

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/328631232>

Resource dispersion influences dispersal evolution of highly insulated insect communities

Article in *Biology letters* · October 2018

DOI: 10.1098/rsbl.2018.0111

CITATIONS

0

READS

61

3 authors:



Vignesh Venkateswaran
Indian Institute of Science

6 PUBLICATIONS 9 CITATIONS

[SEE PROFILE](#)



Anusha L. K. Kumble
Indian Institute of Science

1 PUBLICATION 0 CITATIONS

[SEE PROFILE](#)



Renee Borges
Indian Institute of Science

133 PUBLICATIONS 1,448 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Physical, chemical and behavioural aspects of mound construction by termites [View project](#)



Dispersal in fig wasp communities (PhD thesis) [View project](#)

Research



Cite this article: Venkateswaran V, Kumble ALK, Borges RM. 2018 Resource dispersion influences dispersal evolution of highly insulated insect communities. *Biol. Lett.* **14**: 20180111.
<http://dx.doi.org/10.1098/rsbl.2018.0111>

Received: 16 February 2018
Accepted: 5 October 2018

Subject Areas:
ecology, evolution

Keywords:
resource dispersion, dispersal, community trait, adaptation, fig wasps

Author for correspondence:
Renee M. Borges
e-mail: renee@iisc.ac.in

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4265126>.

Resource dispersion influences dispersal evolution of highly insulated insect communities

Vignesh Venkateswaran, Anusha L. K. Kumble and Renee M. Borges

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

RMB, 0000-0001-8586-7380

Communities in which species are obligately associated with a single host are ideal to test adaptive responses of community traits to host-imposed selection because such communities are often highly insulated. Fig species provide oviposition resources to co-evolved fig-wasp communities. Dispersing fig-wasp communities move from one host plant to another for oviposition. We compared the spatial dispersion of two fig species and the dispersal capacities of their multitrophic wasp communities. Dispersal capacities were assessed by measuring vital dispersal correlates, namely tethered flight durations, somatic lipid contents and resting metabolic rates. We suggest that dispersal-trait distributions of congeneric wasp species across the communities are an adaptive response to host plant dispersion. Larger dispersal capacities of the entire multitrophic community are related to more widely dispersed resources. Our results provide evidence and a novel perspective for understanding the potential role of adaptation in whole-community dispersal-trait distributions.

1. Introduction

Community membership is often dictated by functional traits that allow species to live, breed and coexist within the ecosystems where communities assemble. The distribution of species functional trait values cannot only be important for predicting community composition and diversity [1,2], but can also be important for comparing across communities to understand the influence of differing environmental filters. Environmental filters (any environmental condition that restricts community membership, e.g. salinity, altitudinal pressure or resource dispersion) can dictate species sorting and eventually trait distribution values. However, within the context of environmental filtering, species are often treated as static entities that assemble into communities based on pre-adaptations [1]. The role of ongoing adaptation to a changing environmental filter in (i) maintenance of community membership and (ii) impacting community trait distributions has only recently been gaining importance [3]. Understanding the role of adaptation in affecting community trait distributions requires the characterization of selection on traits. It also requires an understanding of (i) the evolutionary history of inter-species associations within communities including historical contingencies and (ii) the history of the varying selection pressures imposed on community members [4,5]. In insular and specialized biological communities, community–host associations over evolutionary time can lead to adaptive responses in community members to host divergences. In other words, communities can respond to diverging host-imposed selection pressures [3]. For instance, ancient communities obligately associated and speciating with their host species may adapt to such diverging host-imposed selection [5,6].

Insular communities, such as fig wasp assemblages, are valuable candidates for studying the possible role of adaptation in determining the trajectory of functional community traits. Fig wasp communities are obligately dependent on their host

figs (*Ficus* species). They co-adapt and co-speciate with their hosts [6–8] barring some exceptions [9,10]. The tight specificity between *Ficus* and their wasp communities allows related fig species to host closely related, yet highly circumscribed wasp communities. Figs provide oviposition resources for wasps within urn-shaped inflorescences called syconia (singular: syconium); the community usually consists of one pollinating and several non-pollinating species that occupy varied trophic niches [11]. Fig wasp species oviposit into syconia; their offspring exhibit both heterospecific and conspecific interactions (such as parasitoid–prey interactions and mate choice) as they develop in the syconium [5]. This makes the syconial microcosm a convenient unit of investigation within which fig wasp communities largely exist and function [5].

