

Trade-Offs and Coexistence: A Lottery Model Applied to Fig Wasp Communities

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ABSTRACT: Ecological communities in which organisms complete their life cycles on discrete ephemeral patches are common and often support an unusually large number of species. Explaining this diversity is challenging for communities of ecologically similar species undergoing preemptive competition, where classic coexistence mechanisms may not readily apply. We use nonpollinating fig wasps as a model community characterized by high diversity and preemptive competition to show how subadditive population growth and a trade-off between competitor fecundity and dispersal ability can lead to coexistence. Because nonpollinator species are often closely related, have similar life histories, and compete for the same discrete resources, understanding their coexistence is challenging given competitive exclusion is expected. Empirical observations suggest that nonpollinating fig wasp species may face a trade-off between egg loads and dispersal abilities. We model a lottery in which a species' competitive ability is determined by a trade-off between fecundity and dispersal ability. Variation in interpatch distance between figs generates temporal variability in the relative benefit of fecundity versus dispersal. We show that the temporal storage effect leads to coexistence for a range of biologically realistic parameter values. We further use individual-based modeling to show that when species' traits evolve, coexistence is less likely but trait divergence can result. We discuss the implications of this coexistence mechanism for ephemeral patch systems wherein competition is strongly preemptive.

Keywords: storage effect, coexistence, competition, fig wasp, trade-offs.

Introduction

Many organisms complete their life cycles on discrete ephemeral patches of resources. Well-studied examples of such organisms include insects whose larvae consume organic matter in dung or carrion (Beaver 1977; Hanski 1990), in decaying leaves (Heed 1968), or in the living tissues of fungi (Jaenike and James 1991; Wertheim et al. 2000), fruit (Atkinson 1985; Duyck et al. 2004), or flowers (Weiblen 2002; Pellmyr 2003). Additional examples in-

clude insects (Boix et al. 2001; Colburn et al. 2008), crustaceans (Hanski and Ranta 1983; King et al. 1996; Ripley and Simovich 2008), and plants (Collinge and Ray 2009) that rely on ephemerally available vernal pools and parasites that rely on ephemerally available hosts (Hanski 1987; Grenfell and Keeling 2008). The ephemeral patches that these organisms use often support a large number of species (Atkinson and Shorrocks 1981; Hanski 1987; Hartley and Shorrocks 2002), and many theoretical and empirical studies have focused on understanding the mechanisms by which competitors using these resources are able to coexist (Shorrocks et al. 1979; Atkinson and Shorrocks 1981; Chesson 2000a; Woodcock et al. 2002). If resources are heterogeneous, coexistence may occur through resource partitioning, with competitors specializing on different resources within or among patches. But if competitors are limited by identical resources in homogeneous patches, such resource partitioning cannot occur.

For competitors using homogeneous patches, many studies of coexistence in ephemeral patch communities focus on the mechanism of conspecific aggregation (Chesson 2000a). Aggregation intensifies intraspecific competition relative to interspecific competition, potentially leading to competitive coexistence (Atkinson and Shorrocks 1981; Ives 1988; Sevenster 1996; Hartley and Shorrocks 2002). However, plausible aggregating behaviors (Ives 1991; Woodcock et al. 2002) are unlikely to occur when patches are sparsely distributed, as is often the case (Hanski 1990), and when patch competitors cannot afford to be choosy.

In the absence of aggregation among patches, competitors may coexist at the regional scale if competitively superior species are unable to effectively colonize all available patches, and poorer competitors are able to colonize patches that superior competitors cannot (Tilman 1994; Levine and Rees 2002). In the classical competition-colonization trade-off model (Tilman 1994), this mechanism relies on the complete competitive dominance of superior competitors; that is, superior competitors must be able to displace inferior competitors on arrival to an available

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patch. In contrast, when competition is preemptive, organisms that successfully colonize a patch cannot be displaced. Relaxation of the assumption of complete competitive dominance shows that intermediate levels of dominance also allow for coexistence (Calcagno et al. 2006), but when competition is entirely or mostly preemptive, classic competition-colonization trade-off models do not result in coexistence (Yu and Wilson 2001; Calcagno et al. 2006). Preemptive competition is common for organisms that use ephemeral patch habitats (Hanski and Kuusela 1977; Kneidel 1983; Shorrocks and Bingley 1994), suggesting that the classical competition-colonization mechanism is inapplicable for many such systems.

Thus, although several different coexistence mechanisms have been proposed for organisms exploiting ephemeral patches, explaining how diversity is maintained between preemptive competitors that use resources in sparse, mainly homogeneous patches remains a major challenge. Importantly, a significant number of ephemeral patch communities fit this description (Kneidel 1983; Hanski 1990; Marino 1991; Shorrocks and Bingley 1994; Collinge and Ray 2009). Regional coexistence of these species can occur by niche partitioning when different species specialize on different local patch densities (Yu and Wilson 2001). Here we show that coexistence is also possible at the local scale. This occurs when competitors face a life-history trade-off between fecundity and dispersal ability and the required travel distance from patch to patch varies over time. This creates covariance between competitive dominance and interpatch distance, leading to subadditive population growth and the possibility of coexistence via the storage effect (Chesson 1990, 2000b; Chesson and Huntly 1997). Additionally, we model the evolution of competitor traits in these ephemeral patch systems to determine how evolution affects competitor coexistence and possible trait divergence.

Subadditive Population Growth

When the combined effects of environment and competition on population growth are less than additive, population growth is said to be subadditive. Biologically, this describes diminishing returns with respect to population growth as competitive and environmental conditions improve and buffered decreases in population growth as conditions worsen. When the covariance between the effects of environment and competition on population growth is also negative, an interaction between competition and the environment can boost a rare species' growth rate and prevent extinction (Chesson and Huntly 1997).

Coexistence can occur through what is known as the storage effect when subadditivity has this effect for multiple species that are favored under different environmental

conditions. The survival of individuals in long-lived life-history stages—sometimes lasting tens to hundreds of years—that are insensitive to environmental effects and competition can protect populations from excessive decline during unfavorable conditions. Empirical studies have found evidence supporting the storage effect as a coexistence mechanism in a diversity of species including long-lived woody plants (Kelly and Bowler 2002), desert annuals with persistent seed banks (Pake and Venable 1995; Angert et al. 2009), and freshwater zooplankton with dormant stages (Cáceres 1997, 1998). In these systems, as in the classic lottery models of Chesson and Warner (1981) and Chesson (1982), the storage effect relies on some aspect of the environment varying over time, such as precipitation (Pake and Venable 1995; Angert et al. 2009), predator density (Cáceres 1997), or availability of germination sites (Chesson and Warner 1981; Chesson 1982).

In this article, we offer the storage effect as a solution to the puzzle of how ecologically similar species with strong preemptive competition in sparsely distributed ephemeral patches may coexist, using nonpollinating fig wasp communities as a case study. Our study adds to previous work on the storage effect in two important ways. First, we show that the relatively short period of storage typical for ephemeral patch competitors (but see Boix et al. 2001; Bruno et al. 2001) is sufficient for coexistence. Second, we show how the temporal variability needed for coexistence can be generated by spatial processes (here, changing distance between usable patches as they sporadically become available). By drawing on a more subtle source of temporal variability, we highlight the potential for the storage effect to be acting in many more systems than just those with obvious temporal fluctuations in conditions such as weather and predation.

