plant-pollinator-exploiter interactions predict the rate of foundress arrival to affect pollinator, seed, and non-pollinator densities within plants (Bronstein et al. 2003, Morris et al. 2003, Wilson et al. 2003, Duthie and Falcy 2013). When considering non-pollinator density, we included foundresses as a covariate because theory predicts the rate of foundress arrival to decrease non-pollinator production through the production of pollinators. Additionally, pollinator and non-pollinator production were included as covariates when considering seed production, as wasp production might come at the cost of developing seeds.

Effect of fig connectivity on non-pollinator species

The production of any individual species of non-pollinator wasp is likely to be affected by its ability to disperse to receptive fig trees, with weaker dispersers observed most where fig trees are aggregated. In contrast, non-pollinators that are better dispersers will not be observed as much where fig trees are aggregated, and the production of these exploiters may be reduced by the preemption of ovules by pollinators, as well as competition from other non-pollinators. Consequently, while we predict increased pollinator production to decrease non-pollinator production overall where tree connectivity is high, we expect the production of better dispersers to decrease most with tree connectivity (Duthie et al. 2014). Ideally, species dispersal ability would be measured directly, but the small body size of wasps made such measurements infeasible. Instead, we used the wing loadings of *F. petiolaris* non-pollinators as estimated in Duthie et al. (2015a) and published in the Dryad Digital Repository (Duthie et al. 2015b). Wing loadings of *F. petiolaris* non-pollinators calculate the ratio of insect body volume to wing surface area (Duthie et al. 2015a). Wing loadings are typically negatively correlated with dispersal ability in insects (Harrison 1980, Fric et al. 2006), as appears to be the case for the five non-pollinating fig wasps on which we focus (Duthie et al. 2015a). To evaluate support for our prediction that the density of better dispersing non-pollinators will decrease with increasing tree connectivity, we first estimated the slope of a linear regression using r_n as an independent variable and mean non-pollinator species density per crop as a dependent variable. Positive regression slopes are interpreted to indicate a positive effect of r_n on species production, whereas negative regression slopes indicate a negative effect of r_n on production. We tested whether or not species-specific regression slope estimates were positively correlated with wing loadings. In another paper (Duthie et al. 2015a), we used data from 2010 to test this correlation, counting the number of neighbouring trees within a defined radius (e.g. 1 km) of a focal tree, instead of estimating r_n . For consistency, here we estimate r_n , but our results are not qualitatively different between methods. In contrast to Duthie et al. (2015a), regression slopes are obtained using species densities at the level of individual crops rather than syconia, and in addition

to mean syconium volume, we additionally include tree latitude, foundress count, and pollinator production as covariates when estimating regression slopes.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.04416>> (Duthie and Nason 2016).

Results

Histograms illustrating distributions of mean per syconium foundress counts, pollinator production, seed production, and non-pollinator production, are shown in Fig. 1. Foundress counts increased significantly with tree connectivity (r_n ; 76 DF; $p = 0.001$; Fig. 2), with a mean increase of $ca\ 0.03 \pm 0.009$ foundresses per unit r_n (i.e. 0.03 fewer foundresses per km to the nearest 20th tree; \pm indicates standard error). Foundress counts were not affected by syconium volume ($p > 0.1$), but mean foundress count significantly decreased with fig latitude ($p = 0.008$). Overall, greater connectivity among fig trees therefore resulted in more foundresses, and fewer foundresses arrived for trees at higher latitudes.

We observed a mean per syconium increase of 29 ± 9.186 pollinators per foundress ($p = 0.002$; Fig. 3), but pollinator counts were not directly affected by r_n , syconium volume, or tree latitude (75 DF; $p > 0.1$; note, when foundresses were removed from the linear model, r_n had a marginally significant positive effect on pollinator counts, $p = 0.055$). Pollinator production also increased with foundress arrival at the scale of individual syconia (Supplementary material Appendix 1 Fig. A1). We observed a mean per syconium decrease of 0.132 ± 0.048 non-pollinators per pollinator ($p = 0.007$; Fig. 4). Overall, non-pollinators were not directly affected by r_n (74 DF; $p = 0.067$), syconium volume, tree latitude, or foundresses ($p > 0.1$; note, non-pollinator counts significantly decreased with r_n when either pollinators [$p = 0.047$] or both pollinators and foundresses [$p = 0.018$] were removed from the linear model). Seed production per syconium decreased by 0.527 ± 0.133 per pollinator ($p = 0.029$; Fig. 5), and seed production significantly increased or decreased with all covariates except r_n (3 DF; $p > 0.1$). Specifically, on each crop sampled, we observed a mean per syconium increase of 0.044 ± 0.010 seeds per mm^3 syconia volume ($p = 0.021$), a decrease of 303 ± 0.812 seeds per unit of tree latitude ($p = 0.033$), an increase of 71.07 ± 18.92 seeds per foundress ($p = 0.033$), and a decrease of 3.448 ± 0.605 seeds per non-pollinator ($p = 0.011$).