Only female wasps disperse from their natal syconia to other trees that bear suitable syconia for oviposition. Thus, the spatial dispersion (distribution) of syconia-bearing fig trees is expected to select for dispersal of wasp species [5]. Additionally, after development and mating within the fig, all wasp species leave syconia within a relatively short duration [12]. Wasps cannot recolonize their natal trees as individual trees exhibit within-tree reproductive synchrony and population-level reproductive asynchrony [12,13].

By investigating sympatric fig species and their associated wasp communities, we expected a correspondence between dispersion of host trees and dispersal traits of their wasp communities. We discuss the role of adaptation on functional dispersal traits by comparing and contrasting congeneric species across the two wasp communities.

2. Material and methods

(a) Study system

Ficus hispida is dioecious and individuals survive close to parent plants [14]. The wasp community comprises four species in South India [15]. *Ficus racemosa* is a tall free-standing monoecious tree, with flowering phenology similar to *F. hispida* (electronic supplementary material) and seven associated wasp species in South India [11]. Our choice of these fig species is ideal because (i) they are sympatric and belong to the same subgenus *Sycomorus*; (ii) their wasp communities share genera, e.g. *Ceratosolen*, *Apocrypta*—near ideal congeneric comparisons for our test (electronic supplementary material, table S1).

Owing to differences in fig breeding strategies, not all syconia-bearing trees offer oviposition resources. Syconia of functionally monoecious figs bear seeds and pollen-carrying wasps, while functionally dioecious figs are either male, producing syconia with pollen and pollen-vectoring wasps, or female producing syconia with seeds but no wasps [16]. Non-pollinating fig wasps of monoecious figs oviposit into syconia of all hosts, while those of dioecious figs oviposit only into syconia of male hosts [16,17]. Therefore, only the male plants of dioecious fig species provide oviposition resources to their fig-wasp communities while all individuals of monoecious fig species provide such resources.

Resource availability can also be governed by syconium ontogeny with different wasps ovipositing at different times during syconium development [5]. The syconium ontogeny and timing of arrival of congeneric wasps are similar for the fig species in this study (electronic supplementary material).

(b) Spatial dispersion of host-plant species

Spatial dispersions were compared using GPS coordinates of 18 *F. racemosa*, 17 female and 30 male *F. hispida* trees over approximately

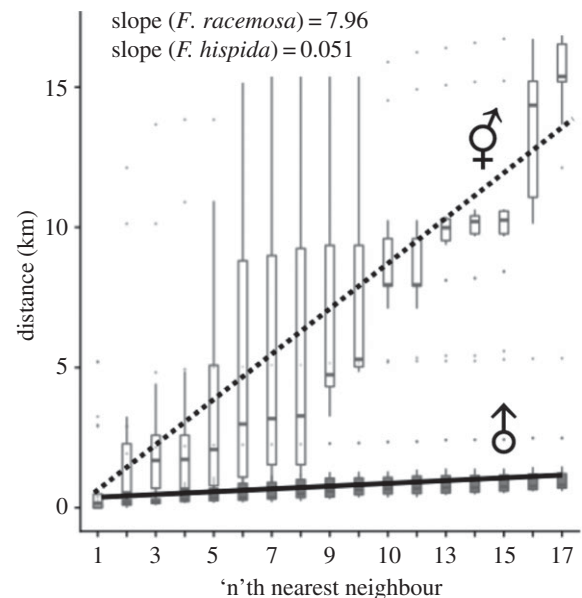


Figure 1. Regression of the average distance between trees with every successive 'n'th nearest neighbour for *F. racemosa* (dotted) and male *F. hispida* plants (solid). The spread at every 'n'th neighbour is indicated in boxplots (*F. racemosa*: white; *F. hispida*: black).

50 km² (2006), in Agumbe Reserve Forest (13°30' N, 75°5' E), Karnataka State, South India (electronic supplementary material, figure S1). The region was sampled with care to avoid any sampling bias (electronic supplementary material). Only naturally established, mature trees were considered. Higher-order nearest-neighbour (HONN) distances were calculated using the *spatstat* package in statistical software R (version 3.2.3). Although the distribution of nearest neighbour distances provides an estimate of spatial dispersion, HONN comparisons, where distances are measured to every succeeding nearest neighbour, provide a more accurate method for comparisons [18]. Since the oviposition window (temporal resource availability) can also confound spatial resource dispersion [5], we accounted for oviposition windows of congeners across the communities and determined that they possessed similar oviposition window lengths (electronic supplementary material).

