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# Trade-Offs and Coexistence in Fluctuating Environments: Evidence for a Key Dispersal-Fecundity Trade-Off in Five Nonpollinating Fig Wasps

A. Bradley Duthie  
*Iowa State University*

Karen C. Abbott  
*Case Western Reserve University*

John D. Nason  
*Iowa State University, jnason@iastate.edu*

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## **Abstract**

The ecological principle of competitive exclusion states that species competing for identical resources cannot coexist, but this principle is paradoxical because ecologically similar competitors are regularly observed. Coexistence is possible under some conditions if a fluctuating environment changes the competitive dominance of species. This change in competitive dominance implies the existence of trade-offs underlying species' competitive abilities in different environments. Theory shows that fluctuating distance between resource patches can facilitate coexistence in ephemeral patch competitors, given a functional trade-off between species dispersal ability and fecundity. We find evidence supporting this trade-off in a guild of five ecologically similar nonpollinating fig wasps and subsequently predict local among-patch species densities. We also introduce a novel colonization index to estimate relative dispersal ability among ephemeral patch competitors. We suggest that a dispersal ability-fecundity trade-off and spatiotemporally fluctuating resource availability commonly co-occur to drive population dynamics and facilitate coexistence in ephemeral patch communities.

## **Keywords**

coexistence, ephemeral patch, competition, trade-offs, *Ficus*, dispersal, fig wasp

## **Disciplines**

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Author(s): A. Bradley Duthie, Karen C. Abbott, John D. Nason

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NOTE

# Trade-Offs and Coexistence in Fluctuating Environments: Evidence for a Key Dispersal-Fecundity Trade-Off in Five Nonpollinating Fig Wasps

A. Bradley Duthie,<sup>1,\*</sup> Karen C. Abbott,<sup>2</sup> and John D. Nason<sup>1</sup>

1. Iowa State University, Ames, Iowa 50011; 2. Case Western Reserve University, Cleveland, Ohio 44106

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**ABSTRACT:** The ecological principle of competitive exclusion states that species competing for identical resources cannot coexist, but this principle is paradoxical because ecologically similar competitors are regularly observed. Coexistence is possible under some conditions if a fluctuating environment changes the competitive dominance of species. This change in competitive dominance implies the existence of trade-offs underlying species' competitive abilities in different environments. Theory shows that fluctuating distance between resource patches can facilitate coexistence in ephemeral patch competitors, given a functional trade-off between species dispersal ability and fecundity. We find evidence supporting this trade-off in a guild of five ecologically similar nonpollinating fig wasps and subsequently predict local among-patch species densities. We also introduce a novel colonization index to estimate relative dispersal ability among ephemeral patch competitors. We suggest that a dispersal ability–fecundity trade-off and spatiotemporally fluctuating resource availability commonly co-occur to drive population dynamics and facilitate coexistence in ephemeral patch communities.

**Keywords:** coexistence, ephemeral patch, competition, trade-offs, *Ficus*, dispersal, fig wasp.

## Introduction

The coexistence of myriad species of competitors with ecologically similar niches has been a longtime focus of community ecology. Hutchinson (1961) observed multiple ecologically similar species in a community as paradoxical, given the principle of competitive exclusion, which states that species competing for identical resources cannot coexist (Hardin 1960).

Hutchinson (1961) proposed that fluctuating environmental conditions could lead to the coexistence of similar competitors, reasoning that competitive exclusion could be

avoided if a fluctuating environment altered the competitive superiority of species rapidly enough for all species to avoid extinction. Subsequent theoretical work has shown Hutchinson's proposal to be supported (e.g., Chesson and Warner 1981; Chesson 1982) but depends on competitor life histories and a covariance between environment and competition (Chesson 1990; Chesson and Huntly 1997). Coexistence in a fluctuating environment is facilitated by trade-offs in the ability of species to thrive under different environmental conditions. Without trade-offs, one species could conceivably maintain competitive dominance in all environments, increasing the likelihood of competitive exclusion. Nevertheless, few studies have identified the functional trade-offs that lead to these species-specific responses (but see, e.g., Angert et al. 2009; Holt and Chesson 2014).