Although non-pollinators as a group did not significantly increase or decrease with tree connectivity, we found among species variation in the effect of tree connectivity on non-pollinator production. Consistent with Duthie et al. (2015a), species with lower wing loadings tended to be more negatively associated with tree connectivity than species with higher wing loadings (Fig. 6; $p = 0.051$; $R^2 = 0.768$). Over all r_n scales considered, only the production of the non-pollinator species with the highest wing loading significantly increased with tree connectivity, with 0.583 ± 0.228

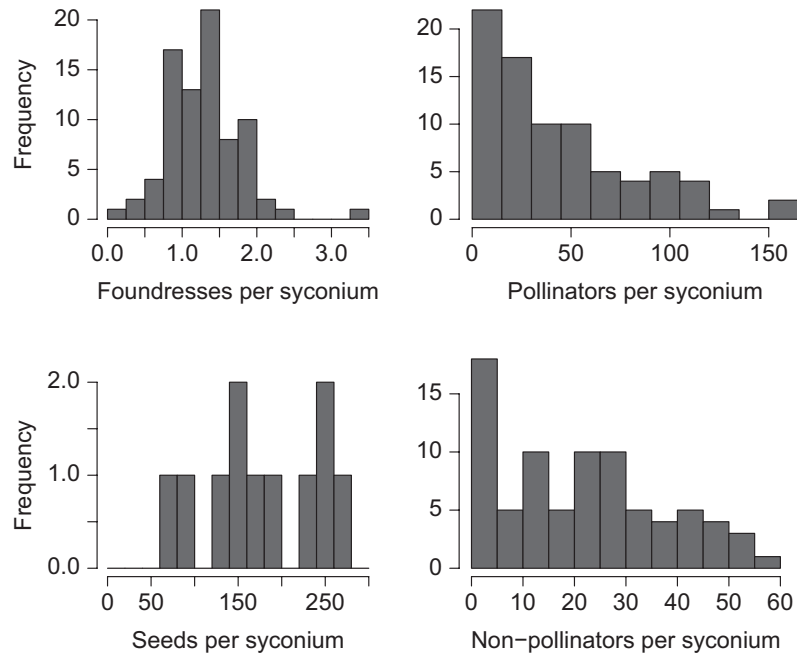


Figure 1. Distributions of the mean per syconium density of arriving pollinator foundresses, pollinator offspring, seeds and non-pollinators on crops of the Sonoran Desert rock fig, *Ficus petiolaris* collected from six sites in Baja, California. Samples include 80 crops from 75 unique trees for foundress, pollinator, and non-pollinator distributions and 11 crops from 11 unique trees for seed distributions.

more individuals produced per syconium per unit r_n (LO1; Fig. 6; $p = 0.011$). The species with the third highest wing loading was the only species of non-pollinator for which the effect of r_n was not significant (SO1; Fig. 6; $p > 0.1$). For the three remaining species of non-pollinators, the effect of r_n was significantly negative, decreasing per syconium species production by 0.073 ± 0.023 (Het2; Fig. 6; $p = 0.002$), 0.318 ± 0.133 (SO2; Fig. 6; $p = 0.019$), and 0.931 ± 0.070 (Het1; Fig. 6; $p < 0.001$). Effects of mean syconium volume,

crop latitude, mean foundress counts, and mean pollinator production are reported in Table 1.

