Journal of Theoretical Biology 617 (2026) 112300

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Intraspecific competition can stabilize asymmetric nursery pollination mutualisms

Jian-Zhong Gao [a,g], Feng Zhang [b,*], Derek W. Dunn [c], Hao Wang [d], K.Charlotte Jandér [e], Rui-Wu Wang [f,g,*]

[a] College of Mathematics and Computer Science, Yan'an University, Yan'an 716000, China
[b] Yunnan Key Laboratory of Forest Ecosystem Stability and Global Change, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China
[c] College of Life Sciences, Northwest University, Xi'an 710069, China
[d] Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB T6G 2G1, Canada
[e] Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Uppsala 75236, Sweden
[f] College of Life Sciences, Zhejiang University, Hangzhou 310058, China
[g] School of Ecology and Environment, Northwestern Polytechnical University, Xi'an 710129, China

ARTICLE INFO

Keywords:
Nursery pollination mutualism
Resource competition
Intraspecific competition
Asymmetric mutualism
Coexistence
Mutualistic relationship

ABSTRACT

A fundamental problem in ecology is to understand how mutualisms remain stable. The density-dependent regulations within interacting species potentially impact the persistence of these interspecific relationships. Yet few studies explore such intraspecific regulations' role in stabilizing mutualisms. In addition, partner species often gain unequal benefits in mutualisms. To what extent such an interspecific asymmetry affects the stability of mutualisms is also poorly understood. We here developed a dynamic model for the asymmetric interaction between plants and their pollinators in nursery mutualisms, considering the intraspecific competition of each mutualist. We found that (i) a mutualism can be stabilized only if both mutualists are subject to the regulation of intraspecific competition; (ii) stabilizing the system also requires that the degree of asymmetry in benefits between mutualists must be limited to a range of 'tolerance', which narrows as intraspecific competition increases and even fades away with strong competition within both mutualistic species; (iii) when intraspecific competition within a species increases, the tolerant range is compressed from the side beneficial for it, with thus its partner species gaining relatively more benefit allocation; (iv) if the plant-pollinator interaction initiates from a small host plant population, these host plants must offer pollinators high levels of benefits, that can be subsequently reduced to favor plants once the mutualism has been successfully established. The agreement of empirical data to theoretical predictions suggests model reliability. These results highlight the role of intraspecific competition and the degree of benefit asymmetry between host plants and symbionts in stabilizing mutualisms.

1. Introduction

Nursery pollination mutualisms, such as Yucca tree–Yucca moth and fig tree–fig wasp, are mutually beneficial interactions between host plants and pollinators, in which pollinators lay eggs within plant reproductive structures when pollinating flowers, using these structures of the host plant as their only breeding sites (Castro and Hoffmeister, 2020; Dufay and Anstett, 2003; Kerdelhue et al., 2000; Pellmyr and Huth, 1994), the result being a mutualism in which both host plant and pollinator obtain net benefits. However, such mutualistic interactions characterized as having positive feedbacks are theoretically prone to instability (Coyte et al., 2015; Sachs and Simms, 2006; Stone, 2020), because mutualistic population increase based on symmetric interaction between mutualists will lead to over-exploitation of the common resource (e.g., flower resources), analogous to resolving the "tragedy of the commons" of humans (Hardin, 1969; Rankin et al., 2007).

Notably, nursery pollination mutualisms are characterized by an inherently asymmetry in the interactions between the two mutualists are inherently asymmetric (Pellmyr and Huth, 1994; Wang et al., 2024). One partner is typically larger and in charge of resources (the "host"),

---

* Corresponding authors.
E-mail addresses: fzhang@xtbg.ac.cn (F. Zhang), wangrw@nwpu.edu.cn (R.-W. Wang).

https://doi.org/10.1016/j.jtbi.2025.112300
Received 21 June 2025; Received in revised form 4 September 2025; Accepted 15 October 2025

and the payoffs to the mutualistic partners are often unequal (Wang et al., 2024). In nursery pollination mutualisms (e.g., Yucca tree–Yucca moth and fig tree–fig wasp) the host provides its reproductive organs (e.g., flowers) as common breeding resources to both mutualists. The number of flowers consumed by seeds and pollinator offspring is often unequal (Addicott, 1986; Herre and West, 1997; Pellmyr et al., 1996a,b; Rosa-Conroy et al., 2019), leading to an asymmetry in benefits to the two partners. If the asymmetry in benefits becomes too skewed, the mutualism shifts into parasitism (i.e., extreme asymmetry). For example, there are several known “cheating” species of fig wasps and yucca moths that have evolved from pollinator lineages and still use the floral resources but no longer pollinate (Compton et al., 1991; Pellmyr et al., 1996; Zhang et al., 2021). However, mechanisms that can moderate the asymmetry in benefits can help prevent overexploitation of the common resource and thus promote mutualism stability (Pellmyr and Huth, 1994; Wang et al., 2011; Wang et al., 2024). One such mechanism is intraspecific competition (Bronstein et al., 1998; Craine and Dybzinski, 2013; Dunn et al., 2015; Gutiérrez et al., 2020; Huth and Pellmyr, 1999; Kinoshita et al., 2002; Wang et al., 2009; Zhang et al., 2021), because intraspecific competition between host plants or between symbionts can reduce their reproductive capacity (Craine and Dybzinski, 2013; Douglas, 1981; Huth and Pellmyr, 1999; Wang et al., 2009; Wang et al., 2011) and thus may alter the degree of the asymmetric benefit allocation between the mutualists, which is likely to impact mutualism stability.

The stability of mutualisms is often linked to complex structural relationships arising from network structure and trait distributions, which can inherently generate competition and asymmetry (Bastolla et al., 2009; García-Algarra et al., 2014; Gracia-Lázaro et al., 2018; Jousselin et al., 2006). While these structures are ecologically critical, they can mask the fundamental principles governing system dynamics. To address this, we develop a simplified, two-species model by employing mean-field assumptions. This model deliberately abstracts from complex network architectures and trait distributions to focus on the isolated effects of two key biological factors: intraspecific competition and asymmetry (modeled as a scalar parameter). This simplification allows us to derive analytical solutions for coexistence thresholds and asymmetry tolerance ranges—a significant advantage over more complex structural models where such metrics are often intractable. This approach achieves a crucial balance between ecological realism and analytical tractability, which is often a challenge in mutualism studies. This study aims to quantify the boundaries of asymmetry tolerance, which are crucial for understanding why some nursery pollination mutualisms remain stable while others evolve into parasitic relationships. Therefore, this research delves into how the externally imposed asymmetry and intraspecific competition jointly shape the dynamics of these mutualistic relationships.

Specifically, this paper will focus on the nursery pollination systems, and we here developed a dynamic model for asymmetric mutualistic interaction in benefit allocation between plants and their pollinators in nursery pollination mutualisms. This model assumes that the plant species compete for nutrients, water, sunlight and space (Craine and Dybzinski, 2013; Gutiérrez et al., 2020) (i.e., resource competition), and that the pollinators compete for access to oviposition sites (Bronstein et al., 1998; Dunn et al., 2015; Huth and Pellmyr, 1999; Kinoshita et al., 2002; Wang et al., 2009). Our aim is to explore how intraspecific competition affects the degree of asymmetry in benefits and determine the tolerance of mutualistic systems to biased benefit allocation. These aspects remain unclear in the biological science community.