The Fig-Fig Wasp System

Figs (genus *Ficus*, family Moraceae) are highly diverse (750-plus species) and widely distributed across tropical and subtropical habitats. Fig wasps (superfamily Chalcidoidea) are obligately associated with figs and include a monophyletic group of obligate pollinators (family Agaonidae), which typically have a one-to-one specificity with their hosts (Janzen 1979; Marussich and Machado 2007). Fig wasps also include a diverse group (multiple families) of nonpollinating exploiters of the mutualism, most of which are also host-specific (Weiblen 2002). When fig flowers become receptive to pollination, volatile cues are released that attract both pollinating (Ware et al. 1993; Grison-Pigé et al. 2002) and nonpollinating (Proffitt et al. 2007) wasps to fig syconia (enclosed inflorescences). In a textbook example of a highly coevolved mutualism, previously inseminated pollinators enter the syconium

through a small opening and provide pollination services to the plant while laying their eggs into a subset of its many ovules. Each ovule can support one developing wasp larva. In addition to the pollinators, a single fig species can support a community of up to 30 species of frequently host-specific nonpollinators; many of these species use fig ovules in seemingly the same way and can be found coexisting within a single syconium (Compton and Hawkins 1992). In monoecious figs, which we model here, wasp offspring mature over several weeks before emerging from ovules and mating within their natal syconia. On emergence from the natal syconia, females must disperse to new receptive syconia to lay their eggs.

How can this diversity of coexisting nonpollinating wasps be maintained where competitive exclusion over access to ovules might be expected? Several hypotheses have been proposed to explain nonpollinator coexistence, including differences in the timing of oviposition (Kerdelhué et al. 2000; Ghara and Borges 2010) and whether it occurs from the exterior or interior of the syconium (Kerdelhué et al. 2000; Ghara et al. 2011). While these differences likely promote niche partitioning to some degree, it is difficult to explain the observed diversity based only on these modest differences. The identification of a more general mechanism explaining the coexistence and diversity of nonpollinating fig wasps remains a challenge.

Rather than focusing on how nonpollinating wasps differ in their exact use of the fig syconia, we suggest a coexistence mechanism dependent on the phenology of host figs and a fundamental trade-off between wasp dispersal ability and fecundity. Except at the environmental limits of the distribution of *Ficus* (Ramírez 1970; Bronstein 1989; Cook and Power 1996; Gates and Nason 2012), syconia development within the crown of a fig usually occurs in synchrony, presumably to increase the total amount of volatile cues available to pollinators (Bronstein 1989) and to promote outcrossing (Bronstein and Patel 1992; McPherson 2005). Because the developmental stages at which syconia are receptive to wasps and emergence of wasps are almost always completely separated in time (but see Cook and Power 1996; Gates and Nason 2012), it is impossible for wasps to cycle on the same fig for more than one generation. Instead, fig wasps must leave their natal fig to locate a new fig bearing receptive syconia. Between bouts of reproductive activity, figs can go through periods of reproductive inactivity in which no syconia are produced for months or even years (Bronstein 1989; Windsor et al. 1989). The initiation of fig syconia is a complex and sporadic process (Kjellberg and Maurice 1989; Windsor et al. 1989) but may be seasonally variable (Bronstein and Patel 1992). For wasps that must migrate from their natal fig to another receptive fig in order to reproduce, this unpredictable phenology introduces much stochasticity in the

distance wasps must disperse. As such, Compton et al. (1994) and McPherson (2005) have argued that within-crown synchrony in syconia development should limit wasp fitness due to dispersal mortality. During periods in which receptive syconia are far away in time or space, short-lived and poorly dispersing wasps will be less likely to find receptive syconia for oviposition; hence, their reproduction will be lowered. In contrast, when receptive syconia are very close, dispersal ability will be less important, and the most fecund wasps will be expected to benefit even if their dispersal abilities are poor. We suggest that the landscape-level variability inherent in the availability of fig ovules can promote coexistence between multiple types of wasps that specialize to different degrees on fecundity or dispersal ability. This coexistence occurs because the competitive superiority of nonpollinating wasp species changes as the distance to the nearest receptive fig changes over time, and periods in which wasp species experience unfavorable conditions for accessing receptive figs are buffered by population storage in figs containing wasps yet to emerge. Additionally, we propose that this mechanism can lead to evolutionary divergence of fecundities and dispersal abilities between competing fig wasps.

Methods

The Population Model

The preemptive competition and discrete resource use involved in interactions between figs and nonpollinating wasps are well described by a lottery competition model. In a lottery model, individuals compete for a limited number of discrete resources (usually empty habitat but here single ovules), and once a resource is claimed, an individual cannot be usurped from it (Sale 1978). In contrast to the lottery competition models of Chesson and Warner (1981) and Chesson (1982), population storage exists not in the form of long-lived adults or a seed bank but in the developed wasps that remain within their natal syconia over multiple time steps. We use a time step of 1 week. The parameter δ_i is biologically interpreted as the proportion of wasps of species i that exit their natal syconia in any given time step to search for newly receptive fig syconia, leaving a proportion of $(1 - \delta_i)$ stored and yet to disperse. Wasps that disperse successfully compete in a lottery for access to φ new ovules, which become available to competitors in each time step. The number of times wasps of species i successfully oviposit at time t is proportional to $\beta_i^*(t)$. An additional parameter, τ , is needed to model wasp development time from oviposition to adulthood, which is assumed to be constant across wasp species developing within syconia of the same host fig species. It is important to note that τ does not directly

contribute to the storage effect (which is made possible by $\delta_i < 1$), but serves as a time lag in the model to reflect the biology of fig wasp development. For k different wasp species, the total population density P_i of wasp species i at time $t + 1$ is

$$P_i(t + 1) = (1 - \delta_i)P_i(t) + \varphi \left[\frac{\delta_i \beta_i^*(t - \tau) P_i(t - \tau)}{\sum_{j=1}^k \delta_j \beta_j^*(t - \tau) P_j(t - \tau)} \right]. \quad (1)$$

Equation (1) tracks newly eclosed adult wasps that are living within fig syconia prior to dispersal because this is the stage that is commonly censused in the field. For simplicity, we focus on the case in which $k = 2$ nonpollinating wasp species, but exploratory simulations show that this model can predict coexistence of >2 species. The storage effect (Warner and Chesson 1985) is made possible by the first term of equation (1), wherein a single cohort of wasps may persist in their ovules over multiple time steps. This term is critical to facilitating coexistence because it limits sharp population decline during unfavorable conditions by allowing the overlapping of generations.