(c) Wasp dispersal capacities

We measured only dispersal traits of *F. hispida* wasps for this study and used dispersal trait values of *F. racemosa* wasps from a previous study [5] (electronic supplementary material, table S1). We measured three dispersal correlates, *viz.* tethered flight durations, somatic lipid content and mass-corrected resting metabolic rates (sRMRs) [5]. Syconia of *F. hispida* were collected in 2016 near the Indian Institute of Science Campus (12°58' N, 77°35' E), Bangalore. Fig wasps are short-lived (some living only 24 h) [11] and, owing to the requirement of live individuals, *F. hispida* wasps were collected near the laboratory. *Philotrypesis* sp. 2 is absent in Bangalore and dispersal traits were not measured for this species (see electronic supplementary material, for methods and sample sizes).

(d) Statistical analysis

Average distances of trees to their 'n'th neighbour were regressed against 'n' for each fig species. Pairwise comparisons were performed to determine significant differences at every 'n'th neighbour between the two species. Slopes of regression lines on the 'n'th nearest neighbour versus distance plot for each group reveal the extent of dispersion; greater slopes indicate higher dispersion. Kruskal–Wallis tests were used to determine significant differences between the dispersion of the two host plants and dispersal traits between

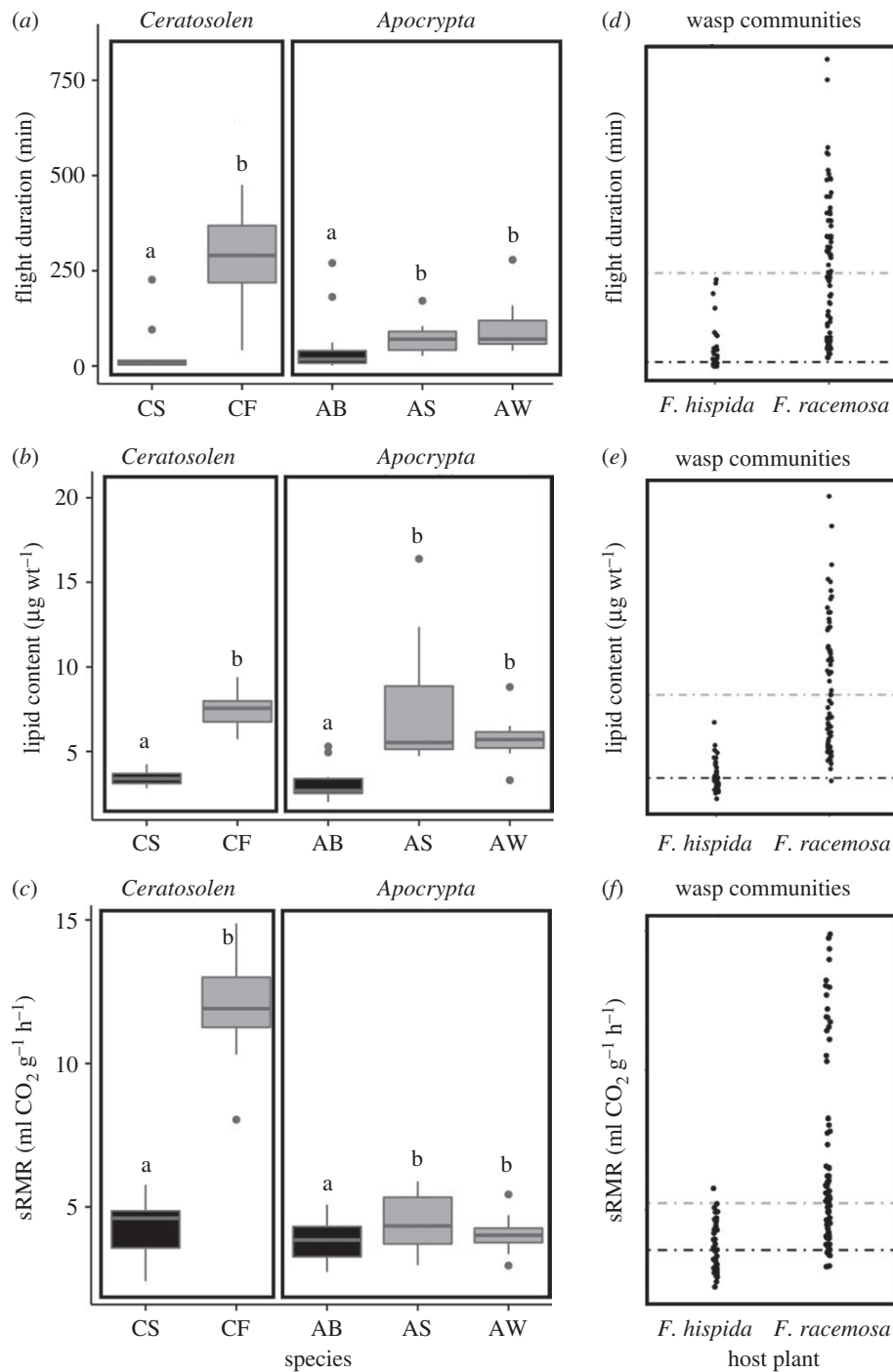


Figure 2. (a) Flight duration, (b) somatic non-polar lipid content and (c) sRMR for the wasp communities. Species abbreviations: CS, *Ceratosolen solmsi*; CF, *Ceratosolen fusciceps*; AB, *Apocrypta bakeri*; AS, *Apocrypta* species 2; AW, *Apocrypta westwoodi*. *Ceratosolen* = pollinating gall; *Apocrypta* = parasitoid. Alphabets and solid circles indicate significant differences by Dunn's test for multiple comparisons and outliers, respectively. (d) Flight durations, (e) lipid content and (f) sRMR comparisons for all wasps pooled in each community; dots indicate individual data points. Dotted horizontal lines indicate median values of dispersal traits. Black and grey indicate membership to *F. hispida* or *F. racemosa* community, respectively.

congeneric wasp species. Pairwise comparisons were conducted using post hoc Dunn's tests and Bonferroni corrections at an adjusted α -level of 0.05 to examine differences between the congeners. Values for each trait were pooled for each community and differences were compared with a Mann–Whitney Wilcoxon test by using both species means and by pooling all values ignoring species identity. Raw data and code are available online [19].

3. Results

Ficus racemosa exhibited greater spatial dispersion than *F. hispida* (males) (figure 1) or *F. hispida* (males and females collectively;

electronic supplementary material, figure S2). With every increasing nearest neighbour for *F. racemosa*, the distance increased by about 0.796 km compared to male *F. hispida* plants in which distance increased only by 0.051 km (indicated by slope values, figure 1; electronic supplementary material, table S2).