Such trade-offs may facilitate coexistence in ephemeral patch communities, which are characterized by competition over patchy resources with rapid turnover (e.g., dung, fruit, carrion, vernal pools). Patch colonization is usually required for reproduction in each generation (Hanski 1987), so spatiotemporal fluctuations in patch distribution may be fundamental to determining competitor success (Chesson 2000; Duthie et al. 2014). Competition for ephemeral patches is often preemptive (Hanski and Kuusela 1977; Kneidel 1983; Shorrocks and Bingley 1994; Dayton and Fitzgerald 2005), giving an advantage to highly mobile competitors when and where colonization is difficult (Yu and Wilson 2001; Duthie et al. 2014). Given trivial colonization difficulty, competition may instead favor high reproductive output within patches. Thus, where constant patch availability might lead to competitive exclusion, spatial (Chesson 2000) or temporal (Duthie et al. 2014) fluctuations in patch availability might instead lead to coexistence, given a trade-off between patch dispersal ability and fecundity.

Trade-offs between dispersal ability and fecundity are well studied theoretically (e.g., Higgins and Cain 2002; Amarasekare 2003; Amarasekare et al. 2004) and established em-

\* Corresponding author; e-mail: [aduthie@abdn.ac.uk](mailto:aduthie@abdn.ac.uk).

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pirically (e.g., Zera and Denno 1997; Hughes et al. 2003; Jervis et al. 2005; Guerra 2011). But for ephemeral patch systems, theory typically includes little mechanistic detail, focusing more generally on whether intraspecific aggregation can stabilize multispecies assemblages (Atkinson and Shorrocks 1981; Sevenster 1996; Heard and Remer 1997; Hartley and Shorrocks 2002; but see Hanski and Kuusela 1977). Hartley and Shorrocks (2002) call for models that incorporate individual-level experiences to predict species dynamics and distributions, in addition to coexistence. Previously (Duthie et al. 2014), we showed how a dispersal ability and fecundity trade-off could facilitate coexistence in ephemeral patch communities, given a fluctuating dispersal distance to receptive patches. Distant patches favored competitor investment in patch colonization (dispersal in our model), and nearby patches favored fecund competitors able to maximize within-patch reproduction. Thus, for ephemeral patch competitors, our model predicts a dispersal-fecundity trade-off, with more accessible patches being dominated by species that invest less in dispersal and more in fecundity.

Here we test whether fecundity and dispersal ability negatively covary among five ephemeral patch species. We then use species trait values to predict species abundances within patches sampled at different densities; more fecund species are predicted where patches are dense, and better dispersers are predicted where patches are isolated. Our results provide empirical support for our previous theoretical work (Duthie et al. 2014) and point to an explicit mechanism underlying the species-specific environmental responses required for coexistence in ephemeral patch communities. We additionally propose a new colonization index for estimating species' abilities to colonize resource patches, which may be useful in situations where direct measurement of dispersal ability poses logistical problems.

## Methods

### *Natural History and High Diversity of Nonpollinating Fig Wasps*

The interaction between figs (*Ficus*, Moraceae) and their pollinating wasps (multiple genera, Agaonidae) is a classic example of an obligate mutualism. Figs rely on typically host species-specific fig wasps for pollination of flowers enclosed in urn-shaped inflorescences (hereafter syconia; Janzen 1979). Pollinating wasps oviposit within fig syconia, with larvae completing development within individual fig ovules. Typical of most mutualisms (Bronstein 2001), figs and their pollinating wasps are exploited by species that use resources at a cost to one or both mutualists. These exploiters include multiple nonpollinating wasp species whose larvae feed on a single fig ovule during development. Like pollinators, non-

pollinator species are usually host fig specific (Weiblen 2002), but one species of fig can host myriad nonpollinating species of wasps (Compton and Hawkins 1992).

Wasps cannot maintain standing populations on individual fig crowns. Within-crown syconia development is never continuous; reproductive bouts are often separated by many months to a few years (Bronstein 1989; Windsor et al. 1989). Instead, wasps must seek new figs with ovules receptive for oviposition (Cook and Power 1996; Gates and Nason 2012). Because most fig species occur at low population densities with highly asynchronous among-tree reproductive activity (Janzen 1979; Nason et al. 1998), wasps must routinely disperse up to tens of kilometers to reach trees bearing receptive syconia (Nason et al. 1996, 1998; Ahmed et al. 2009).