Discussion

The syconia of fig trees are temporally and spatially ephemeral resources for both pollinating and non-pollinating fig wasps. Although some fig species regularly fruit asynchronously

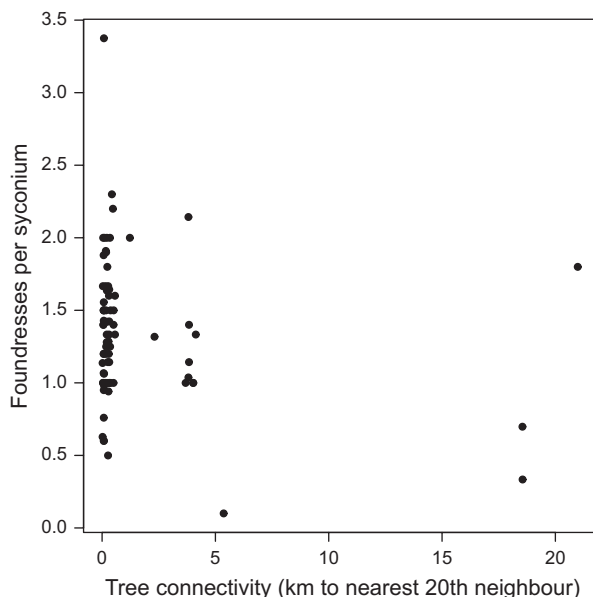


Figure 2. Relationship between tree connectivity (distance in kilometers to the nearest 20th neighbouring tree) and the mean number of arriving pollinator foundresses per syconium collected from 80 crops from 75 unique trees of the Sonoran Desert rock fig.

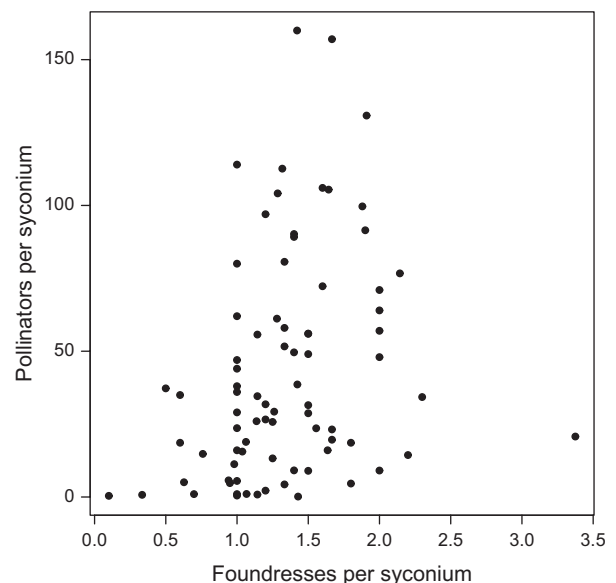


Figure 3. Relationship between the mean number of arriving pollinator foundresses per syconium and mean number of pollinator offspring per syconium collected from 80 crops from 75 unique trees of the Sonoran Desert rock fig.

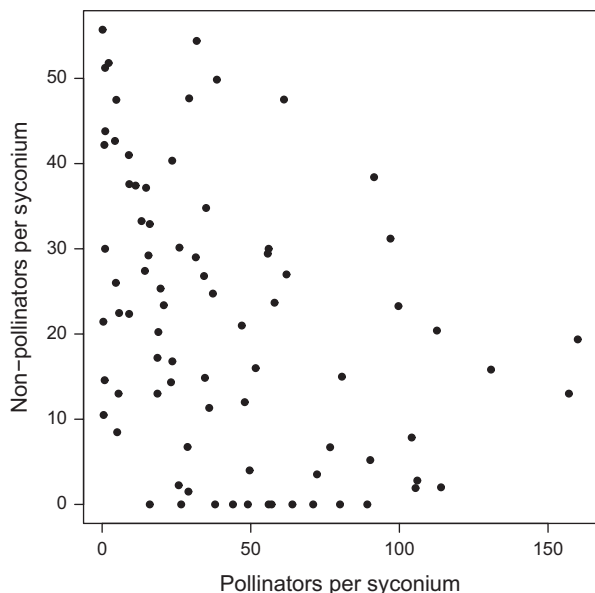


Figure 4. Relationship between the mean number of pollinator offspring per syconium and the mean mean number of non-pollinator offspring per syconium collected from 80 crops from 75 unique trees of the Sonoran Desert rock fig.