2. The models

Let us consider an insect nursery pollination mutualism such as that between a monoecious host fig tree (*Ficus* sp.) and its symbiont pollinating wasp species (Hymenoptera: Agaonidae). The insect species pollinate the plant, and also lay egg in the flowers to nurture their offspring (Biere and Honders, 2006; Castro and Hoffmeister, 2020; Dufay and Anstett, 2003). We here simply assume that the proportion of flowers that the pollinators oviposit into is p $(0 < p < 1)$, and the proportion of flowers pollinated is $1 - p$. Note that the mutualistic interaction occurs through the behavior of the insects (pollination and oviposition). Because there exists the trade-off between the available time for a pollinator to search for flowers, pollinate, oviposit and competitively fight with other conspecific individuals (Dunn et al., 2015; Miao et al., 2023), the Beddington-DeAngelis functional response (hereafter referred to as BD) should be applied to describe the benefit of plants and pollinators from the mutualistic interaction (Beddington, 1975; DeAngelis et al., 1975; Holling, 1959; Zhang et al., 2011). Although the BD framework is a classic approach, it remains underutilized in mutualistic contexts—nevertheless, it provides a flexible framework for capturing saturation effects, as implemented by the first fraction in each equation of Eqn. 1 (see Suppl. Materials S1). Thus, the population dynamics of both host plants and their pollinators can be modeled as the following ordinary differential equations (see Fig. 1 for a diagram and Suppl. Materials S1):

$$\begin{aligned} \frac{dx}{dt} &= \frac{\varepsilon a(1-p)nxy}{1+au(1-p)nx+avpnx+wy}(1-cx)-\gamma x \\ \frac{dy}{dt} &= \frac{\epsilon apnxy}{1+au(1-p)nx+avpnx+wy}-\delta y \end{aligned} \tag{1}$$

Here, x and y are the population densities of host plants and pollinators, respectively; n denotes the number of efficient flowers (either pollinated or oviposited) that an individual plant produces on average. The fraction $\frac{a(1-p)ny}{1+au(1-p)nx+avpnx+wy}$ is the rate at which a flower is pollinated, and $\frac{apny}{1+au(1-p)nx+avpnx+wy}$ is the rate at which a flower is oviposited, where a represents the effort spent by a pollinator searching for flowers, u and v are times that a pollinator spends on pollination and oviposition, respectively, w is the strength of competition between pollinators (the product of the rate of direct interaction between two pollinators and the duration of each interaction). The parameter ε is the probability that a pollinated flower finally becomes a plant, and ϵ is the probability that a pollinator egg successfully translates into an adult female offspring and successfully disperses to next a flowering plant. The term $(1 - cx)$ describes density-dependent regulation on population growth in host

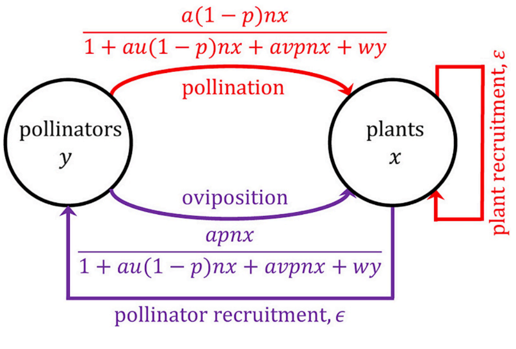

Fig. 1. A schematic diagram for the nursery pollination interaction. Each arrow indicates the direction in which an ecological process (pollination, oviposition, or recruitment) is underway, and the expression close to the line with the arrow shows their occurrence rate per capita. In particular, red and violet respectively identify the reproduction process of plants and pollinators. Where the proportion of flowers that the pollinators oviposit into is $p(0 < p < 1)$, and the proportion of flowers pollinated is $1 - p$. n denotes the number of efficient flowers (either pollinated or oviposited) that an individual plant produces on average. a represents the effort spent by a pollinator searching for flowers, u and v are times that a pollinator spends on pollination and oviposition, respectively, w is the strength of competition between pollinators. The parameter ε is the probability that a pollinated flower finally becomes a plant, and ϵ is the probability that a pollinator egg successfully translates into an adult female offspring and successfully disperses to next a flowering plant.

plants due to resource competition, with competition strength c. The parameter γ and δ are the mortality rates of host plants and symbiont pollinators, respectively. Notably, the life history of plant and pollinator could be different in time scale (e.g., fig tree lives much longer than fig wasp). This can be reflected by letting parameter ε and γ are much smaller than $\in$ and δ in our model (see Table 1).

This model (Eqn.1) integrates three kinds of ecological relationships: the nursery pollination mutualism between plants and pollinators, competition between pollinators, and resource competition between plants. The first two are described by the BD because both of them are associated with the behaviors of pollinators and involved in time trade-off (Beddington, 1975; DeAngelis et al., 1975), while the third one is expressed by the classical form modelling the density-dependent growth (i.e., the factor $1-cx$ in Eqn.1). In addition, we here define an externally imposed asymmetry coefficient

$$A = \log\left(\frac{p}{1-p}\right) \tag{2}$$

to express the asymmetric degree of the mutualistic relationship. Note that the right-hand side of Eqn.2 is mathematically equivalent to the logarithmic difference of both species in benefit, i.e., $\log p - \log(1-p)$. The sign of A indicates whether the mutualism favors pollinator (positive) or plant (negative) over the other, while the degree of deviation indicates the level of asymmetry. In particular, $A = 0$ represents exactly equal benefit allocation between the two mutualists. The asymmetry parameter A allows for systematic exploration of skewed benefit scenarios, which is a valuable feature for understanding mutualisms with unbalanced interactions. Thus, we can use this model to study how the asymmetric degree of the mutualistic relationship impacts the persistence and stability of the system, to what extent the mutualistic system can tolerate the asymmetric deviation in interacting benefit, and what role the intraspecific interactions play in stabilizing and maintaining the mutualistic system.