The *F. racemosa* wasp community correspondingly exhibited greater dispersal abilities than that of *F. hispida* (figure 2a–c; electronic supplementary material, table S1). Pooled values across species for each dispersal trait indicated that the *F. racemosa* community exhibited higher flight durations ($U = 229$, $p < 0.01$), somatic lipid contents ($U = 91$, $p < 0.01$)

and sRMR values ($U = 638$, $p < 0.01$; figure 2*d–f*) than the *F. hispida* community (comparisons of cross-community species means in electronic supplementary material).

4. Discussion

Previous studies have shown that variation in resource dispersion can impact dispersal of single species [20]. We show a clear correspondence between functional dispersal trait distributions of entire fig-wasp communities and their resource dispersion (environmental filter). More spatially dispersed host plants select for and harbour wasp communities capable of greater dispersal capacities. We speculate that these species traits are likely influenced by adaptation to diverging host-imposed selection as indicated by the dispersal capacities of the congeneric species of the two communities.

Extreme specialization, co-diversification and co-adaptation patterns indicate that adaptation to host-imposed selection in fig-wasp communities likely occurs [7–9]. There is also mounting evidence to suggest that monoecious figs are more dispersed in space and have wasps capable of greater dispersal capacities compared to dioecious figs [15,17,18] (more information in electronic supplementary material). Future investigations should rigorously test whether fig-wasp dispersal abilities correlate with fig breeding strategies.

With increasing fig dispersion, selection could have been stronger on traits that make fig wasp species (and by extension fig-wasp communities) better dispersers. Correspondingly, decreasing fig dispersion could have relaxed selection on dispersal traits. More generally, we propose that adaptation over evolutionary time may require explicit consideration while comparing dispersal-related community-trait distributions.

Ethics. Our experiments comply with regulations for animal care in India.

Data accessibility. Additional information is available in the electronic supplementary material. Raw data and code are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3m4k5g0> [19].

Authors' contributions. V.V. conceived the study; A.L.K. and V.V. performed experiments and collected data; V.V. and R.M.B. analysed and interpreted the data; V.V., A.L.K. and R.M.B. were involved in drafting the manuscript, revising it critically for important intellectual content and approving the final version. V.V., A.L.K. and R.M.B. are accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

Funding. The project used funds from the Department of Science and Technology (DST), DST-FIST, Department of Biotechnology, and Ministry of Environment, Forests and Climate Change, Government of India.

Acknowledgements. We thank Karpagam Chelliah, Krishnapriya Tamma and anonymous reviewers for helpful comments on this manuscript, and G. Yathiraj for fig collection.