(Bronstein and Patel 1992, Cook and Power 1996), including *Ficus petiolaris* (Gates and Nason 2012), syconia production is never continuous. Fig wasps must routinely search for new fig trees with receptive syconia, which may be located far from their natal trees (Nason et al. 1996, 1998, Ahmed et al. 2009). This is likely to lead to both high and highly variable dispersal mortality, which will be affected by the location and timing of syconia development in conspecific fig trees. Consequently, the rate at which pollen-bearing foundress wasps arrive to fig syconia is likely to vary greatly in space and time. Further, because the arrival rate of foundresses is predicted to directly affect the production of pollinator offspring, seeds, and exploiter offspring (Bronstein et al. 2003, Morris et al. 2003, Wilson et al. 2003, Duthie and Falcy 2013), the spatio-temporal dynamics of syconia availability may be fundamental to the distributions of species in fig and fig wasp communities. Despite high predicted stochasticity in syconia availability, we found strong support for our four hypotheses. 1) The spatial aggregation of fig trees (tree connectivity) was positively associated with the number of foundresses entering fig syconia, which in turn 2) was positively associated with pollinator production, while pollinator production was negatively associated with both 3) seed production and 4) non-pollinator

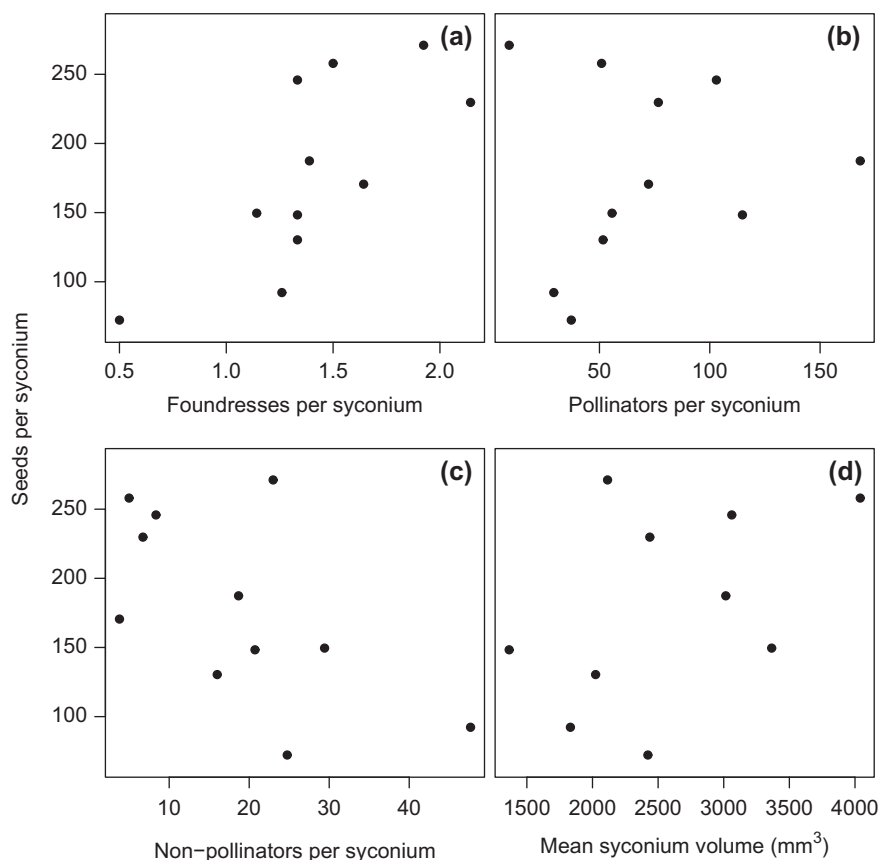


Figure 5. Relationship between mean per syconium seed production and four variables collected from 11 crops from 11 unique trees of the Sonoran Desert rock fig. Panels show how seed production increase with the mean per syconium number of arriving pollinator foundresses (a), decreases with the mean number of pollinators (b) and mean number of non-pollinators (c) per syconium, and increases with mean syconium volume (d).