Probability of Wasp Dispersal Success. The expected reproductive success of wasps (β_i^*) depends on their fecundity, which we define to be the number of eggs a wasp of species i is capable of laying (β_i), and on the probability that a wasp leaving its natal syconium at t successfully disperses to a newly receptive fig syconium (c_i) such that $\beta_i^* = \beta_i c_i$. The probability of successful dispersal is calculated using a diffusion equation. The process of diffusion arises as individuals move in a random walk (or flight) around their environment. We model the fig wasp environment as a two-dimensional landscape on which nonpollinating fig wasps take random flights from their natal fig. For a receptive fig located $r_{\text{dis}}(t)$ from a wasp's natal fig, the probability of successful dispersal for a wasp of species i at time t is defined by an incomplete gamma function,

$$c_i(t) = \frac{r_{\text{tar}}}{\pi l_i} \Gamma\left(0, \frac{r_{\text{dis}}^2(t)}{2l_i \psi_i}\right) \quad (2)$$

(based on an approximation derived by Friedrich 2008). In the above, r_{tar} refers to the radius of the wasp's target, a receptive fig. Here we model the target as the radius of the cloud of volatile cues surrounding the fig, which we assume to be a circle, as recent empirical research has shown that nonpollinating wasps use volatile cues to locate receptive host figs (Proffitt et al. 2007). We do not know of any empirical estimates of r_{tar} , but we found the range of r_{tar} values over which coexistence occurred to be extremely robust. The parameter ψ_i describes the total length of the path that a wasp of species i takes on its flight and

depends on both the velocity and duration of the random flight. Differences in ψ_i between species model different dispersal abilities. We assume that species differences in this path length are related to differences in their longevity and dispersal speed. The variable l_i describes the walk persistence length of species i ; that is, the tendency for a wasp moving in a given direction to continue in that direction (see Friedrich 2008 for details). For very small values of r_{dis} (when the natal fig and receptive fig are very close), equation (2) can lead to values in which $c_i > 1$. When this occurred, c_i values were truncated to unity.

Distribution of Minimum Travel Distance (r_{dis}). Variation in the required dispersal distance to newly available fig syconia ($r_{\text{dis}}(t)$) generates the necessary environmental variation to cause changes in competitive superiority over time. A Poisson process describes independent events occurring over a continuous distance of space or time. For a two-dimensional Poisson process, the square of the distance of the first event will be exponentially distributed, so we use an exponential distribution to model the probability density of the squared distance from a wasp's natal fig to the nearest receptive fig (r_{dis}^2), which contains ovules into which wasps will oviposit in a lottery competition,

$$\Pr(r_{\text{dis}}^2(t) = x) = \frac{1}{\alpha^2} e^{-(1/\alpha^2)x}. \quad (3)$$

The parameter α is the expected distance to the nearest receptive fig. We assume $r_{\text{dis}}^2(t)$ to be uniform within a population (the distance between cross-compatible trees does not vary spatially). Violations of this assumption are likely to further facilitate coexistence (see "Discussion").

Conditions for Species Coexistence. To show that nonpollinating wasp species may coexist, we need to show that the mean geometric growth rate for each species i is positive when $P_i(t)$ is low (Turelli 1978). As pointed out by Chesson and Warner (1981), this is not entirely sufficient because it may allow coexistence when $P_i(t)$ is unrealistically low for a standing population. To avoid unrealistically low population sizes, we define species as coexisting when the mean rate of growth for each species is positive,

$$\mathbb{E}\left[\ln\left(\frac{P_i(t+1)}{P_i(t)}\right)\right] > 0, \quad (4)$$

and when the minimum proportions of each species persists above some threshold, $1/m$, for all time steps,

$$\frac{P_i(t)}{\sum_{i=1}^k P_i(t)} > \frac{1}{m}. \quad (5)$$

Population Model Simulations

The coexistence of species described by our population model was examined via computer simulation with values of model parameters determined by available information on fig wasp fecundity and dispersal. In a recent study of comparative life-history traits from a community of eight nonpollinating fig wasp species, Ghara and Borges (2010) found the egg loads (β_i) of individuals to range between ca. 59 and 263. In our model, β_i values were randomly selected from a uniform distribution between 50 and 300 for each species. To our knowledge, no ecological data exist that describe the velocity, walk length, or walk persistence of dispersing nonpollinating fig wasps, but empirical studies of pollinating fig wasps estimate that pollinators can regularly disperse 5,800–14,200 m (Nason et al. 1998) or farther (Ahmed et al. 2009). This dispersal in pollinators is largely wind-borne, but it is not known to what extent this is also the case for nonpollinators. In our model, we randomly selected ψ_i values between 1,000 and 20,000 for each species.

For a single set of β_i and ψ_i values, coexistence was defined as satisfying the conditions of inequalities (4) and (5) ($m = 1,000$) over 52,000 time steps (1,000 years, wherein we model time steps as a 1-week period) after allowing the simulation to equilibrate for 100 time steps. To ensure that 52,000 time steps was sufficient to judge coexistence, we removed the coexistence-promoting environmental variability by setting $r_{\text{dis}}(t) = \alpha$ for all time steps and verified that the conditions of inequalities (4) and (5) were never satisfied for ecologically distinct species (i.e., species with different β_i , ψ_i). We likewise removed the population storage required for long-term coexistence by setting δ_i equal to unity for all species and verified that coexistence criteria were never satisfied.

Default values for other parameters can be found in table 1; we believe these to be biologically realistic. In the case of α in equation (3), we used geographic coordinates and phenological data from a Mexican population of *Ficus petiolaris* figs to arrive at a reasonable parameter value using maximum likelihood estimation ($\alpha \approx 1,200$). To ensure that our results were not highly sensitive to these specific model parameters, we simulated 52,000 time steps

at randomly selected values of β_i and ψ_i over a variety of different values of α (300, 400, ..., 1,700, 1,800), τ (3, 4, ..., 12, 13), δ_i (0.70, 0.72, ..., 0.98, 1.00), l_i (10, 100, 1,000, 10,000, 100,000), and r_{tar} (10, 100, 1,000, 10,000, 100,000).

To simulate two species of nonpollinating fig wasps (C code available on request), we began by randomly selecting values for β_i and ψ_i and then setting the abundance of each species to 5,000 for τ time steps so that $P_1(0) = P_2(0)$. Every subsequent time step of the simulation proceeded by (1) randomly selecting a value for $r_{\text{dis}}(t)$ from the probability distribution described in equation (3) and then (2) calculating $\beta_i^*(t)$ for each species of wasp. Then (3), these values were used in equation (1) to determine $P_i(t + 1)$. When all time steps had finished, (4) the mean geometric growth rate was calculated, as was (5) the minimum proportional abundance of both species over the course of the simulation. If and only if the conditions in inequalities (4) and (5) were satisfied, we concluded that coexistence was possible at the parameter values used. We simulated 10,000 randomly selected β_i and ψ_i values for all previously mentioned α , τ , δ_i , l_i , and r_{tar} values.

Individual-Based Model Simulations

To explore the consequences of demographic stochasticity, evolution, and individual within-species variation in fecundity and dispersal ability, we constructed an individual-based model (IBM) of the mechanism described above. In the IBM, we replicated the population-level model as closely as possible while allowing for individual variation. At each time step, nonpollinating fig wasps in the IBM disperse to new ovules, which are located at a distance $r_{\text{dis}}(t)$ from their natal ovules (eq. [3]). As in the population model, equation (2) determines the probability that an individual wasp successfully disperses ($c_i(t)$), but the IBM allows for individual variation around the species-specific expected fecundity (β_i) and dispersal ability (ψ_i). In the IBM, each wasp has its own dispersal ability (ψ_{wasp}), so the probability of dispersal success (c_{wasp}) can vary within species. Likewise, a successfully dispersing wasp can produce some number of offspring as determined by the individual

Table 1: Default values for modeling competing nonpollinator fig wasps

Parameter	Description	Default value	Source
α	Expected minimum distance to receptive tree (m)	1,200	Unpublished data
r_{tar}	Tree volatile radius (m)	100	...
l_i	Species walk persistence length (m)	100	...
δ_i	Species emergence rate	.88	Greeff and Ferguson (1999)
ϕ	Ovule abundance	10,000	Janzen (1979)
τ	Wasp development time	5	Janzen (1979)

wasp's fecundity, β_{wasp} . These offspring compete in a lottery along with the offspring of other successfully dispersing wasps wherein each offspring has an equal chance of occupying one of φ ovules. After the lottery competition, offspring develop over τ time steps, after which each individual wasp exits its natal ovule with a probability of $(1 - \delta_i)$ at every subsequent t . To remove any effects of unrealistically long storage, individuals were only allowed to remain in their natal syconia for a maximum of three time steps. After three time steps of storage, wasps were forced to disperse.

