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Integrating simulation modeling and empirical validation to understand the role of population density and isolation in fig-fig wasp mutualism

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Abstract

Obligate mutualisms represent tightly coupled ecological interactions whose persistence depends on both biotic and spatial factors. The fig-fig wasp mutualism is a classic system in which pollination efficiency, reproductive success, and long-term stability are strongly influenced by host population density and spatial structure. In this study, we developed simulation models to explore how population density, spatial isolation, and flowering phenology influence reproductive dynamics in fig-fig wasp systems. These models were parameterized using ecological constraints such as wasp lifespan, dispersal ability, and phenological overlap. Model predictions were subsequently validated using empirical field data collected across multiple density gradients. Results reveal strong density-dependent patterns in pollination efficiency, identify a critical threshold density necessary for sustaining mutualism, and demonstrate that spatial isolation significantly reduces reproductive success. Although phenological asynchrony partially buffers low-density effects, it does not fully compensate for extreme isolation. The integration of simulation and empirical approaches provides a comprehensive framework for predicting mutualism stability under habitat fragmentation and offers critical insights for conservation of keystone fig species.

Keywords: Fig and wasp, mutualism, pollination, population density, spatial isolation, phenology, simulation modeling

Introduction

Mutualistic interactions are fundamental drivers of biodiversity and ecosystem stability, yet their persistence is highly sensitive to ecological context and environmental variability (Ecology; Bascompte & Jordano, 2007; Bronstein, 1994) ^[1, 2]. Among these interactions, the fig-fig wasp mutualism stands out as one of the most specialized and evolutionarily stable systems, characterized by an extraordinary degree of interdependence between partners (Janzen, 1979; Herre *et al.*, 2008) ^[11, 9]. Fig trees (*Ficus* spp.) rely exclusively on species-specific pollinating wasps for successful sexual reproduction, while the wasps are entirely dependent on fig syconia for oviposition and completion of their life cycle (Kjellberg *et al.*, 2005; Weiblen, 2002) ^[12]. This obligate relationship has persisted for millions of years through tightly coupled coevolutionary adaptations (Cruaud *et al.*, 2012) ^[2].

However, despite its evolutionary robustness, the interaction is ecologically fragile due to inherent biological constraints. Pollinator wasps have an extremely short adult lifespan, typically limited to 24-48 hours, within which they must locate a receptive host (Ware & Compton, 1994) ^[18]. Their dispersal ability is also highly restricted, making successful pollination strongly dependent on the spatial proximity of fig trees (Harrison, 2005) ^[7]. Furthermore, the system relies on precise synchronization between wasp emergence and the availability of receptive (B-phase) syconia, adding an additional temporal constraint that can influence reproductive success (Cook & Rasplus, 2003) ^[3].

Previous studies have established that population density and spatial distribution of fig trees are key determinants of pollination efficiency, as they directly influence pollinator movement, encounter rates, and reproductive outcomes (Herre & West, 1997; Holland & DeAngelis, 2010) ^[8, 10]. However, empirical approaches alone are limited in their ability to capture complex ecological processes such as threshold dynamics, long-term extinction risks, and the interactive effects of density, dispersal, and phenology (Okuyama & Holland, 2008) ^[13].

These processes often operate across spatial and temporal scales that are difficult to observe directly in field conditions. Simulation modeling provides a powerful complementary approach by allowing controlled manipulation of ecological variables and exploration of system behavior under a wide range of scenarios, including those that may not be easily replicable in natural settings (Grimm & Railsback, 2005) ^[5].

Nevertheless, models must be grounded in empirical data to ensure ecological realism and avoid oversimplification. Therefore, the present study integrates simulation modeling with field-based validation to develop a comprehensive understanding of the fig-fig wasp mutualism. Specifically, it aims to predict how population density and spatial isolation influence pollination dynamics, estimate the minimum viable density required for sustaining the interaction, and validate these predictions using empirical data collected from natural populations.

Materials and Methods

This study adopts an integrative approach by combining simulation modeling and empirical validation to understand the ecological dynamics of the fig-fig wasp mutualism. Simulation modeling serves as a predictive framework to explore how variations in population density, spatial isolation, and phenological patterns influence pollination outcomes under controlled and repeatable conditions (Grimm & Railsback, 2005; Railsback & Grimm, 2019) ^[5, 14]. In parallel, empirical validation provides field-based evidence to test the accuracy and ecological realism of model predictions (Holland & DeAngelis, 2010) ^[10]. The central hypothesis guiding this study is that pollination efficiency is a function of population density, spatial isolation, and phenological overlap, with these relationships being strongly mediated by the dispersal constraints of pollinating fig wasps, particularly their short lifespan and limited movement range (Harrison, 2005; Kjellberg *et al.*, 2005) ^[7, 12].