3. Results

3.1. Instability for the basic mutualism

We first consider the case in the absence of resource intraspecific competition between plants and intraspecific competition between pollinators (i.e., $c = 0$, $w = 0$). Here, our model (Eqn. 1) describes a basic mutualism between mutualists. The basic mutualism has an extinction equilibrium (0,0) and a unique internal equilibrium $x^* = \frac{\delta}{an[(\in-\delta v+\delta u)p-\delta u]}$ and $y^* = \frac{\gamma[1+au(1-p)nx^*+avpnx^*]}{\varepsilon a(1-p)n}$ if $p > \frac{\delta u}{\in-\delta v+\delta u}$ and $\in > \delta v$, and no internal equilibrium otherwise (see Suppl. Materials S3). In terms of the definition of asymmetry coefficient (Eqn.2), the condition can be rewritten as follows:

$$A > \log\left(\frac{\delta u}{\in-\delta v}\right) \text{with } \in > \delta v \tag{3}$$

According to the stability criteria of dynamics (Hastings and Gross, 2012), the internal equilibrium is an unstable saddle point (see empty circle in Fig. 2A and Suppl. Materials S3), and extinction equilibrium (0,0) is always a locally stable equilibrium for Eqn.1 (see Suppl. Materials S2). There exists a threshold line on the phase plane (see right boundary of the cyan region in Fig. 2A), the system (both partners) grows infinitely when the density combination of both mutualists is above the threshold line, but the system goes extinct when it falls below (see Fig. 2A). The inequality (Eqn.3) holds only if the probability that a pollinator egg successfully translates into an adult female offspring and successfully disperses to next a flowering plant is greater than a pollinator's mortality multiplied by the time it takes to lay eggs (i.e., $\in > \delta v$), this shows that the potential development of this symbiotic relationship requires relatively high fitness benefits for symbiont pollinators. That is to say, pollinators need to oviposit sufficient eggs ($p > \frac{\delta u}{\in-\delta v+\delta u}$, see the vertical black dashed line in Fig. 3A), and each egg may translate into an adult female offspring sufficiently and successfully disperses to next a flowering plant ($\in > \delta v$) (see Fig. 3A). Moreover, it is noteworthy that the basic system is unstable with both species either becoming extinct or both growing infinitely depending on mutualist population densities (i.e., the system grows infinitely when the density combination of both mutualists is above the threshold line, but the system goes extinct when it falls below, see Fig. 2A). Thus, intraspecific competition in both mutualists may play a role in stabilizing mutualisms.

Table 1

Parameter values and their biological significance.

Para.	Descriptions	Values
a	The effort spent by a pollinator searching for flowers	10
ε	The probability that a pollinated flower finally becomes a plant	0.00001
$\in$	The probability that a pollinator egg successfully translates into an adult female offspring and successfully disperses to next a flowering plant	5
p	The proportion of flowers that the pollinators oviposit	0.9
n	The number of efficient flowers (either pollinated or oviposited) that an individual plant produces on average	500
c	The strength of competition between plants	0.1
w	The strength of competition between pollinators	0.0001
u	The time that a pollinator spends on pollination	0.001
v	The time that a pollinator spends on oviposition	0.0015
δ	The mortality rates of symbiont pollinators	50
γ	The mortality rates of host plants	0.01

3.2. Factors stabilizing a nursery plant-pollination mutualism

Here, we assess the role of intraspecific resource competition among host plants and competition between pollinators in stabilizing a mutualism. First, if $c > 0$ but $w = 0$ in Eqn.1 (i.e., there is resource competition among host plants but no competition between pollinators), the system has an extinction equilibrium (0,0) and a unique internal equilibrium $x^* = \frac{\delta}{an[(\in-\delta v+\delta u)p-\delta u]}$ and $y^* = \frac{\gamma[1+au(1-p)nx^*+avpnx^*]}{\varepsilon an(1-p)(1-cx^*)}$ if satisfying the condition $p > \frac{an\delta u+\delta c}{an(\in-\delta v+\delta u)}$, $\in > \delta v$, and $0 < c < \frac{an(\in-\delta v)}{\delta}$, and no internal equilibrium otherwise (see Suppl. Materials S4). The condition, using the definition of the asymmetry coefficient (Eqn.2), can be rewritten as:

$$A > \log\left(\frac{an\delta u+\delta c}{an(\in-\delta v)-\delta c}\right)$$
$$\text{with } \in > \delta v \text{ and } 0 < c < \frac{an(\in-\delta v)}{\delta} \tag{4}$$

Note that if $c = 0$, the condition (4) returns to the condition (3). According to the stability criteria of dynamics (Hastings and Gross, 2012), the internal equilibrium is still an unstable saddle point (see empty circle in Fig. 2B and Suppl. Materials S4), and extinction equilibrium (0,0) is always a locally stable equilibrium for Eqn.1 (see Suppl. Materials S2). Thus, similar to when $c = w = 0$, the system (both partners) goes extinct when the density combination of both mutualists is below a threshold line on the phase plane, but grows infinitely when is above the line (see Fig. 2B). Notably, in this case, the population of host plants converges to $\frac{1}{c}$ when the pollinator population increases infinitely (see vertical red dashed line in Fig. 2B and Suppl. Materials S4). A necessary condition that the system is able to grow like this is the pollinators produce sufficient offspring ($p > \frac{an\delta u+\delta c}{an(\in-\delta v+\delta u)}$, $\in > \delta v$ and see the vertical black dashed line in Fig. 3B), as well as limited competition among host plants ($c < \frac{an(\in-\delta v)}{\delta}$). However, comparing condition (4) with (3), it is clear that intraspecific competition among host plants ($c > 0$) elevates the minimum requirement of the asymmetry coefficient for the emergence of an unstable internal equilibrium (see compare the position of the vertical black dashed line in Fig. 3A and Fig. 3B), this means that intraspecific