Evolutionary Dynamics. We allow hereditary variation to influence the evolution of species-specific expected fecundity and dispersal ability. Following Wood and Ackland (2007), we prevent unrealistic evolution by constraining individuals not to exceed a set maximum expected product of fecundity and dispersal probability ($c_{\text{wasp}}(t)$). This expected product ($E[\beta^*]$) is calculated as

$$E[\beta^*] = \beta_{\text{wasp}} \int_0^{\infty} (c_{\text{wasp}}(t) | r_{\text{dis}}^2(t) = x) \times \Pr(r_{\text{dis}}^2(t) = x) dx. \quad (6)$$

We consider five different maximum $E[\beta^*]$ values, and for each, we find the trade-off line defined by β_{wasp} , ψ_{wasp} combinations that yield the maximum $E[\beta^*]$ at the expected intertree distance (fig. 1). In the simulations, females were mated with a randomly selected conspecific from her natal syconium. Trait values for their offspring were selected at random from a normal distribution with mean equal to the mean trait value of the parents and standard deviations as described in the appendix. If after selection the trait values were above the trade-off line, then either fecundity or dispersal ability was randomly selected with equal likelihood to be lowered so that $E[\beta^*]$ fell back on the trade-off line. Trait values of offspring are rounded to the nearest integer. It was necessary before simulating the effect of evolving traits on coexistence to find trait variances that did not bias evolution toward one trait and away from the other. Trait variance selection and additional model details can be found in the appendix.

We ran multiple simulations to compare the probability of long-term coexistence in evolving and nonevolving populations. If simulations in which evolution was permitted result in a higher proportion of communities with long-term coexistence, our model suggests that evolution may facilitate coexistence in the presence of the storage effect. We additionally tested whether ecologically similar species diverge in their trait values over time under the conditions of our model. To test whether evolution leads to character

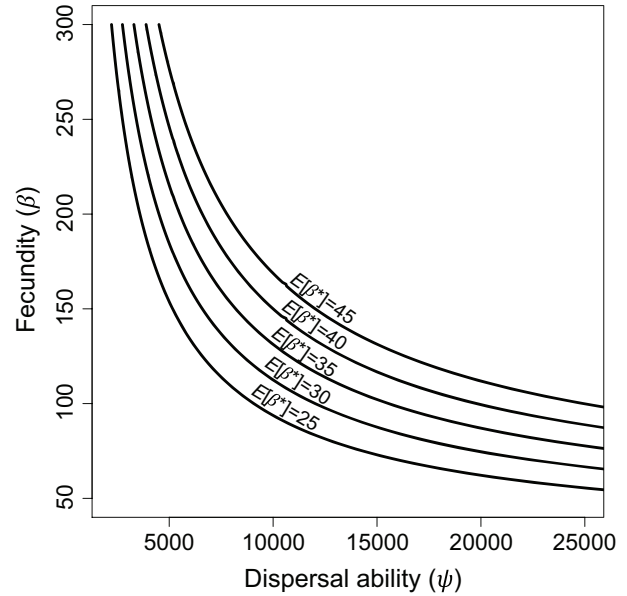


Figure 1: Trade-off lines showing the maximum expected fecundity values allowed in the individual-based model simulations of non-pollinating fig wasps. Combinations of individual β and ψ that resulted in values above $E[\beta^*]$ lines were not permitted.

divergence, we ran 100 simulations in which species had identical initial starting trait values: $\beta = 150$ and $\psi = 8,197$. Each simulation was allowed to run until either one species became extinct or 52,000 time steps had passed. For each of these simulations, we used a trade-off line value of $E[\beta^*] = 35$. If ecologically similar species diverge in one or both traits, this divergence will be observable as an increase in the difference between species traits from t to $t + 1$ (e.g., $|\beta_1(t + 1) - \beta_2(t + 1)| - |\beta_1(t) - \beta_2(t)| > 0$). If the expected difference in trait difference from one time step to the next is positive, then we conclude that trait divergence is occurring. From the 100 simulations, we collected changes in trait values from a total of 541,801 time steps. We estimated the mean change in fecundity and dispersal ability difference, and 95% confidence intervals around the mean. In addition to looking at the mean trait divergence in a time step, we also recorded long-term divergence that occurred for each of the 100 simulations. Because net divergence is assured when species have initially identical traits, and sample size is small when a population is nearing extinction, we excluded the first and last 500 time steps from each simulation when looking for long-term change. We report the mean of long-term trait change and the proportion of simulations in which long-term trait divergence occurred.

Results

Population Model Simulations

Over all simulations, the pattern of coexistence across $\beta_i - \psi_i$ space was qualitatively the same. Two species were able to coexist only if there was an inverse relationship between β_i and ψ_i and simulations in which one species was superior to the other in both of these randomly selected values led to the extinction of the inferior competitor. In simulations in which long-term coexistence occurred, storage led to higher growth rates at lower population sizes, buffering rare species against extinction (e.g., fig. 2). Although coexistence criteria were met at least some of the time for all parameter combinations (with the exception of $\delta_i = 1$, which removed all population storage), some parameter values were more likely to facilitate coexistence. Coexistence became less likely as the expected dispersal distance to the nearest tree (α) increased (fig. 3a) and more likely as development time (τ) increased (fig. 3b). The probability of coexistence decreased as the proportion of wasps stored in each time step was reduced (fig. 3c). The relationship between coexistence and flight persistence did not have a clear directional trend (fig. 3d), and coexistence was only slightly augmented with an increase in the size of the attractive cloud of volatiles around the fig (fig. 3e).

To visualize the range of β_i and ψ_i values that one species could take given the values of a second, we set $\beta_1 = 150$ and $\psi_1 = 10,000$ at default parameter values and then

tested whether species could coexist when $\beta_2 = (50, 51, \dots, 299, 300)$ and $\psi_2 = (1, 2, \dots, 19,999, 20,000)$. A plot showing the interaction between β_i and ψ_i coexistence values reveals a pattern that has a concave parabolic shape that widens at the ends and shrinks to a point in the center where $\beta_1 = \beta_2$ and $\psi_1 = \psi_2$ (fig. 4). This pattern of coexistence was retained over multiple simulated parameter combinations (results not shown).

Individual-Based Model Simulations

Our individual-based model consistently reproduced the coexistence results of our population models. Individual-based model simulations (fig. 5) were slightly more likely to result in coexistence than population model simulations (fig. 3) because in the IBM, we immediately rejected randomly selected trait values above a prespecified trade-off line (fig. 1). The probability of coexistence generally increased with increasing $E[\beta^*]$ when traits were fixed or allowed to evolve (fig. 5). The probability of coexistence was consistently lower for all $E[\beta^*]$ values when populations were allowed to evolve, but some coexistence was observed in all cases.