Simulation model design

Simulation models were developed using R and Python programming environments to replicate ecological processes observed in natural fig populations (Grimm *et al.*, 2006) ^[6]. The model was structured to capture the essential biological and spatial dynamics governing the fig-fig wasp interaction (Herre *et al.*, 2008) ^[9].

Model structure

The simulation framework consists of three interconnected modules:

Fig tree population module

This module represents the spatial and temporal structure of fig populations. Each tree is assigned geographic coordinates within a simulated landscape, allowing explicit modeling of spatial relationships (Turner *et al.*, 2001) ^[17]. Populations are categorized into low, medium, and high density based on tree abundance per unit area. Additionally, each tree is assigned a phenological state corresponding to the developmental stages of the syconium (A-E phases), enabling temporal tracking of reproductive availability (Cook & Rasplus, 2003) ^[3].

Pollinator (Wasp) module

This module simulates the life cycle and movement of pollinating fig wasps. Wasps emerge from D-phase syconia carrying pollen and have a strictly limited lifespan (Typically 24-48 hours), imposing strong constraints on dispersal (Ware & Compton, 1994) ^[18]. Movement is modeled probabilistically, with wasps searching for receptive B-phase syconia within their dispersal range. The probability of successful movement decreases with increasing distance between trees (Harrison, 2005) ^[7].

Interaction module

This module governs the outcomes of fig-wasp encounters. It calculates the probability of successful host location, determines whether pollination occurs, and simulates oviposition within the syconium. Reproductive output is quantified in terms of seed production (Fig fitness) and gall formation (Wasp fitness), allowing evaluation of mutualistic efficiency (Herre & West, 1997) ^[8].

Key assumptions

To simplify complex ecological processes while retaining biological realism, the following assumptions were incorporated:

- Wasps disperse randomly, but with success decreasing as a function of distance (Okuyama & Holland, 2008) ^[13]
- The probability of locating a receptive host declines exponentially with increasing inter-tree distance (Holland & DeAngelis, 2010) ^[10].
- Pollination occurs only when wasps successfully reach B-phase (receptive) syconia (Kjellberg *et al.*, 2005) ^[12]

Reproductive success is represented by the seed-to-gall ratio within syconia, reflecting the balance between plant and pollinator fitness (Herre & West, 1997) ^[8].

Model parameters

Model parameters were derived from a combination of empirical observations and published literature (Harrison, 2005; Kjellberg *et al.*, 2005) ^[7, 12]. These include:

- **Tree density:** Number of fig trees per unit area, representing population size.
- **Isolation distance:** Spatial distance between neighboring trees.
- **Wasp lifespan:** Fixed at approximately 24-48 hours, limiting dispersal opportunities (Ware & Compton, 1994) ^[18].
- **Dispersal range:** Distance-dependent movement probability of wasps.
- **Phenological overlap:** Degree of synchrony between receptive (B-phase) and pollen-releasing (D-phase) syconia (Cook & Rasplus, 2003) ^[3].
- **Pollination success:** Number of viable seeds produced per syconium.

These parameters collectively determine the probability of successful pollination and reproduction within the simulated environment.

Simulation experiments

To systematically evaluate ecological dynamics, four major simulation scenarios were implemented:

- **Density gradient:** Populations were simulated across low, medium, and high density levels to assess how increasing tree density influences pollination efficiency and reproductive output (Herre *et al.*, 2008)^[9].
- **Isolation gradient:** Inter-tree distances were progressively increased to evaluate the effects of spatial isolation on wasp dispersal and pollination success (Harrison, 2005)^[7].
- **Phenological variation:** Different flowering patterns were modeled to examine the role of temporal overlap in facilitating pollination (Cook & Rasplus, 2003)^[3].
- **Combined effects:** Interactions between density, isolation, and phenology were analyzed to capture realistic ecological scenarios (Okuyama & Holland, 2008)^[13].

Each simulation scenario was repeated across multiple iterations to incorporate stochastic variability and ensure robustness of results (Grimm & Railsback, 2005)^[5].