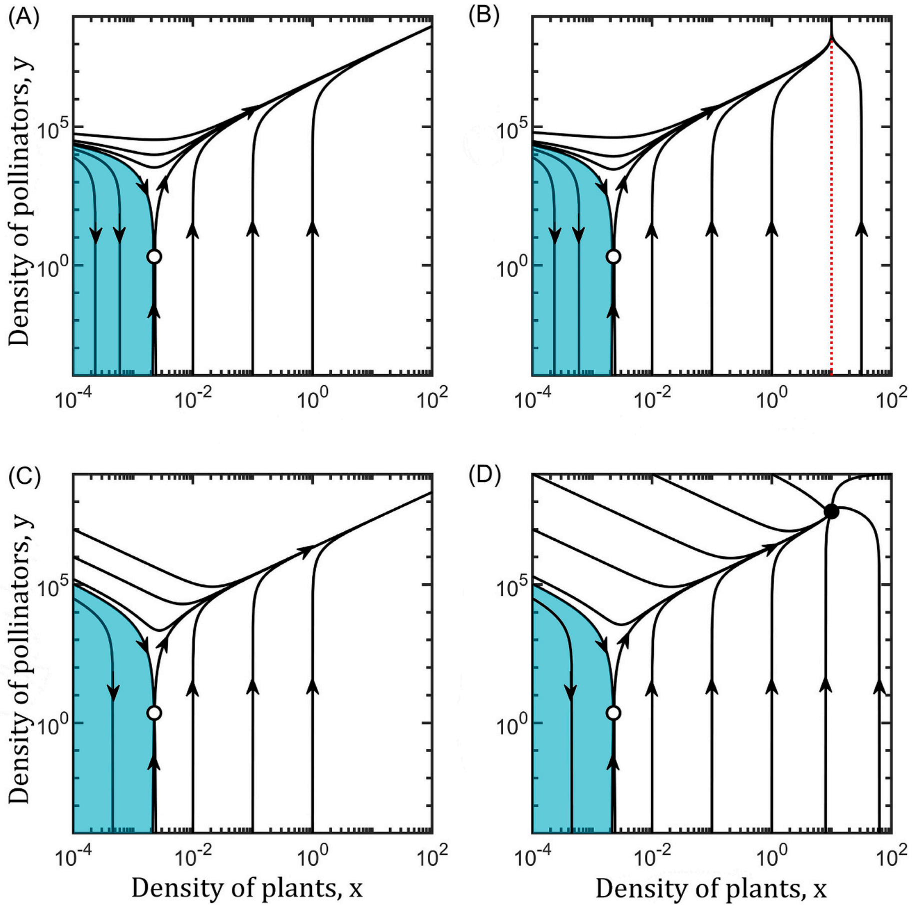

Fig. 2. Population dynamics of plants and pollinators on phase plane respectively when $c = w = 0$ (A), $c > 0$ but $w = 0$ (B), $c = 0$ but $w > 0$ (C), and $c > 0$ and $w > 0$ (D). Empty circles denote unstable equilibria, and the solid circle is a stable equilibrium; cyan region indicates extinction region, and right boundary of the cyan region represents a threshold line; arrows point out the direction of the trajectories. The vertical red dashed line shows an asymptotical line that trajectories converge (B). This figure shows solutions (arrow lines) starting from different initial values, which either tend to extinction (cyan region), infinity (white region in A-C), or stability (solid circle in D). Parameters are $a = 10$, $n = 500$, $u = 0.001$, $v = 0.0015$, $\varepsilon = 0.00001$, $\epsilon = 5$, $\gamma = 0.01$, $\delta = 50$, and $p = 0.9$ for all panels; $c = w = 0$ for (A), $c = 0.1$ and $w = 0$ for (B), $c = 0$ and $w = 0.0001$ for (C), $c = 0.1$ and $w = 0.0001$ for (D).

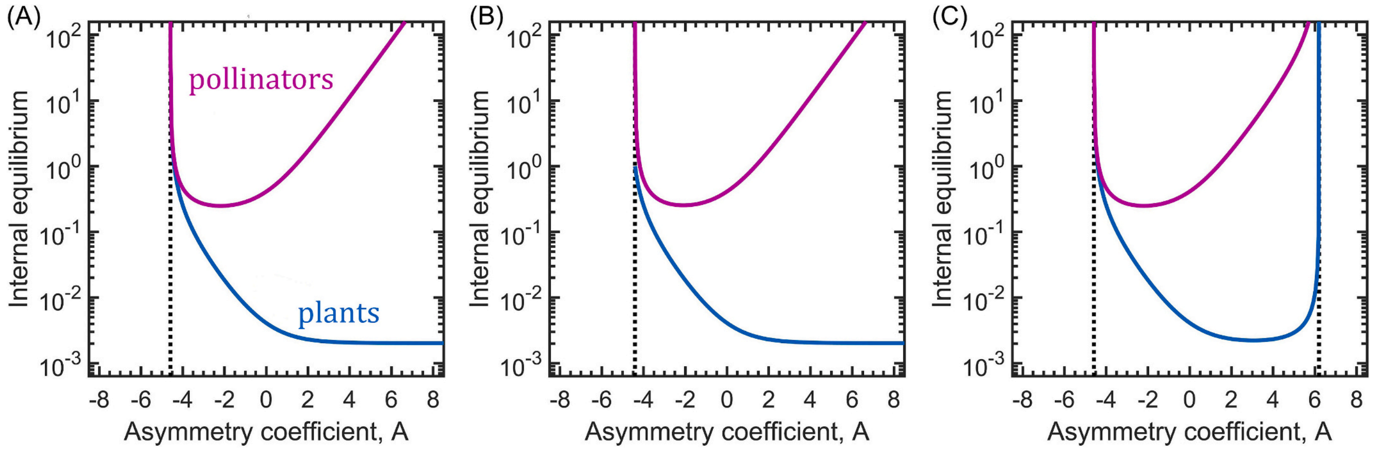

Fig. 3. Dependence of unique internal equilibrium (unstable) on asymmetry coefficient (defined by Eqn.2) when $c = w = 0$ (A), $c > 0$ but $w = 0$ (B), and $c = 0$ but $w > 0$ (C). Dashed lines indicate maximum or minimum threshold of asymmetry coefficient that the internal equilibria emerge. That is, the upper and lower bounds of the asymmetric range in which the species can grow, i.e., dashed lines: $A = \log\left(\frac{\delta u}{\epsilon - \delta v}\right)$ for (A), $A = \log\left(\frac{an\delta u + \delta c}{an(\epsilon - \delta v) - \delta c}\right)$ for (B), the upper and lower bounds of the inequality (Eqn. 5) for (C). Parameters are $a = 10$, $n = 500$, $\varepsilon = 0.00001$, $\epsilon = 5$, $u = 0.001$, $v = 0.0015$, $\gamma = 0.01$, and $\delta = 50$ for all panels. Parameter $c = w = 0$ for (A), $c = 1$ and $w = 0$ for (B), $c = 0$ and $w = 0.01$ for (C).

competition among host plants narrows the range of species that can grow. It is noteworthy that intraspecific competition between host plants cannot unilaterally stabilize the mutualism; both host plant and symbiont pollinator populations either go extinct or grow infinitely depending on mutualist population densities.

Second, if $c = 0$ and $w > 0$ in Eqn.1 (i.e., including competition among pollinators but excluding competition among host plants), the system has an extinction equilibrium (0,0) and a unique internal equilibrium $x^* = \frac{\varepsilon(1-p)\delta}{an\varepsilon(1-p)(\Omega p-\delta u)-w\gamma\in p}$ and $y^* = \frac{\gamma\in p}{an\varepsilon(1-p)(\Omega p-\delta u)-w\gamma\in p}$ when $\frac{an\varepsilon(\Omega+\delta u)-w\gamma\in-\sqrt{\Delta}}{2an\varepsilon\Omega} < p < \frac{an\varepsilon(\Omega+\delta u)-w\gamma\in+\sqrt{\Delta}}{2an\varepsilon\Omega}$, $\in>\delta v$, and $0<w<\frac{an\varepsilon(\Omega+\delta u-2\sqrt{\delta u\Omega})}{\gamma\in}$, where $\Omega=\in-\delta v+\delta u$ and $\Delta=[an\varepsilon(\in-\delta v)-w\gamma\in]^2-4an\varepsilon\delta uw\gamma\in$ (see Suppl. Materials S5). In the terminology of the asymmetry coefficient (Eqn.2), the condition can be rewritten as:

$$\log\left(\frac{an\varepsilon(\Omega+\delta u)-w\gamma\in-\sqrt{\Delta}}{an\varepsilon(\Omega-\delta u)+w\gamma\in+\sqrt{\Delta}}\right) < A < \log\left(\frac{an\varepsilon(\Omega+\delta u)-w\gamma\in+\sqrt{\Delta}}{an\varepsilon(\Omega-\delta u)+w\gamma\in-\sqrt{\Delta}}\right)$$
$$\text{with } \in > \delta v \text{ and } 0 < w < \frac{an\varepsilon\left(\Omega+\delta u-2\sqrt{\delta u\Omega}\right)}{\gamma\in} \tag{5}$$

Notably, letting $w = 0$, condition (5) returns to condition (3). According to the stability criteria of dynamics (Hastings and Gross, 2012), the internal equilibrium is still an unstable saddle point (see empty circle in Fig. 2C and Suppl. Materials S5), and extinction equilibrium (0,0) is always a locally stable equilibrium for Eqn.1 (see Suppl. Materials S2). Both mutualists increase infinitely only if the density combination exceeds a threshold line on the phase plane but both become extinct otherwise (see Fig. 2C). It is noteworthy that when the system only includes competition between pollinators, the potential growth of both mutualists requires the asymmetry coefficient that not only exceeds a lower bound but also fails to reach an upper bound (see Eqn. (5) or two vertical black dashed lines in Fig. 3C). Therefore, competition among pollinators cannot unilaterally stabilize a mutualism; both host plants and symbiont pollinators either go extinct or grow infinitely depending on mutualist population densities.