Reproductive success for ovule-feeding nonpollinators is therefore affected by two life-history stages. First, wasps must colonize a receptive fig crown. Second, following successful colonization, wasps must oviposit into ovules. Resource use is thus described by a lottery system, where species population growth is determined by the number of ovules claimed. Interspecific competition occurs if species overlap in their use of ovule resources, the accessibility of which is limited by other species at least some of the time (Sale 1974). Because ephemeral patch communities are defined by spatiotemporally fluctuating resource availability, the strength of competition is also expected to vary geographically and over time (Thompson and Cunningham 2002; Thompson 2005). While the strength of competition among nonpollinating fig wasps has not been estimated, interspecific competition among nonpollinators should be comparable to that of pollinators where ovule resources are limiting and overlapping (e.g., Ghara et al. 2014). Observations from wild populations find that nonpollinators regularly compete with pollinators for access to overlapping ovule resources (e.g., West and Herre 1994; Kerdelhué and Rasplus 1996; West et al. 1996; Kerdelhué et al. 2000; Ghara and Borges 2010), and experimental manipulations suggest that observational studies likely underestimate competition (Raja et al. 2014).

### *Data Collection for Sonoran Desert Test Case*

The nonpollinating fig wasp community surrounding the Sonoran Desert rock fig *Ficus petiolaris* (subgenus *Urostigma*) is ideal for testing the predicted trade-off between fecundity and dispersal ability. *Ficus petiolaris* is sparsely distributed throughout its range in the Sonoran Desert of Baja California and adjacent mainland Mexico; we limit our observations to Baja California, where *F. petiolaris* is the only endemic species of fig. *Ficus petiolaris* is pollinated by a single unnamed species of *Pegoscapus* wasp and hosts a diverse and host-specific nonpollinating fig wasp commu-

nity (figs. A1, A2 in appendix, available online). Five of these nonpollinators oviposit from the outside of syconia and produce larvae that each feed on a single ovule. They include three unnamed species of *Idarnes* (Sycophaginae) and two unnamed species of *Heterandrium* (Pteromalidae) and form the basis of our study. Species are distinguishable by morphology and mitochondrial DNA sequence and are regularly found within the same fig syconia using the same ovule resources for larval development. None of these species are parasitized by other nonpollinators, thus minimizing the potential confounding impact of indirect species interactions (e.g., Holt 1984; Abrams and Matsuda 1996). The nonpollinator community also includes *Aepocerus* (Pteromalidae)—which appears to gall the outer tissue of fig syconia—and its specialist parasitoid *Physothorax* (Torymidae), neither of which was included in our analyses.

In summer 2010, we sampled wasps from *F. petiolaris* trees in five sites located from far southern (latitude 23.736) to north-central (latitude 29.265) Baja California. Sampling was restricted to 17 trees in which wasps were mature but had not exited syconia. Sampled trees were surrounded by varying densities of previously mapped (Gates and Nason 2012) trees that were either in different reproductive phases or between reproductive bouts. Following the methods of Bronstein and Hoffmann (1987), we estimated that sampled trees produced 130–10,696 ( $\hat{\mu} = 2,906$ ) syconia (syconia collected per tree: minimum = 4,  $\mu = 25.7$ , maximum = 48; 451 total syconia sampled). After collection, syconia were partially cut open and placed in individual vials overnight (minimum 12 h) to allow wasps to emerge. Emerged wasps were preserved in 95% ethanol and shipped to Iowa State University, where species abundances were recorded. We observed positive counts for all species in syconia absent of pollinators, suggesting that all species can complete larval development in unpollinated syconia.

#### Estimating Egg Load as a Proxy for Fecundity

Travel between natal and receptive trees likely results in high dispersal mortality (Compton et al. 1994; McPherson 2005), but upon successful colonization, search time for suit-

able oviposition sites will be low among densely distributed syconia. Therefore, wasp fecundity is likely to be frequently limited by egg load following colonization (Minkenberg et al. 1992; Heimpel and Rosenheim 1998; Rosenheim et al. 2008). Lifetime egg load can be estimated by counting mature and immature oocytes at emergence (Jervis et al. 2005), as has been used to compare potential fecundity broadly across holometabolous insects (Jervis et al. 2007) and specifically among nonpollinating fig wasps (Ghara and Borges 2010). We therefore use egg load as a proxy for fecundity, following the procedure of Ghara and Borges (2010), dissecting 10–15 wasps of each species in a phosphate buffer saline solution and under a stereomicroscope. An acetocarmine stain was used to help count mature and immature oocytes under a compound microscope. Four species of nonpollinators were observed to be proovigenic, having all eggs mature at eclosion (table 1). One species of *Heterandrium* was observed to be synovigenic, having some immature eggs at eclosion. We define egg load as the number of eggs that are mature and therefore available to oviposit upon wasp eclosion.