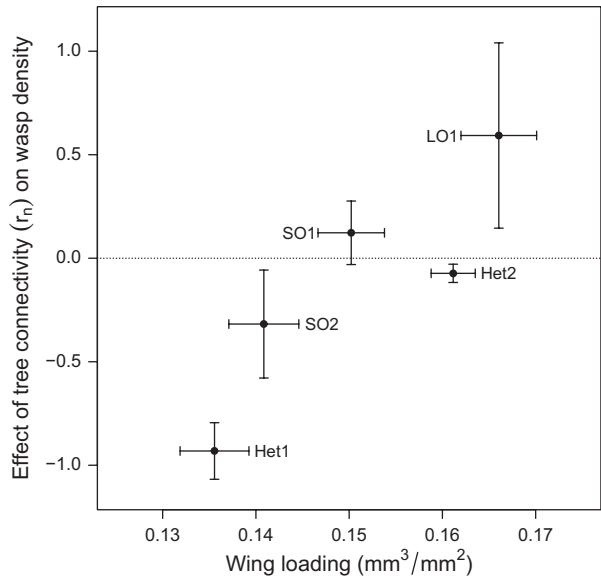


Figure 6. Relationship between the wing loadings of five non-pollinating fig wasps associated with the Sonoran Desert rock fig, and the effect that tree connectivity (r_n = distance to the nearest 20th neighbouring tree) has on the per syconium density of each species. The effect of tree connectivity on non-pollinator species density is estimated by regressing r_n against the mean per syconium density of an individual non-pollinator species on a crop. Positive values on the y-axis indicate that tree connectivity increased the density of a non-pollinator species, and negative values indicate that connectivity decreased density. Error bars show 95% confidence intervals.

production. Overall, these patterns are strongly consistent with plant-pollinator-exploiter theory, which predicts that the aggregation of plants will attract high rates of foundress visitation, increasing the production of pollinator offspring and in turn decreasing seed and overall non-pollinator production (Duthie and Falcy 2013).

We conclude that the distribution of foundresses among trees is likely to be a fundamental predictor of pollinator, non-pollinator, and seed distributions on the landscape of figs and related systems. Where foundress arrival is relatively high, pollinators are expected to be relatively more abundant, and where foundress arrival is low, non-pollinators are likely to be relatively more abundant. Consequently,

pollinators are likely to be spatially aggregated in areas of high tree connectivity, and non-pollinators are more likely to be spatially aggregated in areas of low tree connectivity. The spatial aggregation of pollinators and non-pollinators may have broad implications for the ecology and evolution of fig–fig wasp mutualisms and related systems. When nearby wasps compete directly for access to developing flowers, pollinator and non-pollinator spatial aggregation is expected to result in higher intraspecific competition. Morris et al. (2003) modelled the impact of intraspecific competition on community dynamics and coexistence in seed-eating mutualisms that include a species of exploiter. They found increasing intraspecific competition for both pollinators and non-pollinating exploiters to greatly widen the range of demographic parameters over which stable coexistence occurs, even given the competitive superiority of pollinators. The spatial aggregation of pollinators and exploiters may therefore facilitate coexistence through intraspecific competition in the *F. petiolaris* community. Additionally, regions where fig trees are sparser and visited less frequently by foundresses may be especially influential in maintaining populations of non-pollinators. Our results showing an increase in overall non-pollinator production where fig trees have fewer nearby conspecifics are comparable to those of Wang et al. (2005), who examined the production of pollinating and non-pollinating fig wasps associated with *F. racemosa* in primary forest, fragmented forest and highly fragmented forest in Xishuangbanna, Yunnan, China. They observed the proportion of non-pollinating wasps to be significantly higher in highly fragmented forest habitat than in primary forest habitat. We hypothesise that high non-pollinator abundance in such fragmented populations may be driven by decreased foundress arrival caused by low tree connectivity.