Finally, we assess how intraspecific competition among both plants and pollinators may interact in contributing to mutualism stability. Letting $c > 0$ and $w > 0$ in Eqn.1 (i.e., including both resource competition among host plants and competition among pollinators), the system has an extinction equilibrium (0,0), and two internal equilibria, and no internal equilibrium otherwise (see Fig. 2D and Fig. 4). Because the conditions for the existence of internal equilibria are complex but we here only provide a brief overview (see Suppl. Materials S6 for full details). The existence of internal equilibria first requires that at least one of the parameters c and w is small enough and $\in > \delta v$; specifically, the larger one of these two parameters is, the smaller the other needs to be (see the gray region in Fig. 5). On satisfying this condition, a further requirement is that the parameter p must be between a lower and an upper bound (respectively denoted by p_L and p_U; see Suppl. Materials S6 for their specific expressions and the surfaces in Fig. 5 for an intuitive presentation). Using the asymmetry coefficient (Eqn.2), this condition can be expressed as:

$$\log\left(\frac{p_L}{1-p_L}\right) < A < \log\left(\frac{p_U}{1-p_U}\right) \quad \text{with } \in > \delta v \text{ and } 0 < w < f(c) \tag{6}$$

where $f(c)$ is a concave decreasing function with regards to parameter c, expressing the boundary curve of gray region in Fig. 5. These conditions suggest that both mutualists are subject to strong intraspecific competition (see white region, i.e., unsolvable region in Fig. 5), or the extreme asymmetry in benefit allocation beyond the bounds (i.e., asymmetric intervals where species cannot coexist, see Fig. 4), which can result in the mutualistic system going extinct (because of no internal equilibrium in these cases). Otherwise, the mutualism has two internal equilibria: the larger one is locally stable (see solid circle in Fig. 2D), and the smaller one is an unstable saddle point (see empty circle in Fig. 2D), forming a bistable situation (Fig. 2D, see Suppl. Materials S6; note that extinction equilibrium is always stable, see Suppl. Materials S2). That is to say, the survival of species is not possible in smaller or extinction equilibrium, whereas species can thrive in larger and stable equilibrium (see solid circle in Fig. 2D). That is, the two mutualists can coexist stably only if initial density combinations are beyond a threshold line on the

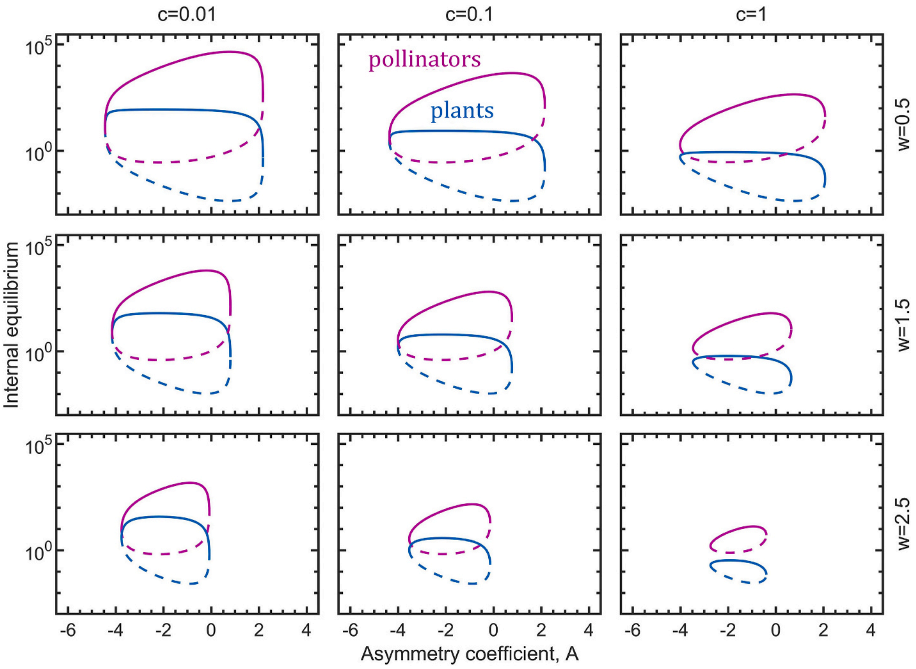

Fig. 4. Internal equilibria of plant-pollinator system (Eqn.1) when both the species are subject to intraspecific competition, expressed as a function with regards to asymmetry coefficient. Solid lines represent stable equilibria, and dashed lines unstable ones. The upper and lower bounds of the inequality (Eqn. 6) are the upper and lower bounds of the asymmetric range of species coexistence. Parameters are $a = 10$, $n = 500$, $u = 0.001$, $v = 0.0015$, $\varepsilon = 0.00001$, $\in = 5$, $\gamma = 0.01$, $\delta = 50$.

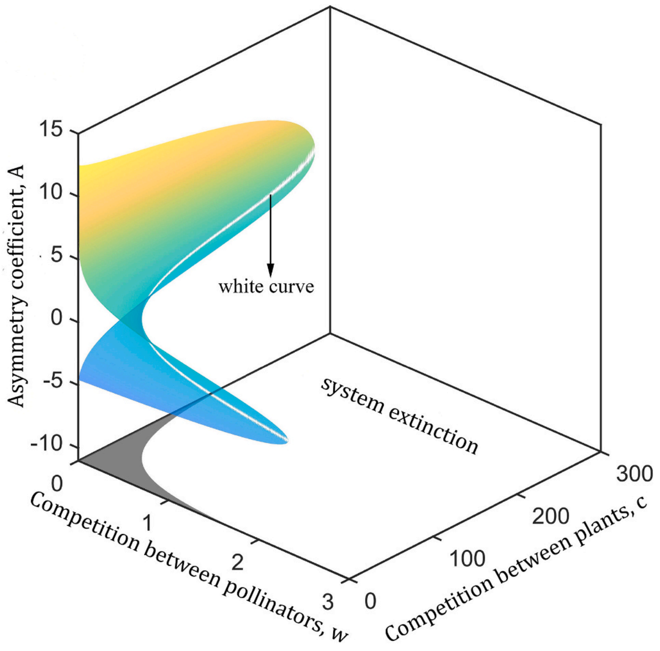

Fig. 5. Effect of intraspecific competition on the range of asymmetry coefficient emerging internal equilibria. The color gradient represents the magnitude of the asymmetry coefficient A (see Eqn. (2)) that permits stable coexistence, ranging from $A \approx -4.9$ (blue) to $A \approx 12.7$ (yellow). Surface above white curve is the upper limit of the range, and surface below them is its lower limit. Gray region (coexistence region) on floor plane indicates the projection of the surfaces, representing the system can persist potentially, whereas white region (extinction region) on the floor plane indicates parameter combinations (w, c) where no coexistence is possible for any value of A. Parameters are $a = 10$, $n = 300$, $\varepsilon = 0.00001$, $\epsilon = 5$, $\gamma = 0.01$, $\delta = 50$; $u = 0.001$ and $v = 0.0015$.

phase plane (see right boundary of the cyan region in Fig. 2D), otherwise they die out. Notably, only in the case of both mutualists being subject to intraspecific competition, it is possible that the mutualism has a stable internal equilibrium (see Fig. 2D and gray region in Fig. 5), otherwise it either goes extinct or grows infinitely (see Fig. 2A-C), whilst strong competition in any one species can potentially trigger the system to go extinct (see white region in Fig. 5). This suggests that moderate levels of intraspecific competition within each mutualist species may play a role in stabilizing the mutualism.