Estimation of minimum viable density

A key objective of the simulation analysis was to determine the minimum viable population density required to sustain mutualism. This threshold was defined as the lowest density at which:

- Pollinator populations remain stable across generations
- Pollination events occur consistently
- Reproductive output is sufficient to maintain both fig and wasp populations

Below this threshold, simulations predicted increasing pollination failure, declining wasp populations due to unsuccessful dispersal, and eventual collapse of the mutualistic interaction (Holland & DeAngelis, 2010)^[10]. Threshold values were further examined under varying levels of isolation and phenological overlap to understand context-dependent stability.

Empirical validation

To test the validity of simulation predictions, empirical data collected from field studies were used for comparison (Herre *et al.*, 2008)^[9]. Field measurements were conducted across sites representing different density categories and degrees of isolation.

Measured variables

The following parameters were quantified:

- **Pollen load on wasps:** Indicator of pollination potential
- **Number of foundress wasps per syconium:** Measure of pollinator arrival success
- **Seed and gall counts:** Indicators of reproductive success for figs and wasps (Herre & West, 1997)^[8].

These metrics provide a comprehensive assessment of pollination efficiency and mutualistic outcomes.

Statistical analysis

Statistical analyses were performed to evaluate relationships between ecological variables and pollination outcomes (Zar, 2010):

- Linear regression was used to examine the relationship between fig tree density and pollination efficiency
- Analysis of Variance was employed to compare reproductive success across different density categories

- Model validation analysis involved comparing predicted values from simulations with observed field data

Together, these analytical approaches ensured a rigorous evaluation of both simulation outputs and empirical observations, providing a robust framework for understanding the ecological dynamics of the fig-fig wasp mutualism.

Results

Density-dependent pollination efficiency

Simulation results revealed a strong positive relationship between fig tree population density and pollination success. As tree density increased, pollinator encounter rates with receptive syconia also increased due to reduced inter-tree distances and greater host availability within the short lifespan of fig wasps.

This enhanced encounter rate led to:

- Increased foundress entry
- Higher pollen deposition
- Greater oviposition success

Consequently, reproductive output improved significantly, reflected in higher seed production and increased wasp offspring. However, the relationship followed a non-linear trend (Fig 1), with rapid gains at low to moderate densities and saturation at higher densities, indicating diminishing returns beyond a threshold.

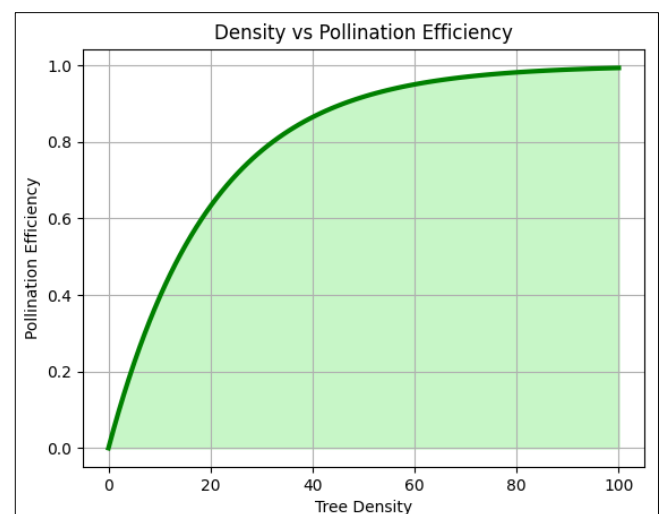


Fig 1: Density vs Pollination Efficiency (Conceptual)

Extinction probability dynamics

Simulation results (Fig. 2) demonstrated that the probability of extinction of the fig-fig wasp mutualism is strongly influenced by both Ficus tree density and wasp dispersal distance. Extinction risk was highest under conditions of low tree density and limited dispersal ability, where probabilities approached 1.0, indicating near-certain system collapse over the 100-year simulation period.

At low dispersal distances (0.25-0.5 km) and low tree densities (<100 trees), extinction probability remained extremely high, reflecting severe dispersal limitation and reduced likelihood of pollinator encounter. As tree density increased (≥ 200 trees), extinction probability declined sharply, even at shorter dispersal distances, indicating that

higher host availability partially compensates for limited movement. Similarly, increasing wasp dispersal distance (1-2 km) significantly reduced extinction probability across all density levels. Under conditions of moderate to high density combined with greater dispersal capacity, extinction probability approached zero, suggesting stable persistence of the mutualism.

Overall, the results highlight a strong interaction between spatial connectivity and dispersal ability, where both factors jointly determine long-term system stability.