#### Estimating Dispersal Ability

Given the small body size of fig wasps, direct observation of dispersal was not feasible. Therefore, we used two indirect methods to estimate the dispersal ability of each species. First, we estimated species wing loadings. Second, we inferred tree colonization ability, using the distributions of species abundances.

Wing loading is a metric that captures the lift associated with wing size and the burden associated with body size to infer an insect's flying ability (Betts and Wootton 1988). Normally, wing loading is calculated as the ratio of body mass to wing area; high values suggest poor flying ability. Fig wasp mass is difficult to estimate with precision, so we used body volume instead (for details, see appendix; Yao 2011; Yao and Katagiri 2011).

Flying ability may be only one of multiple traits that affect successful colonization of receptive patches. Patch colonization success will directly affect resource exploitation

**Table 1:** Gallling fig wasps associated with *Ficus petiolaris* in Baja California, Mexico (all species unnamed)

Label	Genus	Egg load mean $\pm$ SD	Ovigeny index	Total wing area (mm <sup>2</sup> )	Wing length (mm)	Volume (mm <sup>3</sup> )	Ovipositor length (mm)
LO1	<i>Idarnes</i>	75.8 $\pm$ 2.3	1.0	2.085 $\pm$ .069	1.75 $\pm$ .04	.351 $\pm$ .029	5.52 $\pm$ .09
SO1	<i>Idarnes</i>	50.2 $\pm$ 2.7	1.0	1.575 $\pm$ .050	1.48 $\pm$ .03	.239 $\pm$ .015	3.03 $\pm$ .06
SO2	<i>Idarnes</i>	47.1 $\pm$ 7.0	1.0	1.640 $\pm$ .061	1.51 $\pm$ .03	.234 $\pm$ .018	2.84 $\pm$ .04
Het1	<i>Heterandrium</i>	33.7 $\pm$ 2.1	.56 $\pm$ .04	2.862 $\pm$ .131	1.95 $\pm$ .04	.388 $\pm$ .029	.34 $\pm$ .01
Het2	<i>Heterandrium</i>	53.8 $\pm$ 1.5	1.0	2.191 $\pm$ .131	1.69 $\pm$ .03	.355 $\pm$ .020	.65 $\pm$ .01

Note: Values  $\pm$  SEs, unless otherwise indicated. Egg load means and SDs are shown for each species. Ovigeny index is calculated by dividing the number of mature wasp eggs by the total number of eggs upon wasp eclosion; SE is reported where it is nonzero. Total wing area includes two forewings and two hindwings for each species. Wing length describes forewing only. Volume measures total body volume. Ovipositor length measures the external sheath of each species.

and hence has a key effect on population dynamics and competition if resources are limiting. We therefore developed and calculated a new metric that we call the colonization index (defined below), which encompasses traits relevant to colonization success that are unknown or difficult to measure. We propose this index to estimate relative species colonization ability in ephemeral patch communities, especially where dispersal cannot be directly observed.

To calculate the colonization index, we first infer how difficult each fig tree was to colonize when receptive and then determine how successful each wasp species was at colonizing each tree. We used the mean density of emerging wasps (including all pollinators and nonpollinators) within the syconia of the 17 fig trees to estimate how difficult each tree was to colonize, with low densities indicative of trees that were difficult to colonize. Colonization should be relatively easy for wasps emerging from nearby trees, but unmeasured or unknown environmental variables—such as prevailing winds—may also contribute to the ease of colonization. A similar technique is well known and widely used in estimating spatial heterogeneity in parasitism risk (Pacala and Hassell 1991) and is acknowledged to be advantageous in encompassing risk factors that are difficult to measure or unknown (Hassell 2000).