In addition to affecting species population dynamics and coexistence, increased exploitation from non-pollinators in regions where figs trees are sparse may have long-term consequences for the evolutionary stability of the fig–fig wasp mutualism. In mutualism, theory predicts competitive asymmetry between mutualists and exploiters to be critical to evolutionary stability (Ferrière et al. 2002). When mutualists are not competitively superior to exploiters, selection is expected to reduce the amount of goods or services provided by mutualists to their partners, ultimately driving the mutualism to

Table 1. Effects of five independent variables on within-crop (crop is defined as a single bout of reproduction observed on a tree) per syconium densities of five non-pollinating fig wasps associated with *Ficus petiolaris*. For each species, non-pollinator density is estimated as a function of tree connectivity (r_n = distance to the nearest 20th neighbouring tree), mean syconium volume, the latitude of the crop from syconia were sampled, the mean number of pollinating foundresses arriving per syconium on the crop, and the mean number of pollinator offspring produced per syconium on the crop. Data were collected from 859 syconia on 80 *F. petiolaris* crops from 75 trees in Baja, California. Numbers indicate multiple regression coefficients for each covariate and for each species. Significance is indicated at the 0.05 (*), 0.01 (**), and 0.001 (***) levels, and \pm indicates standard errors.

Exploiter species		LO1		Het2		SO1		SO2		Het1	
Description		<i>Idarnes</i>		<i>Heterandrium</i>		<i>Idarnes</i>		<i>Idarnes</i>		<i>Heterandrium</i>	
Genus											
Variable											
Tree connectivity		0.593* \pm 0.228		-0.073** \pm 0.023		0.123 \pm 0.078		-0.318* \pm 0.133		-0.931*** \pm 0.697	
Syconium volume		0.001 \pm 0.001		0.000 \pm 0.000		-0.001* \pm 0.000		-0.001 \pm 0.001		0.000 \pm 0.000	
Crop latitude		1.473* \pm 0.602		-0.003 \pm 0.059		-0.808*** \pm 0.21		-0.326 \pm 0.351		-0.124 \pm 0.184	
Foundress count		-0.744 \pm 2.818		0.171 \pm 0.278		1.201 \pm 0.966		2.403 \pm 1.642		-0.164 \pm 0.861	
Pollinator production		-0.041 \pm 0.033		-0.005 \pm 0.003		-0.025* \pm 0.011		-0.037 \pm 0.019		-0.025* \pm 0.010	

extinction. Thus, even if mutualist communities that include exploiters are ecologically stable, the long-term evolutionary persistence of these communities is not guaranteed (Ferrière et al. 2002, Jones et al. 2009). Jones et al. (2009) examined the role of mutualist and exploiter intraspecific competition in long-term mutualism evolutionary stability. They found increased intraspecific competition of mutualists and exploiters to be highly stabilising, leading to coevolutionary stable equilibria that result in the coexistence of all species. Among competitors, intraspecific competition is expected to be increased when species aggregate spatially near limiting resources. The spatial aggregation of pollinators and non-pollinators observed here and in other fig wasp associations (Wang et al. 2005) therefore predicts increased intraspecific competition, and may contribute to the coevolutionary stability of the fig–fig wasp mutualism, and mutualisms that include exploiters more generally.

Pollinator production had a negative effect on the production of each species of non-pollinator, but this effect was statistically significant for only two of five non-pollinator species considered individually (Table 1). Additionally, tree connectivity was negatively associated with the production of three non-pollinator species, and positively associated with one species. This pattern is consistent with a previous study (Duthie et al. 2015a) that identified a life history tradeoff between species dispersal abilities and egg loads of the five non-pollinators observed here, and which focused on potential competition among non-pollinators. Overall, species with phenotypes associated with low dispersal ability (e.g. high wing loading) have higher egg loads, but are less likely to be found where tree connectivity is low due to dispersal limitations. In contrast, species with high dispersal abilities will have lower egg loads, but will be less restricted by tree connectivity. As such, although tree connectivity might increase the rate at which foundresses arrive at a receptive fig tree, thereby increasing pollinator offspring production and decreasing non-pollinator offspring production as a whole (Fig. 4), the consequences of tree connectivity might differ among individual species of non-pollinators. Highly fecund, less mobile, non-pollinating fig wasps might be competitively superior to other non-pollinators where dispersal distances between natal and receptive fig trees are low (Duthie et al. 2014, 2015a), resulting in a net benefit in these species' growth rates. In contrast, less fecund but highly mobile non-pollinator species might benefit where tree connectivity is low due to limited competition from pollinators and highly fecund non-pollinators. Although more work is needed to determine the nature and strength of competition among pollinators and the non-pollinator species included in this study, it is likely that fig ovules are shared limiting resources at least some of the time, and that competition therefore occurs between pollinators and the five non-pollinator species on which we focused. Further, although species of *Idarnes* and *Heterandrium* on other *Ficus* hosts are observed to be cleptoparasites (attacking already parasitised tissue) of pollinators rather than competitors (Elias et al. 2008, Cruaud et al. 2011), this is unlikely for the five species we observe on *F. petiolaris*. All species of *Idarnes* and *Heterandrium* were observed within syconia in which no foundresses arrived and no pollinator offspring were produced, meaning that