For the 100 simulations in which we tested whether trait divergence was expected over time for initially identical species, we found a mean increase in the difference between trait values for fecundity ($2.765 \times 10^{-4} \pm 7.980 \times 10^{-5}$) and dispersal ability ($2.428 \times 10^{-2} \pm 6.900 \times 10^{-3}$) from one time step to the next. Despite this trend toward trait

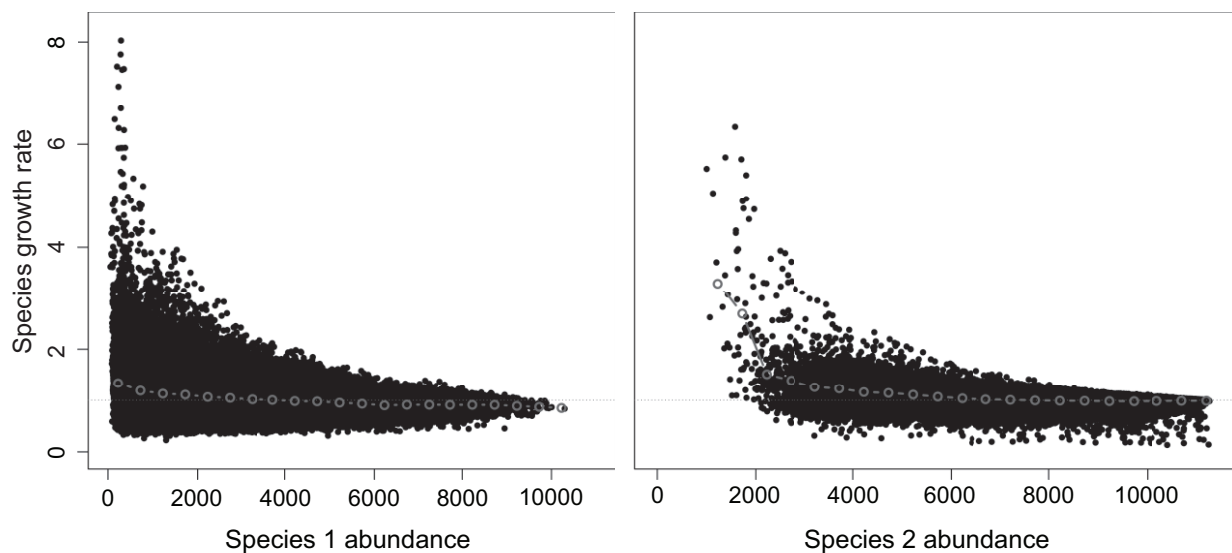


Figure 2: Relationship between species growth rate, $P(t + 1)/P(t)$ and abundance for two populations of simulated nonpollinating fig wasp competitors that display long-term coexistence. Populations have negatively correlated fecundities ($\beta_1 = 134$, $\beta_2 = 188$) and dispersal abilities ($\psi_1 = 17,977.41$, $\psi_2 = 12,846.89$). Open circles show the mean species growth rates in bins of 500 along the X-axis. Points above the dotted horizontal line indicate positive species growth rates.

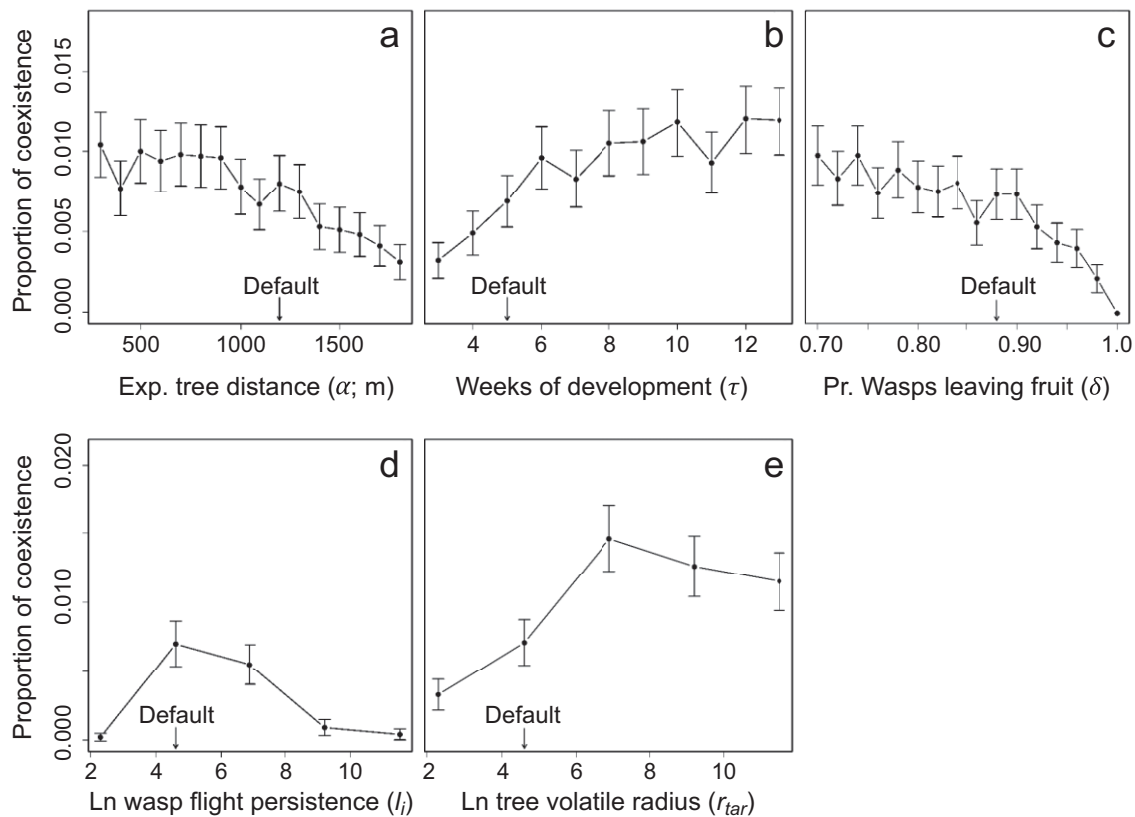


Figure 3: Proportion of simulations in which coexistence criteria were upheld at different expected minimum distances to a receptive fig (α ; a), durations of wasp development (τ ; b), eclosion rates (δ ; c), flight persistence values (l_f ; d), and receptive fig volatile radii (r_{tar} ; e) for simulated competitor fig wasps. Error bars show 95% confidence intervals.

divergence, trait evolution was highly variable. Trait divergence occurred in only slightly over half of time steps for fecundity (50.2%, 271,987 of 541,801) and dispersal ability (50.2%, 271,889 of 541,801). As such, evolutionary trait divergence was not consistent over time in simulations. Rather, trait evolution was highly variable with regular divergence and convergence in evolving species trait values. Despite this variability from one time step to the next, traits tended to diverge over the long term. The difference between species dispersal values increased by 62.90 on average and in 92% of simulations. The difference between species fecundity values increased an average of 0.76 and in 90% of simulations. As expected, a species' increase in one trait was associated with a decrease in the second. For example, when one species evolved to increase its dispersal ability relative to its competitor, its competitor typically evolved to increase its superiority in fecundity (fig. 6).

Discussion

Here we model an ephemeral patch system in which the minimum travel distance for successful dispersal to a new

patch varies over time. With this varying travel distance, the probability of successful dispersal also varies, and species that use ephemeral patches as a resource for larval development face a trade-off in the degree to which they invest in dispersal ability and fecundity. When combined with Chesson's model of coexistence (Chesson and Warner 1981; Chesson 1982), this trade-off can result in multiple coexisting species that specialize to different degrees on dispersal ability and fecundity. To model this mechanism, we use a lottery competition focusing on the interactions within a community of nonpollinating fig wasps that compete for access to the ovules of figs for larval development. We show that variation in the minimum travel distances facilitates coexistence between competing wasp species with different life-history trade-offs for dispersal ability and fecundity. These results offer an explanation for the extensive and widespread diversity of nonpollinating fig wasps that use fig syconia as a resource for larval development.