Connectivity and Extinction Threshold (*Ficus religiosa* and *Ficus benghalensis*)

All study sites exhibited connectivity index (K) values far below the critical threshold ($K_{crit} \approx 45$) for *Ficus*

religiosa, indicating widespread instability.

- GKVK (K = 3) showed extremely low connectivity and functioned as a highly sub-viable sink, with a very high extinction risk.
- Hebbal (K = 7.5), although still below the threshold, demonstrated relatively improved connectivity and was categorized as sub-viable but comparatively more stable.
- Kaivara forest (K = 4.25) also remained below the threshold and functioned as a sub-viable sink.

These results suggest that *Ficus religiosa* populations across all sites are unlikely to sustain stable mutualistic interactions without increased density or connectivity (table 1).

Table 1: Connectivity index (K) relative to the species-specific extinction threshold for *Ficus religiosa* populations across study sites.

Location	Trees N	K = N/4	Compare with $K_{crit} \approx 45$	Status
GKVK	12	3	$\ll 45$	Highly sub-viable sink
Hebbal	30	7.5	$\ll 45$	Sub-viable, but relatively better
Kaivara forest	17	4.25	$\ll 45$	Sub-viable sink

The connectivity analysis for *Ficus benghalensis* indicates that all study sites fall below the critical extinction threshold ($K_{crit} \approx 20$), suggesting that none of the populations are fully viable under current conditions (Table 2).

- GKVK (K = 5.75) showed low connectivity and functioned as a strong reproductive sink, indicating limited pollinator movement and reduced chances of successful pollination.
- Hebbal (K = 4.25) exhibited the lowest connectivity among the sites and was classified as a sub-viable sink, reflecting a high risk of local mutualism failure.

- Kaivara forest (K = 8.5) had the highest connectivity among the three sites. Although still below the critical threshold, it was categorized as sub-viable but relatively better, suggesting comparatively improved conditions for persistence.

Overall, the results demonstrate that while *Ficus benghalensis* performs better than *Ficus religiosa* in terms of connectivity, all populations remain below the threshold required for long-term stability. This indicates that increased tree density or improved spatial connectivity is necessary to sustain viable fig-fig wasp interactions.

Table 2: Connectivity index (K) relative to the extinction threshold for *Ficus benghalensis* populations across study sites.

Location	Trees N	K = N/4	Compare with $K_{crit} \approx 20$	Status
GKVK	23	5.75	$\ll 20$	Sub-viable; strong sink
Hebbal	17	4.25	$\ll 20$	Sub-viable; sink
Kaivara forest	34	8.5	< 20	Sub-viable, but best of the three

Species-specific connectivity and persistence

Connectivity analysis revealed clear differences in persistence between species and locations (Table 3):

Ficus benghalensis

- Showed relatively higher K values across sites.
- Kaivara forest (K = 8.5) was the only site classified as stable, indicating sufficient connectivity for persistence.
- GKVK (K = 5.75) was near the viability threshold but remained fragile.

- Hebbal (K = 4.25) approached a collapse zone, suggesting high vulnerability.

Ficus religiosa

- Displayed consistently lower connectivity.
- GKVK (K = 3) indicated high extinction risk.
- Hebbal (K = 7.5) showed moderate stability, likely due to relatively higher tree numbers.
- Kaivara forest (K = 4.25) remained fragile, despite better conditions for *F. benghalensis*.

Table 3: Connectivity index (K) values and predicted persistence of *Ficus benghalensis* and *Ficus religiosa* populations across study sites.

Location	Species	K = N×0.25	Prediction
GKVK	<i>Ficus benghalensis</i>	5.75	Near viability threshold, but still fragile
	<i>Ficus religiosa</i>	3	Below threshold → high extinction risk
Hebbal	<i>Ficus benghalensis</i>	4.25	Near collapse zone
	<i>Ficus religiosa</i>	7.5	Moderately stable
Kaivara forest	<i>Ficus benghalensis</i>	8.5	Stable
	<i>Ficus religiosa</i>	4.25	Fragile

Consistency across connectivity analyses

Results in Table 4 reaffirm patterns observed in Table 2 and 5, demonstrating consistency across simulations:

- *Ficus benghalensis* consistently performed better than *Ficus religiosa* in terms of connectivity and persistence.
- Kaivara forest emerged as the most stable site overall, particularly for *F. benghalensis*.

- GKVK and Hebbal showed limited connectivity, with several populations near or below collapse thresholds.
- *Ficus religiosa* remained highly vulnerable across all sites, reinforcing its sensitivity to low density and fragmentation.