It is noteworthy that our ‘basic’ mutualism is unstable, with either both mutualists going extinct or growing infinitely (see Fig. 2A) depending on mutualists population densities. Furthermore, neither resource competition between host plants nor competition between symbiont pollinators can unilaterally stabilize the mutualism (see Fig. 2B, C), with either both mutualists going extinct or growing infinitely depending on mutualists population densities. Only when both mutualists are subject to intraspecific competition can the mutualism be stabilized by the avoidance of infinite growth (see Fig. 2D).

3.3. System tolerance for asymmetric benefits

Our previous models show that a ‘basic’ mutualism is unstable, and intraspecific competition of either host plants or symbiont pollinators alone cannot stabilize the system. Stable coexistence occurs only when both mutualists are subject to intraspecific competition (see Fig. 2). This also requires an asymmetry coefficient exceeding a lower bound but below an upper bound (see Eqn. (6) and Fig. 4). The interval range of the asymmetry coefficient (namely the tolerance of the mutualism to the degree of asymmetric benefits between host plants and symbionts) largely depends on the strength of intraspecific competition in each mutualist (i.e., the size of parameters c and w). When intraspecific competition in either host plants or symbiont pollinators gradually increases, the range of asymmetric coefficient allowing mutualism stability will narrow (see Fig. 4) and even disappear when competition is intense (see white region in Fig. 5). Fig. 5 further illustrates that the color gradient quantifies how the tolerable asymmetry coefficient A varies with the competition strengths. Low asymmetry (blue surface) expands the viable parameter space, whereas high asymmetry (yellow surface) severely constrains the possibility of coexistence. In particular, increased intraspecific competition in host plants results in the lower bound of the range of the asymmetry coefficient to increase significantly (move rightwards, i.e., benefits to plants are reduced), whilst increased intraspecific competition among symbiont pollinators results in the range upper bound to decline significantly (move leftwards, i.e., benefits to pollinators are also reduced) (see Fig. 4). That is to say, when the intraspecific competition within one of species moderately strengthens, the range of asymmetric degree that interacting species can tolerate and persist will be compressed from the side beneficial for this species, which suggests that the partner species would gain relatively more benefit allocation in the process of mutualistic interaction. Additionally, increasing the asymmetry coefficient (i.e., when benefits tend to be gained by pollinators), the stable equilibrium size of the pollinator population increases sharply, but that of host plant population remains almost unchanged (see solid lines in Fig. 4). On the contrary, the unstable equilibrium size of the host plant population decreases as the asymmetry coefficient increases, but that of the symbiont pollinator population remains almost unchanged (see dashed lines in Fig. 4). These results suggest that, if a plant-pollinator mutualism evolves initially with few host plants, these plants need to offer high benefits in order to attract sufficient pollinators. After the mutualism is established, the allocation of benefits becomes more biased to host plants due to enhancing intraspecific competition among pollinators resulting from increased population density. Therefore, intraspecific competition within both mutualists can stabilize a mutualism as long as the degree of asymmetric benefits is kept between the lower and upper bounds, and further significantly impacts the range of tolerance that both mutualists can coexist stably by adjusting the position of lower and upper bounds. However, strong intraspecific competition results in the disappearance of the range of tolerance and population extinction (see white region in Fig. 5). Intraspecific competition can therefore be a ‘double-edged sword’, which adds to our understanding of mutualisms.

3.4. Empirical evidences for theoretical predictions

To validate our model, we here compiled data on 64 different plants from five nursery species, such as figs (Anstett et al., 1996; Herre, 1989; Herre and West, 1997; Wang and Wang, 2022), yuccas (Pellmyr et al., 2020), senita cactus (Pellmyr et al., 2020), leafflowers (Pellmyr et al., 2020), trollius europaeus (Pellmyr, 1989). Each data point includes the average number of seeds and pollinators’ eggs in per flower or fruit of each population (see Table S1 in Suppl. Materials S7). Here we assume that the average total number of seeds and eggs denotes n in the model. The proportion of eggs is p in the model ($p = \frac{\text{the average number of eggs}}{\text{the average total number of seeds and eggs}}$). The asymmetry coefficient (A) of each data can be calculated by bringing p into the Eqn. (2). Statistical analyses show a significant asymmetry in benefit between the host plants and pollinators (see Fig. 6A), with more plant seeds relative to the number of pollinators’ eggs (t-test, seeds and eggs: $P < 0.001$). Notably, most of asymmetry coefficients are smaller than zero (90.62 % with mean -3.9573), further suggesting that the benefits are skewed towards the host plants in the nursery mutualisms (see Fig. 6B). According to the results from our model, such a deviation in benefit to host plants implies strong competition within pollinators ($c = 0.02$, $w = 8$ in Fig. 6C). Furthermore, these experimental data can be covered by the predictions of the model (see Fig. 6C). This shows that our model, despite simplicity, captures the essential aspects of the nursery pollination mutualisms. It