Because of their remarkable diversity, nonpollinating fig wasp communities have been the focus of multiple ecological studies. An interesting feature of this diversity is

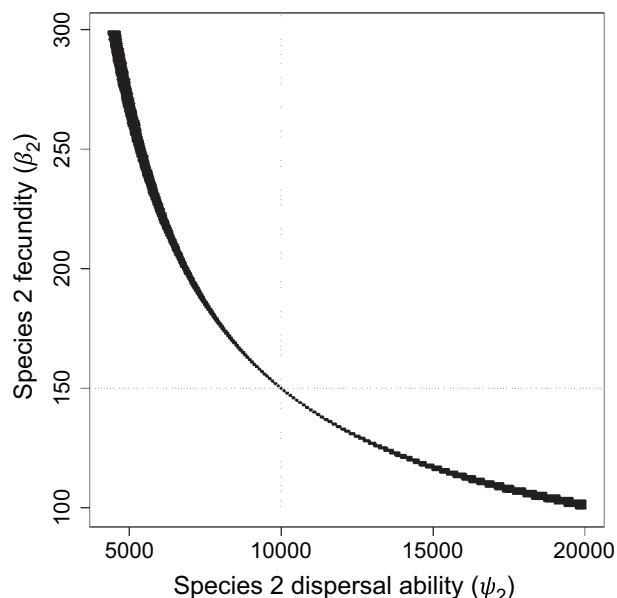


Figure 4: Coexistence along the ranges of β_2 and ψ_2 simulated given $\beta_1 = 150$ and $\psi_1 = 10,000$. The solid black band represent simulations that resulted in coexistence. The horizontal dotted line shows where $\beta_1 = \beta_2$, and the vertical dotted line shows where $\psi_1 = \psi_2$.

the variability of nonpollinator species richness across taxonomic and geographical scales. Among South African fig species, for example, nonpollinator species richness has been found to range between 3 and 30 (Compton and Hawkins 1992), and high variability in wasp species richness has been observed among individuals within species of figs as well (Hawkins and Compton 1992). In a study of nonpollinating wasp diversity between fig species, Compton and Hawkins (1992) suggest that variability in species richness may be due to historical factors that limit the richness of nonpollinators that develop in a particular fig species. A similar study showed evidence for the undersaturation of fig wasp communities, and the variability of local nonpollinator species richness led the authors to suggest that wasp life histories strongly constrain host-finding ability (Hawkins and Compton 1992). Our model shows how this constraint can be a coexistence-promoting mechanism when fig phenology is also considered. Because individual figs remain unreceptive to fig wasps for an extended length of time and become receptive for only a short period of time, the distance over which a fig wasp is required to travel to reach a receptive tree can vary greatly from one natal fig and wasp generation to the next. Our results show that a trade-off between dispersal ability and fecundity can provide a mechanism for coexistence in such a variable landscape. We hypothesize that when the travel distance to a receptive tree is low, wasps that

invest more resources in fecundity will have the highest fitness, and when travel distance is high, wasps that are especially good dispersers will be favored.

We have focused on explaining the diversity of non-pollinating fig wasp communities, but pollinating fig wasps must also successfully disperse and oviposit into fig syconia. As such, a trade-off between dispersal ability and fecundity might also be expected for pollinating fig wasps. Pollinators are represented by a single family (Agaonidae), while nonpollinators are represented by multiple families. A plausible explanation for the difference in diversity at this scale is that the specificity of fig hosts to their agaonid wasps preceded the evolution of the mutualism, as appears to be the case for yuccas and their pollinating moths (Pellmyr and Thompson 1992; Bogler et al. 1995). But within-family nonpollinator diversity is also generally higher than that of pollinators within host fig species. In contrast to nonpollinators, pollinating fig wasps typically exhibit a one-to-one host specificity with their mutualist fig (Weiblen 2002). The paucity of pollinators sharing a host fig likely requires additional explanation. One possibility is that pollinating fig wasps have arisen too recently to permit their diversification on individual hosts. This explanation seems unlikely, however, given that the fig-fig wasp mu-

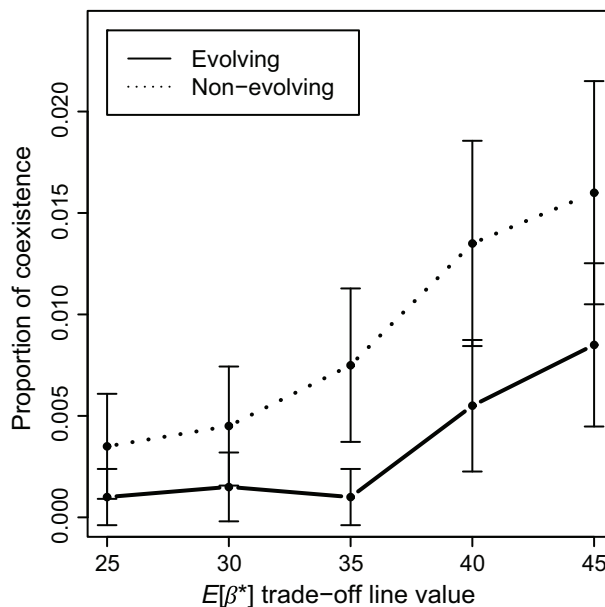


Figure 5: Relationship between the maximum expected net reproductive rate ($E[\beta^*]$) of competing simulated fig wasps and their probability of coexistence. In all simulations, the initial life-history values of two competing species are randomly selected, and combinations of fecundities (β) and dispersal abilities (ψ) are restricted so that wasps cannot increase $E[\beta^*]$ above a maximum value. Simulations in which traits are allowed to evolve are compared to simulations in which traits do not evolve. Error bars show 95% confidence intervals.

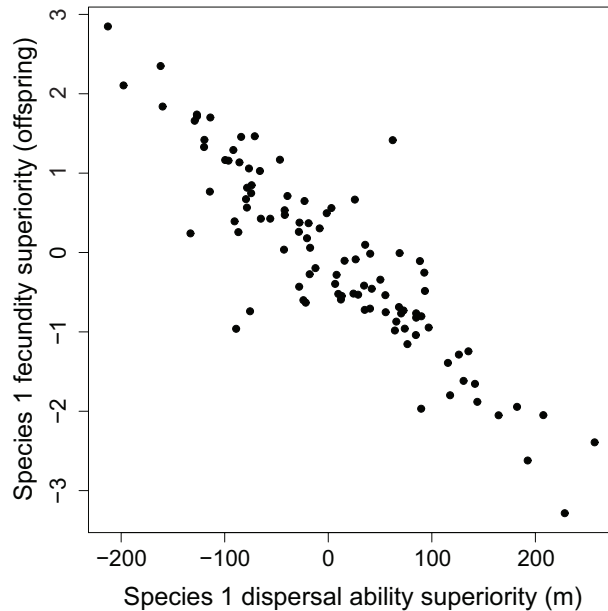


Figure 6: The long-term evolved change in the dispersal ability (meters of distance dispersed) and fecundity (number of offspring produced) superiority of a single species of simulated fig wasp relative to a competitor species for ephemeral patch resources in 100 simulations. Both species begin simulations with identical trait values, and long-term trait evolution is analyzed after 500 generations have passed until 500 generations before the extinction of one species.