Table 4: Connectivity index (K) values and predicted persistence of *Ficus benghalensis* and *Ficus religiosa* populations across study sites.

Location	Species	K = N×0.25	Prediction
GKVK	<i>Ficus benghalensis</i>	5.75	Near viability threshold, but still fragile
	<i>Ficus religiosa</i>	3	Below threshold → high extinction risk
Hebbal	<i>Ficus benghalensis</i>	4.25	Near collapse zone
	<i>Ficus religiosa</i>	7.5	Moderately stable
Kaivara forest	<i>Ficus benghalensis</i>	8.5	Stable
	<i>Ficus religiosa</i>	4.25	Fragile

Low connectivity (low K values) is a primary driver of extinction risk

- Tree density and dispersal distance interact synergistically to determine persistence
- *Ficus religiosa* is more vulnerable than *Ficus benghalensis*
- Most study sites currently fall within sub-viable or fragile conditions

These findings emphasize the importance of enhancing landscape connectivity and maintaining sufficient tree densities to ensure long-term stability of the fig-fig wasp mutualism.

Density-dispersal dynamics governing extinction risk in fig-wasp mutualism

Figure 2 illustrates the probability of extinction of the fig-fig wasp mutualism over a 100-year period as a function of *Ficus* tree density and wasp dispersal distance within a 10-km radius landscape. The results reveal a strong interaction between these two factors in determining system persistence. At low tree densities (≤ 100 trees) and short dispersal distances (0.25-0.5 km), extinction probability is extremely high (approaching 1.0), indicating near-certain collapse of the mutualism. This reflects severe dispersal limitation, where pollinating wasps fail to locate sufficient

receptive syconia within their short lifespan. As tree density increases (≥ 200 -300 trees), extinction probability declines sharply, even under limited dispersal conditions. Higher host density enhances encounter rates, partially offsetting constraints imposed by restricted movement. A similar trend is observed with increasing wasp dispersal distance. At 1-2 km dispersal, extinction probability drops substantially across all density levels, approaching zero under moderate to high densities. This indicates that improved dispersal ability enhances landscape connectivity and stabilizes the mutualism.

Notably, the lowest extinction probabilities occur under combined conditions of high density and long dispersal distance, where the system remains consistently stable over time. In contrast, low density combined with poor dispersal represents the most vulnerable scenario, leading to persistent system failure.

Overall, the figure demonstrates that:

- Tree density and dispersal distance jointly regulate mutualism persistence
- High density can compensate for low dispersal to some extent
- Increased dispersal significantly reduces extinction risk
- Critical thresholds exist below which the system collapses rapidly

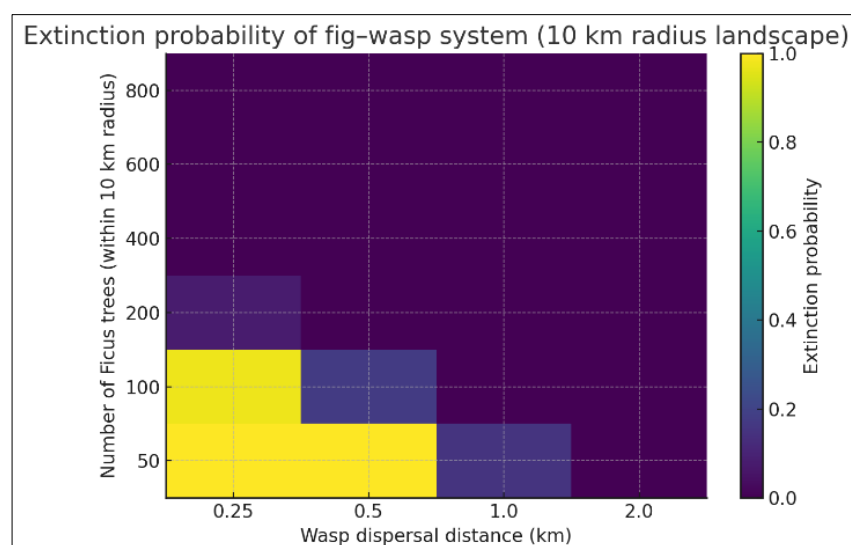


Fig 2: Probability of extinction of the fig-fig wasp mutualism over 100 years across combinations of *Ficus* tree density and wasp dispersal distance within a 10-km radius landscape

Discussion

The present study highlights the critical role of tree density, spatial connectivity, and pollinator dispersal in maintaining the stability of the fig-fig wasp mutualism. This obligate interaction is highly sensitive to ecological constraints, particularly under fragmented landscape conditions, as also reported in earlier studies on fig-wasp dynamics (Herre & West, 1997; Holland & DeAngelis, 2010)^[8, 10].