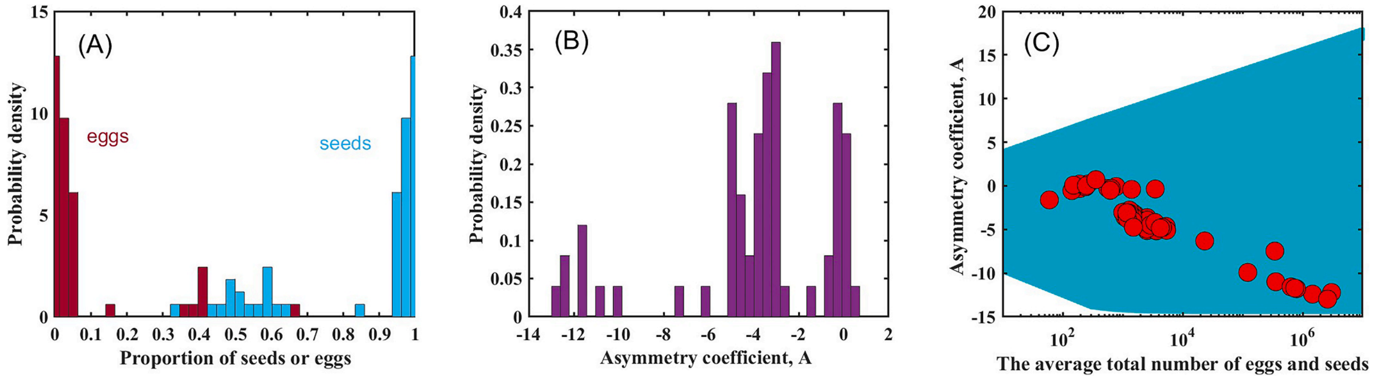

Fig. 6. We compiled data on 64 different plants from five nursery species, and each data point includes the average number of seeds and pollinators' eggs in per flower or fruit of each population (see Table S1 in Suppl. Materials S7). Probability density of proportion of seeds or eggs for (A); Probability density of Asymmetry coefficients (B); According to Eqn. (6) in the text, the tolerance range (cyan region) can be calculated, see (C); the average total number of seeds and eggs within per flower or fruit is equal to n in model, see (C). The cyan region represents the coexistence region, the white region represents the extinction region, and red solid dots represent 64 data points, see (C). Parameters are $a = 10$, $u = 0.00001$, $v = 0.000001$, $\varepsilon = 0.05$, $\in = 500$, $\gamma = 0.01$, $\delta = 27$, $c = 0.02$, $w = 8$ for (C).

should be noted here that the comparison between this model and the empirical data is qualitative and static. It successfully captured static patterns such as the uneven distribution of benefits, but it did not fit or contrast time series, stability patterns, dynamic trajectories, or bifurcation structures with real data.

4. Discussion

The stability and resource allocation between the mutualists in nursery mutualisms have received much past attention (Dunn, 2020; Kulkarni et al., 2024; Li et al., 2016; Pellmyr and Huth, 1994). Some negative-feedback interactions such as competition (Coyte et al., 2015; Stone, 2020; Thompson, 2003), predation (Heithaus et al., 1980; Kawata and Takimoto, 2022; Thompson, 2003), parasitism (Gutiérrez et al., 2020; Little, 2010), and host sanctions (Jandér et al., 2012; West et al., 2002), have been shown to play a role in stabilizing some mutualisms. In host sanctions, the host plant allocates more resources to cooperative pollinators than to individuals that do not pollinate (cheaters) (Frederickson, 2013; Jandér and Herre, 2016; Jandér et al., 2012; Wang et al., 2014). The above literatures present more experimental analysis and does not fundamentally understand how negative feedback affects stability and asymmetric benefit allocations. This article will theoretically or fundamentally address these issues. Our model here revealed: first, the mutualistic system can be stable only if the two species are subject to intraspecific competition; second, intraspecific competition profoundly impacts the range of asymmetry in benefit allocation that mutualistic system can tolerate; third, the degree of both intraspecific competition and asymmetry in benefit allocation must be moderate in order to maintain the long-term stability of the mutualistic system. Moreover, we confirmed the consistency between theoretical predictions and empirical data, indicating the effectiveness of the model in predicting the range of tolerance in nursery pollination systems. In addition, we have derived the analytical coexistence conditions (see Suppl. Materials for details), revealing the precise mechanism behind them. This goes beyond the limitations of numerical simulations, not only enabling the prediction of system coexistence but also providing in-depth mechanistic explanations, thereby significantly enhancing the interpretability and pedagogical value.

Intraspecific competition has been shown to affect as diverse areas as niche expansion (Jones and Post, 2016), species diffusion (Grabowska et al., 2019), resource use diversity (Svanbck and Bolnick, 2007), life-history evolution (Gribbin and Thompson, 1990; Kleunen et al., 2001), soil nutrient improvement (Wu et al., 2023), intraspecific variation (Bolnick, 2004; Roughgarden, 1972), trophic polymorphism (Smith and Skulason, 1996), and speciation (Dieckmann et al., 2004; Rosenzweig, 1978). We here further show the role of intraspecific competition in stabilizing mutualism. We obtained that the mutualistic system cannot be stabilized only by the interspecific reciprocity between the mutualists (see Fig. 2A), nor by only resource competition among host plants or by only competition among pollinators (see Fig. 2B, C) – the mutualistic system can be stable only if both mutualists are subject to intraspecific competition (see Fig. 2D). Intraspecific competition can only stabilize the mutualistic system when the degree of bias in the benefit allocation is moderate (within the upper and lower bounds calculated in Eqn. (6)) – more extreme asymmetry in the benefit allocation beyond these bounds results in species extinction, in fact, some species only acquire host resources without returning them, which can lead to extreme asymmetry and ultimately result in species extinction, for example, the cheater bees obtain floral nectar without pollinating plants (Maloof and Inouye, 2000; Sakhalkar et al., 2023); some fig wasps only oviposit in the syconia of figs rarely providing pollination service for figs (Zhang et al., 2021; Zhang et al., 2019). Therefore, mutualism can be stabilized only when both mutualists are subject to intraspecific competition and the degree of asymmetry in benefit allocation is moderate.

Furthermore, increased intraspecific competition within any one species, the range of asymmetry in benefit allocation that benefits this species is compressed (see the upper (lower) bound moves to the left (right) in Fig. 4), makes its partner gain more benefit allocation. For example, increased competition among pollinating fig wasps/yucca moth resulted in fewer eggs laid per pollinator (Huth and Pellmyr, 1999; Wang et al., 2009; Wang et al., 2011) (i.e., the upper bound moves to the left in Fig. 4), but can increase pollinators dispersal, which to some extent improves pollination efficiency and promotes pollen transmission (Moore et al., 2005), or may lead to them visiting flowers more frequently, thereby increasing the chances of pollination. Similarly, increased competition between plants can lead to an uneven allocation of resources such as light, water, and nutrients, thereby inhibiting the reproduction of plants (Craine and Dybzinski, 2013; Douglas, 1981) (i.e., the lower bound moves to the right in Fig. 4), the study suggests that pollinators have a clear preference for plants when foraging, as the absolute resource density of plants makes them more efficient foraging targets, therefore, it can be speculated that competition between plants may encourage them to better utilize these advantages to attract pollinators, thereby providing them with more food resources and increasing their reproductive opportunities (Donkersley, 2019). Anyway, increased intraspecific competition within one of the mutualist species narrows the range of asymmetric bias in benefit allocation. But too strong intraspecific competition results in the species utilizing very little or no resources, leading to costs exceeding the basic growth needs, this leads to extreme asymmetric benefits so that the system collapses (see white region in Fig. 5). Therefore, intraspecific competition is closely related to the degree of asymmetry, influencing the stability of nursery systems. For mutualistic systems to remain stable, this competition must be kept at a moderate level.