A species' colonization index corresponds to how constant its relative abundance is across patches with different colonization difficulties. The abundance of good dispersers will not decrease dramatically in difficult-to-colonize patches, but the abundance of poor dispersers will drop relatively quickly. We regressed each wasp species' mean per syconium density on a tree against the ease of tree colonization (total density of all species per syconium volume). More positive slope values indicate that a species' density is especially sensitive to ease of crop colonization and thus that the species is a poor disperser. We therefore used the negative slope from this regression as our colonization index (i.e., we multiplied the slope by  $-1$ ), so that higher index values reflect higher species' colonization abilities. Because males of the three *Idarnes* species cannot currently be distinguished on the basis of morphology, only female wasps were used in constructing each species' colonization index. Neither the inclusion of males from known species nor the assignment of all *Idarnes* males entirely to any single *Idarnes* species qualitatively affected our results.

#### *Wasp Distributions on Ephemeral Patches*

If a dispersal-fecundity trade-off underlies population dynamics, then these traits should predict the spatial distributions of species. The abundance of species with high egg loads should be disproportionately high where patches (trees) are dense, and the abundance of better dispersing species should be high where patches are sparse. To test

this prediction, we estimate the number of reproductive-sized conspecific trees within a 1-km radius for all syconia sampled ( $\mu = 41$ ;  $SD = 29.5$ ; range, 0–85; scale did not qualitatively affect our results between 0.5 and 2.0 km; broader scales were not used because of mapping limitations). We then regress wasp species densities from syconia (number per volume syconia) against conspecific neighboring tree density. Relatively high slopes indicate that local species abundance increases with patch density, relative to other species. Lower slopes indicate relatively low local species abundance, given high patch density. We tested to see whether slopes estimating the effect of neighboring trees on species density were correlated with wing loading and egg load.

Additionally, species with similar traits should be correlated in their densities among patches. We therefore test whether the absolute differences in mean species' egg loads and mean species' wing loadings covary with species among tree density correlations (e.g., there are  ${}^5C_2 = 10$  possible species pairs, so data points include 10 absolute differences in species egg load vs. 10 correlations between species abundances among trees). All analyses were conducted using R (R Development Core Team 2011). All data collected and used in analyses are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4dj10> (Duthie et al. 2015).

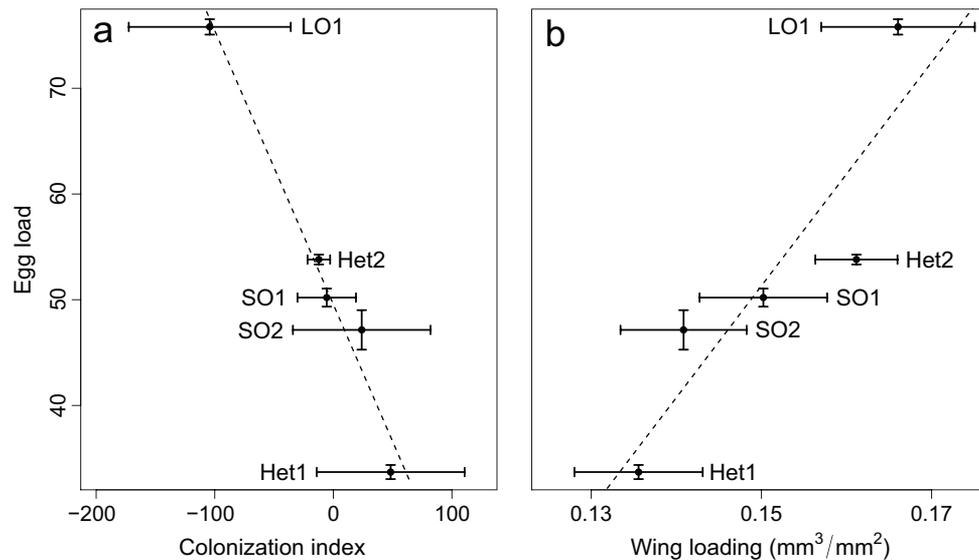
#### Results

Species egg load was strongly correlated with both metrics of dispersal ability. Egg load was negatively correlated with our colonization index ( $P = .0022$ ,  $R^2 = 0.9702$ ; fig. 1a) and positively correlated with wing loading ( $P = .0387$ ,  $R^2 = 0.8058$ ; fig. 1b). Colonization index and wing loading were negatively correlated ( $P = .0404$ ) among species.