tualism originated roughly 70–90 million years ago (Rønsted et al. 2005, 2008), leading us to seek an alternative explanation for specificity in the ecological dynamics of the interaction. We suggest that differences between pollinator and nonpollinator life histories relevant to population storage might limit pollinator diversity. Our model shows that some portion of a wasp population must be stored over changing environmental conditions (dispersal distances) for multiple species to coexist. In contrast to nonpollinators, some of which can live for multiple weeks (Ghara and Borges 2010), pollinator longevity is only 2–3 days (Kjellberg et al. 1988; Dunn et al. 2008). Pollinators also emerge from syconia much more rapidly. In a study of *Ficus ingens*, Greeff and Ferguson (1999) observed pollinator emergence to stretch over a period of only 4 days, with the overwhelming number of pollinators leaving within 24 h. In contrast, nonpollinator emergence extended over a much longer period of time. One week after emergence began, some wasps of all nonpollinator species were still emerging, and between 4.5% and 19.6% of wasps remained within their natal syconia, depending on species (Greeff and Ferguson 1999). In addition to lower longevity and population storage, pollinator diversity may be lower due to species interactions. While the nonpollinators we

model simply compete for oviposition space in fig syconia, coexisting pollinators using a single fig species as a host have the additional complexities associated with the differential costs and benefits associated with mutualism. Multiple pollinators, for example, might vary in their investments in pollination efficiency. Interactions between multiple pollinators and figs may be ecologically or evolutionarily unstable due to these mutualistic interactions (the evolutionary atrophy of mutualism; see Ferrière et al. 2002).

Many insects face a trade-off between fecundity and longevity at both intraspecific (Rose 1984; Kaitala 1991; Tatar et al. 1993; Ellers and Alphen 1997) and interspecific (Jervis et al. 2001, 2007; Pexton and Mayhew 2002) levels. A large number of mature eggs at emergence has been suggested to limit insect mobility in multiple ways (see Jervis et al. 2005 for review), such as by increasing abdominal mass (Sattler 1991) or reducing body space for thoracic muscles (Kaitala 1988). Unfortunately, because fig wasps are extremely small and often far-dispersing (Nason et al. 1998; Ahmed et al. 2009; Yu et al. 2010), direct measures of individual mobility can be difficult to obtain (but see Kjellberg et al. 1988). Recently, Ghara and Borges (2010) examined life-history traits of fig wasps in the community ovipositing in *Ficus racemosa*. They found variation in fecundity and longevity between these species, and while they did not measure the dispersal ability of species in the community, they noted that the abundances of species varied both locally and seasonally. Ghara and Borges (2010) suggest that the life-history traits of community members will be affected by spatiotemporal variation in figs. Egg load and wing loading estimates from the non-pollinator community associated with *Ficus petiolaris* strongly support the hypothesis of a dispersal ability and fecundity trade-off (Duthie 2013).

Competition-Colonization Dynamics

Subadditive population growth is well known to facilitate species coexistence (Chesson 2000a, 2000b; Fox 2013). Chesson (2000a) shows a general model of how subadditive population growth can apply to a class of ephemeral patch models, suggesting that ephemeral patches may be differently preferred or accessible to competitors in space, or that competitor survivorship in patches may differ between species. A central goal of Chesson's (2000a) work was to show how a spatial storage effect could be applied to understanding coexistence in a class of ephemeral patch models. In contrast, we focus on a temporal storage effect, modeling the overlapping of generations that occurs when competitors of a single cohort leave patches over multiple time steps. We show that short-term population storage and variation in between-patch dispersal distance is suf-

ficient for competitor coexistence for biologically reasonable parameter values. This coexistence is possible at the population level, even given complete preemptive competition. Our results shed new light on competition-colonization dynamics, showing a plausible biological mechanism that can facilitate coexistence at the population level for many communities that include a diversity of ephemeral patch competitors.

Kelly and Bowler (2002) contrast models of habitat patchiness, such as those of Nee and May (1992) or Pacala and Tilman (1994), with storage models such as those of Chesson and Warner (1981) or Chesson and Huntly (1989). Our model shows that the mechanisms generating coexistence in these models can act in tandem. A storage effect is generated when species differ in their abilities to colonize new patches and compete following successful colonization and when generations overlap such that a single cohort staggers its dispersal over multiple time steps. A varying dispersal distance between patches is the environmental variable that generates the change in competitive dominance on which the storage effect depends in our model, and we present an extreme case in which patches are identical and population storage is short. For many ephemeral patch competitors, patch heterogeneity may lead to different types of environmental variation, which will likely further facilitate coexistence caused by a storage effect. For example, multiple species of copepods inhabit temporary ponds and must survive extended periods of desiccation, often through egg dormancy (Santer 1998; Bruno et al. 2001). Bruno et al. (2001) observed multiple species of copepods that inhabit ephemeral ponds of Everglades National Park (Florida). Population growth in these species may be influenced by species' fecundities and abilities to successfully disperse to new ephemeral ponds, but also by different species specific responses to varying levels of ephemeral pond hydration (Bruno et al. 2001), which may lead to differential survivorship of competitors in different ponds. As noted by Chesson (2000a), such differential survivorship between ephemeral patch competitors may also facilitate coexistence. Given the multiple ways that the storage effect may operate in species of ephemeral ponds, the storage effect may be of great importance to understanding coexistence in these systems—perhaps as much or more so than classical resource partitioning. Because vernal pool ecosystems are of great importance for maintaining biodiversity and ecosystem functioning (Hunter 2008), understanding the factors that maintain copepod biodiversity may have important implications for conservation.

Buffered population growth caused by storage and a trade-off between dispersal ability and fecundity may also have broader applications for understanding host-parasitoid interactions. A substantial component of the Earth's

total biodiversity is composed of phytophagous insects and the insects that parasitize them; parasitoids account for more than 10% of metazoan species, and most insects are host to multiple parasitoid species (Hassell 2000). In general, ecological theory indicates that the spatial aggregation of parasitoids can increase parasitoid intraspecific competition and facilitate the persistence of host and parasitoid populations (Hassell and May 1973; May 1978; Hassell et al. 1991). Equilibrium conditions for the coexistence of multiple parasitoids on a single host have also been examined. May and Hassell (1981) found coexistence to be facilitated by the intraspecific aggregation of parasitoid species and when later-attacking parasitoid species have equal or greater host searching efficiency. Lei and Hanski (1998) found evidence for a competition-colonization trade-off in two specialist parasitoids of the Glanville fritillary butterfly, *Melitaea cinxia*. They concluded that this competition-colonization trade-off facilitated parasitoid coexistence at both the population and metapopulation level (Lei and Hanski 1998).

Individual-Based Model and Evolutionary Dynamics

A comprehensive understanding of ephemeral patch competitor diversity will almost certainly require an understanding of many ecological and evolutionary processes and a deeper understanding of the natural history of the complex system we have modeled here. Although the storage effect is an important mechanism for maintaining biodiversity in a variety of taxa (Cáceres 1997; Kelly and Bowler 2002; Angert et al. 2009), how evolution acts to promote or hinder the persistence of populations maintained by the storage effect has only recently been considered (Snyder and Adler 2011; Svardal et al. 2011; Abrams et al. 2012). Evolution relies on individual variation within species, which may promote population stability by widening the breadth of conditions under which at least some individuals can survive (Lankau 2011). Adaptive evolution may also be expected to make species persistence more likely through evolutionary rescue (Bell and Gonzalez 2009, 2011; Vasseur et al. 2011).