Density-dependent mutualism stability

The strong positive relationship between fig tree density and pollination efficiency supports the concept of density-dependent mutualism, where increased host availability enhances pollinator encounter rates. At low densities, pollination success is limited due to greater inter-tree distances and reduced probability of wasp arrival within their short lifespan (Harrison, 2005)^[7]. As density increases, pollination efficiency improves through higher foundress entry, pollen transfer, and oviposition success. However, the observed saturation at higher densities indicates diminishing returns, consistent with ecological models of mutualistic interactions (Holland & DeAngelis, 2010; Kjellberg *et al.*, 2005)^[12, 10].

Role of spatial isolation and dispersal limitation

The results clearly demonstrate that spatial isolation strongly constrains pollination success, primarily due to the short lifespan and limited dispersal ability of fig wasps. Increasing inter-tree distance reduces the likelihood of successful host location, leading to higher proportions of unpollinated syconia (Ware & Compton, 1994; Harrison, 2005)^[18, 7].

The extinction probability patterns observed in Fig. 2 align with metapopulation and landscape ecology theories, where dispersal plays a key role in maintaining persistence across fragmented habitats (Okuyama & Holland, 2008)^[13]. Increased dispersal distance significantly reduced extinction risk in the simulations, suggesting that improved landscape connectivity can compensate for local density limitations.

Threshold effects and mutualism collapse

A major outcome of this study is the identification of critical connectivity thresholds below which the fig-fig wasp mutualism becomes unstable. Both *Ficus religiosa* ($K_{crit} \approx 45$) and *Ficus benghalensis* ($K_{crit} \approx 20$) populations across all study sites exhibited K values well below these thresholds, indicating sub-viable conditions.

Below these thresholds:

- Pollination becomes inconsistent
- Wasp populations decline due to dispersal failure
- Fig reproduction is severely reduced

Such threshold-dependent dynamics are characteristic of obligate mutualisms and have been widely reported in ecological modeling studies (Holland & DeAngelis, 2010; Herre *et al.*, 2008)^[9, 10]. Once connectivity falls below a critical level, populations may function as reproductive sinks, unable to sustain long-term persistence.

Species-specific differences in vulnerability

The results indicate that *Ficus benghalensis* is relatively more resilient than *Ficus religiosa*, as reflected by higher connectivity values and better persistence in some sites (e.g., Kaivara forest). In contrast, *F. religiosa* consistently showed lower connectivity and higher extinction risk.

These differences may be attributed to variations in:

- Population density
- Spatial distribution
- Phenological patterns

Previous studies have also highlighted species-specific differences in fig-wasp systems, influenced by ecological and evolutionary factors (Cook & Rasplus, 2003; Herre *et al.*, 2008)^[3, 9].

Interaction between density and dispersal

The study demonstrates a strong interactive effect of density and dispersal on mutualism persistence. High tree density increases the probability of pollinator encounter, while greater dispersal enhances connectivity across fragmented landscapes. Importantly, neither factor alone is sufficient under extreme conditions.

This interaction supports theoretical predictions that mutualistic systems are jointly regulated by demographic and spatial processes (Okuyama & Holland, 2008)^[13]. The lowest extinction probabilities occurred only under conditions of both high density and high dispersal, highlighting the need for combined ecological stability.

Implications for conservation and landscape management

The consistently low connectivity values observed across study sites indicate that current populations are below viable thresholds, making them highly vulnerable to extinction. Conservation strategies should therefore prioritize:

- Increasing fig tree density through restoration programs
- Enhancing habitat connectivity to facilitate pollinator movement
- Maintaining landscape heterogeneity to support phenological overlap

Figs are considered keystone species in many ecosystems, supporting a wide range of frugivores and ecological interactions (Herre *et al.*, 2008). Therefore, conserving fig-wasp mutualism has broader implications for ecosystem stability and biodiversity conservation.

Conclusion

Overall, this study demonstrates that the persistence of the fig-fig wasp mutualism is governed by a combination of density-dependent processes, spatial connectivity, and dispersal constraints. The presence of clear thresholds and strong interaction effects highlights the fragility of this system under current landscape conditions. Without improvements in connectivity and density, many populations may remain trapped in sub-viable states, with a high risk of long-term collapse.

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