Species distributions reflected local tree density. The effect that the number of neighboring trees had on wasp species density from a sampled tree was positively correlated with both wing loading ( $P = .0379$ ,  $R^2 = 0.8085$ ; fig. 2a) and egg load ( $P = .0371$ ,  $R^2 = 0.8111$ ; fig. 2b). Additionally, among tree correlations between wasp species densities negatively covaried with species' differences in wing loading ( $P = .0462$ ,  $R^2 = 0.4097$ ; i.e., pairs of species that were more different in wing loading were less correlated in their among tree abundances) but not egg load ( $P > .1$ ,  $R^2 = 0.0985$ ; figs. A1, A2).

#### Discussion

Communities characterized by individuals developing within—then dispersing between—patchy and ephemeral resources are ubiquitous and species rich (Beaver 1977; Hanski 1987). They include species that develop within carrion (Beaver 1977), dung (Hanski 1990), fruit (Atkinson



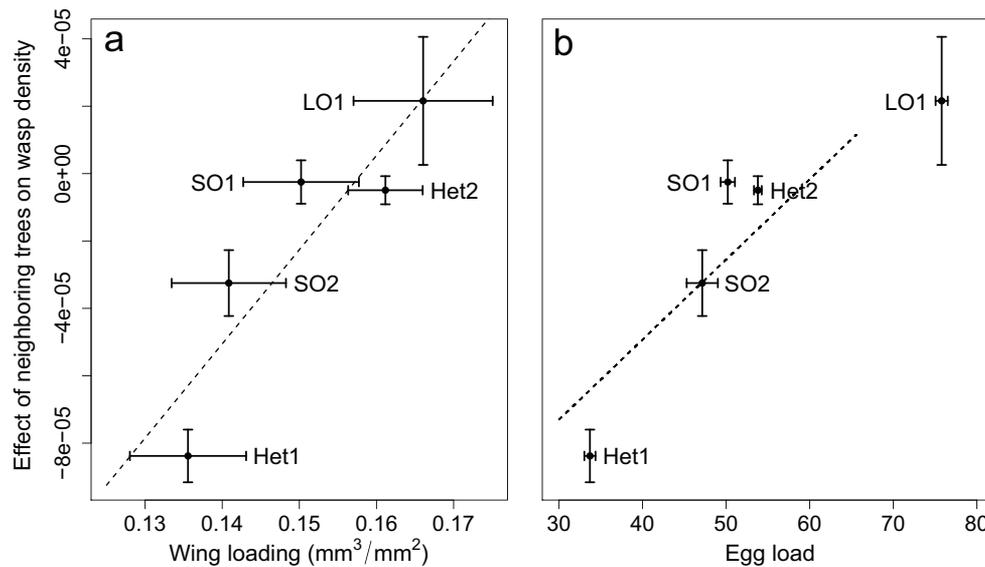
**Figure 1:** Correlation between wasp immediate fecundity and colonization index (a) and wasp immediate fecundity and wing loading (b) in the nonpollinating galler community associated with *Ficus petiolaris*. Immediate fecundity is defined as the mature egg load upon wasp eclosion. Galling wasps include one long ovipositor species of *Idarnes* (LO1), two short ovipositor species of *Idarnes* (SO1 and SO2), and two species of *Heterandrium* (Het1 and Het2). Error bars show standard errors.

1985; Duyck et al. 2004), fungi (Jaenike and James 1991; Wertheim et al. 2000), flowers (Weiblen 2002; Pellmyr 2003), and temporary wetlands (Hanski and Ranta 1983; Collinge and Ray 2009). They also include the many parasites and parasitoids that develop within ephemerally available hosts (Hanski 1987; Grenfell and Keeling 2008). The environment experienced by individuals in these communities routinely fluctuates because resource accessibility is dynamic in space and time. Such environmental fluctuations can facilitate competitor coexistence if functional trade-offs cause species to vary in their competitive superiority (e.g., Yu and Wilson 2001; Angert et al. 2009; Holt and Chesson 2014).