The effect of adaptive evolution on population persistence in the presence of interspecific competition may depend on specific ecological conditions (Osmond and de Mazancourt 2013). For example, de Mazancourt et al. (2008) modeled a lottery competition for a diverse guild of competitors in a patchy environment to determine the effect of biodiversity on species' evolutionary responses to environmental change. They found that higher biodiversity, in the form of a higher number of competing species, decreased adaptive evolution by making it more likely that a species would be outcompeted by a superior competitor, ultimately limiting diversification (de Mazancourt et al.

2008). While a detailed analysis of the effect of adaptive evolution on competitive exclusion is beyond the scope of this article, superior competitors in our model likely limited the ability of poorer competitors to adapt by preempting ovules that could otherwise have been used by some individuals of the poorer-competing species. Additionally, more rapid adaptive evolution of superior competitors was likely facilitated by higher population sizes, giving them a further competitive advantage.

Recent evolutionary models that incorporate the storage effect show that disruptive selection can lead to the evolutionary branching of a phenotypic trait in a single population (Svardal et al. 2011) or in a population of two initially identical species whose competitive abilities in a specific environment are governed by a single trait (Abrams et al. 2012). Our individual-based model supported the general conclusions of these studies, but the extent to which populations diverged was minimal. This low trait divergence in initially identical populations was likely influenced by the limited population sizes of competitors. Similar results were observed by Wakano and Iwasa (2013) and Claessen et al. (2007), in part by demographic stochasticity leading to random genetic drift away from the evolutionary branching point. In our model, competitor population size was limited by the number of ovules available to competing fig wasps at each time step ($\varphi = 10,000$), which likely weakened character displacement. Additionally, the phenotypic effects of drift were likely increased in our model by the existence of two unlinked traits (as opposed to a single trait), further inhibiting evolutionary branching (Dieckmann and Doebeli 1999). Previous work has shown that evolutionary branching is more likely for strong trade-offs (high average specialist fitness relative to generalist fitness; Abrams et al. 2012), high overlap in generations, and a strong selection against suboptimal phenotypes relative to the variance in selective optima (i.e., the less the environmental optimum varies over time, the stronger selection against suboptimal competitors must be for branching to occur; Svardal et al. 2011). Although a full analysis of how competing populations are expected to diverge evolutionarily is beyond the scope of this article, it would be interesting to consider the effect different species emergence rates (δ_i), minimum dispersal distance requirements (r_{dis}), and trade-off curves (fig. 1) have on species trait divergence or convergence.

Spatial Storage

For ease of modeling and proof of concept, we model competitive coexistence using only a temporal storage effect. Our model shows that given a minimal set of assumptions, competing nonpollinator fig wasps can maintain positive growth rates and viable population sizes over

time. For natural communities of nonpollinating fig wasps, spatial storage mechanisms and spatial heterogeneity will very likely facilitate competitor coexistence further. In our model, we assume competing wasps in a given time step move from a single fig with eclosing wasps to another fig with receptive syconia. In nature, multiple figs with eclosing wasps and figs receptive to incoming wasps are likely to overlap temporally, leading to spatial variation for wasps in travel distance to the nearest receptive fig. When such spatial effects are present, the dynamics of populations will be the arithmetic mean of local spatial processes (Hassell et al. 1991; Chesson 2000a). For competing species in nonpollinating fig wasp communities, and ephemeral patch communities in general, such spatial processes should have the effect of further buffering population growth against extinction. This additional buffering of population growth will arise because different competing species may be competitively superior in different localities, leading to less dramatic population-wide changes in competitive dominance over time. Applying the spatial storage effect outlined in Chesson (2000a) to our fig wasp system indeed suggests that spatial variability should further promote coexistence (A. B. Duthie, unpublished results).

Conclusions

Our model shows that long-term coexistence between competitors in homogeneous ephemeral patch systems is possible at the local scale when competition is preemptive. Long-term coexistence is achieved when competitors vary in their fecundities and dispersal abilities because of the variability of patch distances. At times when a receptive patch is near a competitor's natal patch, competitors with high fecundity will have a competitive advantage even if their dispersal ability is poor. When a receptive patch is more distant, competitors that invest to a greater degree in the ability to disperse will have a competitive advantage. We propose this mechanism as a broadly applicable hypothesis for explaining diversity in ephemeral patch communities, including the 750-plus communities of nonpollinating fig wasps. Within nonpollinating fig wasp communities, a number of other elements of fig ecology will be relevant to understanding wasp coexistence. In addition to dispersal/fecundity trade-offs, some nonpollinating fig wasps vary in resources use (Kerdelhué et al. 2000) and oviposition timing (Ghara and Borges 2010; Ranganathan et al. 2010), both of which may limit competitive exclusion. Given this diversity of nonpollinator life histories, and the diversity in nonpollinator community composition among fig species, we emphasize the utility of these communities as a model for the study of com-

petitive coexistence (Hawkins and Compton 1992; Kerdelhué et al. 2000) and the evolution of diversity.

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APPENDIX

Individual-Based Model Evolution Details

To avoid evolution being biased toward either increasing fecundity or dispersal ability, it is necessary to select trait variances that have equivalent effects on fitness. To accomplish this goal, prior to simulations between competing species, we modeled a single population in which the fecundity variance was set to unity with the initial starting conditions of $\beta = 150$ and $\psi = 8,197$ (two points on the $E[\beta^*] = 35$ trade-off line; fig. 1). Multiple simulations with different dispersal standard deviations were tested, and in each simulation the population was allowed to evolve over multiple generations. When the standard deviation of ψ from parent to offspring was ca. 93, the population did not evolve significantly toward maximizing either fecundity or dispersal ability over 52,000 generations. Lower dispersal ability standard deviations led to increasing fecundities (and decreasing dispersal abilities), and higher dispersal standard deviations led to increasing dispersal abilities (and decreasing fecundities) along the trade-off line. Therefore, offspring β values were chosen from a distribution with standard deviation 1 while offspring ψ values were chosen with standard deviation 93.

To begin a single run of one of these simulations, initial fecundity and dispersal ability values are randomly and independently selected. For each of two competing species, values of β ranged between 50 and 300, and values of ψ ranged between 1,000 and 20,000. Combinations of fecundity and dispersal ability values that result in $E[\beta^*]$ values greater than allowed are immediately rejected, and new values are selected before the simulation run proceeds. When acceptable values are found for each species, 10,000 individuals are randomly assigned to one of two species with an equal likelihood of being assigned to each. All individuals within a species are assigned the same fecundity and dispersal ability. The developmental stage of each individual is randomly assigned to a week of development

time from 0 to τ . For each maximum $E[\beta^*]$ trade-off line (fig. 1), we ran 2,000 simulations, each with 5,200 time steps, in which both species were allowed to evolve, and 2,000 simulations in which no evolution occurred. In simulations without evolution, trait values of offspring were identical to those of the parental mean and initial trait values were uniform within species. We compare the probability of long-term coexistence in communities that were allowed to evolve and in communities in which no evolution occurred.

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Artist’s rendering of a nonpollinating fig wasp such as *Idarnes* sp., which lays its eggs into the ovules of *Ficus petiolaris* flowers. Credit: A. Catherine Duthie, <http://www.mandikat.net>.