they cannot rely on pollinators to complete their development. Further, all species of *Idarnes* and *Heterandrium* were observed in the absence of each other species within syconia, meaning that species are also unlikely to be cleptoparasites of one another. Nevertheless, further studies will benefit from a more detailed investigation of how ovules are used and species interact within fig syconia (Ghara et al. 2011, 2014), and how wasps differ in their time of arrival to (Elias et al. 2008, Ghara and Borges 2010) and departure from (Greeff and Ferguson 1999) syconia. Seasonality may also be important for predicting species interactions and distributions (Warren et al. 2010, Wang et al. 2015). Overall, however, we conclude that tree connectivity will be an important factor affecting wasp distributions and population dynamics.

Our results may also have broad implications for the ability of plants associated with seed-eating pollinators to adapt to new habitats, especially at the margins of plant ranges. Areas where plants are especially aggregated are likely to be high quality habitat. If high habitat quality leads to both high local plant density and, in turn, disproportionately high pollinator production, then plant populations will be gender dimorphic, with plants in higher habitat quality being functionally more male than plants in lower habitat quality. At the landscape level, aggregated plants in high quality habitats will be net exporters of pollinators, and more sparsely distributed plants in lower quality habitats will be net exporters of seeds. Depending on the degree to which pollen versus seed dispersal contributes to total gene flow, the genetic structure of plants may be dominated by gene flow from high density locals (if pollen contributes more total gene flow) or from more sparsely distributed plants in less high quality habitats (if seeds contribute more total gene flow). For most plants, gene flow via pollen flow is typically over an order of magnitude higher than gene flow via seed flow (Petit et al. 2005). Figs appear to be no exception, with genetic evidence indicating that pollen transfer contributes more strongly to gene flow than seed dispersal among fig populations (Yu et al. 2010, Yu and Nason 2013). In a study of *F. hirta*, the ratio of pollen to seed migration was observed to be 16.2–36.3 (Yu et al. 2010). Given the dominance of gene flow from pollen transfer, the genetic structure of fig populations is likely to be influenced disproportionately by trees in aggregated patches where habitat quality is high. Such disproportionate gene flow from areas of high habitat quality to low habitat quality may erode the influence of natural selection on local adaptation, limiting adaptation to novel environments at the margins of fig ranges (Gaston 2009). In the northernmost parts of the range of *F. petiolaris*, plants often occur in small and fragmented populations (Gates and Nason 2012), where foundress arrival is expected to be low. Consistent with these observations, we found that the arrival of pollinating foundresses decreased with increasing latitude. Because foundress visitation increases pollinator production, plants on the northernmost edge of the range of *F. petiolaris* might contribute relatively little to gene flow. Instead, high gene flow contributed by pollen carried by foundresses originating from lower latitudes of higher habitat quality may swamp local selection in northern regions, thereby limiting adaptation in marginal habitats (Kirkpatrick and Barton 1997, Polechová and Barton 2015).

In conclusion, we find predictions of Duthie and Falcy (2013) to be strongly supported by data collected from *F. petiolaris* and its associated fig wasps. When conspecific fig trees are aggregated, syconia receive higher numbers of foundresses to pollinate and oviposit into flowers. More foundresses result in a relatively high proportion of flowers used for developing pollinators. Where trees are relatively isolated, fewer foundresses arrive to syconia, leading to increased exploitation of the mutualism. Our results show that the connectivity of plants that rely on seed-eating pollinators is central to understanding the distributions of mutualists and exploiters. We conclude that the spatial connectivity of mutualists is likely a key driver of mutualist distributions, and of mutualist susceptibility to exploitation.

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Supplementary material (available online as Appendix oik-02905 at <www.oikosjournal.org/appendix/oik-02905>). Appendix 1–2.