References

- Cadotte MW, Arnillas CA, Livingstone SW, Yasui S-LE. 2015 Predicting communities from functional traits. *Trends Ecol. Evol.* **30**, 510–511. (doi:10.1016/j.tree.2015.07.001)
- Garnier E *et al.* 2004 Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**, 2630–2637. (doi:10.1890/03-0799)
- Johnson MTJ, Stinchcombe JR. 2007 An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* **22**, 250–257. (doi:10.1016/j.tree.2007.01.014)
- Jousselin E, Van Noort S, Berry V, Rasplus J-Y, Rønsted N, Erasmus JC, Greff J. 2008 One fig to bind them all: host conservatism in a fig wasp community unraveled by cospeciation analyses among pollinating and nonpollinating fig wasps. *Evolution* **62**, 1777–1797. (doi:10.1111/j.1558-5646.2008.00406.x)
- Venkateswaran V, Shrivastava A, Kumble ALK, Borges RM. 2017 Life-history strategy, resource dispersion and phylogenetic associations shape dispersal of a fig wasp community. *Mov. Ecol.* **5**, 25. (doi:10.1186/s40462-017-0117-x)
- Cruaud A *et al.* 2012 An extreme case of plant–insect codiversification: figs and fig-pollinating wasps. *Syst. Biol.* **61**, 1029–1047. (doi:10.1093/sysbio/sys068)
- Jousselin E, Rasplus J-Y, Kjellberg F. 2003 Convergence and coevolution in a mutualism: evidence from a molecular phylogeny of *Ficus*. *Evolution* **57**, 1255–1269. (doi:10.1111/j.0014-3820.2003.tb00334.x)
- Machado CA, Jousselin E, Kjellberg F, Compton SG, Herre EA. 2001 Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. *Proc. R. Soc. Lond. B* **268**, 685–694. (doi:10.1098/rspb.2000.1418)
- Machado CA, Robbins N, Gilbert MTP, Herre EA. 2005 Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *Proc. Natl Acad. Sci. USA* **102**, 6558–6565. (doi:10.1073/pnas.0501840102)
- Cook JM, Segar ST. 2010 Speciation in fig wasps. *Ecol. Entomol.* **35**, 54–66. (doi:10.1111/j.1365-2311.2009.01148.x)
- Ghara M, Borges RM. 2010 Comparative life-history traits in a fig wasp community: implications for community structure. *Ecol. Entomol.* **35**, 139–148. (doi:10.1111/j.1365-2311.2010.01176.x)
- Bronstein JL, Gouyon P-H, Gliddon C, Kjellberg F, Michaloud G. 1990 The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* **71**, 2145–2156. (doi:10.2307/1938628)
- Gates DJ, Nason JD. 2012 Flowering asynchrony and mating system effects on reproductive assurance and mutualism persistence in fragmented fig–fig wasp populations. *Am. J. Bot.* **99**, 757–768. (doi:10.3732/ajb.1100472)
- Dev SA, Kjellberg F, Hossaert-Mckey M, Borges RM. 2011 Fine-scale population genetic structure of two dioecious Indian keystone species, *Ficus hispida* and *Ficus exasperata* (Moraceae). *Biotropica* **43**, 309–316. (doi:10.1111/j.1744-7429.2010.00704.x)
- Proffitt M, Schatz B, Borges RM, Hossaert-Mckey M. 2007 Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. *J. Anim. Ecol.* **76**, 296–303. (doi:10.1111/j.1365-2656.2007.01213.x)
- Harrison RD, Yamamura N. 2003 A few more hypotheses for the evolution of dioecy in figs (*Ficus*, Moraceae). *Oikos* **100**, 628–635. (doi:10.1034/j.1600-0706.2003.11829.x)
- Wang Q, Jiang Z-F, Wang N, Niu L, Li Z, Huang D-W. 2013 Host sex-specific parasites in a functionally dioecious fig: a preference way of adaptation to their hosts. *Ecol. Evol.* **3**, 2976–2984. (doi:10.1002/ece3.682)
- Grossbart SL, Mittelstaedt RA, Murdock GW. 1978 Nearest neighbor analysis: inferring behavioral processes from spatial patterns. *Assoc. Consum. Res. North Am. Adv.* **5**, 114–115.
- Venkateswaran V, Kumble ALK, Borges RM. 2018 Data from: Resource dispersion influences dispersal evolution of highly insulated insect communities. Dryad Digital Repository. (<http://dx.doi.org/10.5061/dryad.3m4k5g0>)
- Fountain T, Nieminen M, Sirén J, Wong SC, Lehtonen R, Hanski I. 2016 Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. *Proc. Natl Acad. Sci. USA* **113**, 2678–2683. (doi:10.1073/pnas.1600951113)