We previously showed how fluctuating patch accessibility leads to coexistence among ephemeral patch competitors, given a trade-off between fecundity and dispersal ability (Duthie et al. 2014). The negative correlation between egg load and our colonization index and the positive correlation between egg load and wing loading strongly support a dispersal-fecundity trade-off in nonpollinators associated with *Ficus petiolaris*. Qualitative observations also support this trade-off; the only synovigenic species we observed also had the highest colonization index and lowest wing loading. Synovigenic species are typically longer lived than proovigenic species (Jervis et al. 2001, 2007) and therefore likely better patch colonizers. Additionally, egg load and wing loading predict local species densities. Species with higher egg loads and wing loadings are relatively more abundant where local patch density is high, and species with lower egg loads and

wing loadings are more common where patches are isolated. Species with dissimilar wing loadings were also less positively correlated in their within-patch abundances. Overall, we present strong evidence supporting a dispersal-fecundity trade-off among five species that share a patchy ephemeral resource. We suggest that fluctuating patch accessibility regularly drives population dynamics in ephemeral patch communities and likely facilitates species coexistence.

The observed trade-off between egg load and dispersal ability—and its ability to predict local species distributions—shows how these traits can be fundamental to understanding population dynamics in ephemeral patch communities. Where competition occurs, this trade-off will also facilitate species coexistence (Duthie et al. 2014). Given the high diversity and resource overlap of nonpollinators associated with *F. petiolaris*, species interactions are likely to be competitive. Nevertheless, despite high species richness (Compton and Hawkins 1992), Hawkins and Compton (1992) suggest that nonpollinating fig wasp communities may be unsaturated and interspecific competition often weak because of a lack of resource limitation. It is therefore important to note that it is possible for the trade-off we observe to arise in the absence of competition. For example, a wasp's investment in egg load versus dispersal ability might simply maximize expected reproductive success along a trade-off line rather than at specific trait values (e.g., fig. 1 of Duthie et al. 2014), potentially leading to unique trait values along this common trade-off line even if no competition occurs. The importance of competition will be deter-



**Figure 2:** Correlation between wasp species wing loading and the effect that neighboring trees have on wasp density on a fig crown (a) and between wasp species egg loads and the effect of neighbors on density on a crown (b) in the nonpollinating galler community associated with *Ficus petiolaris*. All species develop within enclosed inflorescences (syconia) of *F. petiolaris* trees. The effect of neighboring trees on wasp density (Y-axis) is estimated by regressing the number of reproductive-sized conspecific trees within a 1-km radius against the density of wasps collected on a tree. Higher slope values indicate that species production increases when conspecific trees are nearby. Error bars show standard errors.

mined by the extent to which ephemeral patch resources are overlapping and limiting (Sale 1974; Cook and Power 1996).

To more quantitatively predict how fluctuating resource availability drives population dynamics and competitive exclusion or coexistence in ephemeral patch communities, additional theory and empirical studies are needed. Theory demonstrates that spatial (Chesson 2000) and temporal (Duthie et al. 2014) resource fluctuations can lead to coexistence on a local scale, but no tactical models exist to predict their effect on the dynamics of specific ephemeral patch systems. Ideally, such models could be applied to communities amenable to experimental manipulation or long-term observation, as has been done for competition-colonization dynamics at a regional scale (e.g., Yu et al. 2001; Livingston et al. 2012).

At local scales, population dynamics will be affected by species' abilities to colonize and then use patch resources. We introduce a novel metric to assess the relative abilities of species to colonize patches. Instead of estimating traits directly affecting dispersal, this colonization index quantifies relatively how much colonization ability contributes to species growth (i.e., it encompasses species dynamics as affected by patch colonization and excludes effects of within-patches interactions). This index is relative, so it cannot be compared across communities, but it produces results consistent with an estimate based on species physiology. The colonization index may be useful in encompassing

unknown mechanisms affecting patch colonization, especially where colonization is difficult to observe because sampling is restricted to individuals that have yet to disperse from their natal patches (e.g., Kneidel 1983; Shorrocks and Bingley 1994; Woodcock et al. 2002; Inouye 2005).

Our results are novel in revealing a dispersal-fecundity trade-off that rigidly defines an entire guild of species sharing an ephemeral patch resource and predicts local species distributions. This trade-off likely facilitates coexistence when resources are limiting. We suggest that the fluctuating availability of ephemeral patch resources is likely a critical driver of population dynamics in many related ephemeral patch communities. Because such communities are common and unusually species rich, further development toward a comprehensive mechanistic and predictive theory of ephemeral patch dynamics will have broad applicability for evolution and ecology.

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