Additionally, stable region predicted by the relatively strong competition within pollinators covers all empirical data (see cyan region in Fig. 6C). Statistical analysis suggests that benefits are skewed towards the host plants, which is consistent with the theoretical result that relatively strong intraspecific competition within pollinators results in the benefits being tilted towards host plants (comparison between Fig. 4 and Fig. 6B). Therefore, in nursery systems, it is common for intraspecific competition between pollinators to be relatively strong compared to intraspecific competition among host plants. Anyway, differences in intraspecific competition between mutualistic species lead to asymmetric benefits tilted toward partner species. In addition, there is a point that cannot provide a scientific explanation: why there is a negative correlation between the degree of asymmetric bias (A in Eqn. 2) and total resources (n in Eqn. 1) in nursery mutualisms? (see Fig. 6C) we speculate that this may be related to other ecological relationships (not shown in model). Additionally, it is noteworthy that we found it sufficient to validate the model using data on 64 different plants from five nursery species (see Fig. 6C), because adjusting the parameter values in the model appropriately can obtain a stable region covering data from different types of nursery systems, and the result obtained must be similar to Fig. 6C. This indicates that the generalization ability and parametric flexibility of the model are sufficient to explain the effects of intraspecific competition and asymmetric benefits on the stability of nursery mutualisms.

In mutualism research, studies have explored various mechanisms determining species coexistence and stability. García-Algarra et al. (2014) introduced an implicit form of mutual regulation within a logistic framework, avoiding singularities and offering an integrated interpretation of competition (García-Algarra et al., 2014); Certain network architectures (e.g., nestedness or modularity) can effectively reduce competition and enhance coexistence (Bastolla et al., 2009). Importantly, competition can arise from topological overlap in bipartite mutualistic networks, with Gracia-Lázaro et al. (2018) demonstrating that such structure-based competition can lead to biodiversity loss at high mutualism strength (Gracia-Lázaro et al., 2018). Other research has modeled competition through externally imposed parameters, as seen in Fishman and Hadany suggested that pollinator efficiency requires a supercritical value, and stability stems from a balance between reciprocity and plant mortality (Fishman and Hadany, 2010), and Johnson and Amarasekare found that competition can stabilize systems within the same species (Johnson and Amarasekare, 2013). Our study similarly employs an externally imposed scalar parameter to model competition intensity, finding that system stability requires both species to experience intraspecific competition.

A key distinction in our approach concerns how asymmetry is modeled. Although we impose asymmetry externally through a scalar parameter, many empirical systems exhibit structurally derived asymmetries. These emerge from network architecture and trait distributions (e.g., specialization or degree heterogeneity). Such structural factors can create asymmetric tolerance ranges (Bastolla et al., 2009), and stabilize systems through trait complementarity (García-Algarra et al., 2014; Jousselin et al., 2006; Segar et al., 2013; Wang et al., 2024). Instead of relying on complex structural models, our study constructed, using the mean-field formula, a simplified two-species model. Consequently, we were able to derive analytical solutions for the tolerance range and coexistence threshold—a feat that is typically unattainable with more complex network or trait-structured models (Bastolla et al., 2009; García-Algarra et al., 2014; Gracia-Lázaro et al., 2018; Jousselin et al., 2006). Thus, our model balances ecological realism and analytical tractability, overcoming the limitations of complex, high-dimensional network models.

In conclusion, intraspecific competition within host plants and symbiont pollinators can stabilize mutualism as long as the degree of asymmetry in benefit allocation is kept between the upper and lower bounds that the mutualistic system can tolerate, but extreme asymmetry in benefit allocation beyond these bounds results in species extinction. Moderate intraspecific competition makes partner species get relatively more asymmetric benefit allocation. Moreover, as intraspecific competition increases, the range of tolerance narrows and even fades away with strong competition within both mutualistic species. Therefore, the degree of intraspecific competition and asymmetry in benefit allocation between mutualists must be moderate in order for the mutualistic system to be stable in the long run. The agreement of empirical data to theoretical predictions suggests model reliability. For nursery pollination mutualisms, this study innovates by clarifying two critical points. We demonstrate that intraspecific competition is essential for curbing unbounded population growth and maintaining system stability. Furthermore, we define the tolerance range of benefit asymmetry and elucidate how this range is influenced by competition. These findings link theoretical models more closely with empirical data observations, providing new dimensions for understanding the universal mechanisms of mutualistic stability. (The codes for all the Figures are described in Suppl. Materials S8).

CRediT authorship contribution statement

Jian-Zhong Gao: Writing – original draft, Software, Resources, Methodology, Formal analysis, Data curation. **Feng Zhang:** Writing – review & editing, Writing – original draft, Software, Funding acquisition, Formal analysis. **Derek W. Dunn:** Writing – original draft, Resources, Formal analysis. **Hao Wang:** Writing – original draft, Methodology, Funding acquisition. **K.Charlotte Jandér:** Writing – original draft, Methodology, Data curation. **Rui-Wu Wang:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work is supported by the National Natural Science Foundation of China [grant numbers U2102221, 11931015, 32070453]; Xishuangbanna Tropical Botanical Garden [grant numbers RC2023056BN], the NSERC Individual Discovery Grant [grant numbers RGPIN-2020-03911]. We are grateful to the anonymous reviewers for their insightful comments and constructive suggestions, which have significantly improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtbi.2025.112300.

References

Addicott, J.F., 1986. Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. Oecologia 70, 486–494.

Anstett, M.C., Bronstein, J.L., Hossaert-Mckey, M., 1996. Resource allocation: a conflict in the fig/fig wasp mutualism? J. Evol. Biol. 9, 417–428.

Bastolla, U., Fortuna, M.A., Pascual-García, A., et al., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018–1020.

Beddington, J.R., 1975. Mutual interference between parasites or predators and its effect on searching efficiency. J. Anim. Ecol. 44, 331–340.

Biere, A., Honders, S.C., 2006. Coping with third parties in a nursery pollination mutualism: Hadena bicruris avoids oviposition on pathogen-infected, less rewarding Silene latifolia. New Phytol. 169, 719–727.

Bolnick, D.I., 2004. Can intraspecific competition drive disruptive selection? an experimental test in natural populations of sticklebacks. Evolution 58, 608–618.

Bronstein, J.L., Vernet, D., Hossaert-Mckey, M., 1998. Do fig wasps interfere with each other during oviposition? Entomol. Exp. Appl. 87, 321–324.

Castro, C.V.D., Hoffmeister, T.S., 2020. Friend or foe? a parasitic wasp shifts the cost/benefit ratio in a nursery pollination system impacting plant fitness. Ecol. Evol. 10, 4220–4232.

Compton, S.G., Holton, K.C., Rashbrook, V.K., et al., 1991. Studies of ceratosolen galili, a non-pollinating agaonid fig wasp. Biotropica 23, 188–194.

Coyte, K.Z., Schluter, J., Foster, K.R., 2015. The ecology of the microbiome: Networks, competition, and stability. Science 350, 663–666.

Craine, J.M., Dybzinski, R., 2013. Mechanisms of plant competition for nutrients, water and light. Funct. Ecol. 27, 833–840.

Deangelis, D.L., Goldstein, R.A., O'neill, R.V., 1975. A model for tropic interaction. Ecology 56, 881-892.

Dieckmann, U., Doebeli, M., Metz, J.a.J., et al., 2004. Adaptive speciation, New York, NY: Cambridge University Press.

Donkersley, P., 2019. Trees for bees. Agric. Ecosyst. Environ. 270–271, 79–83.

Douglas, D.A., 1981. The balance between vegetative and sexual reproduction of mimulus primuloides (scrophulariaceae) at different altitudes in california. J. Ecol. 69, 295–310.

Dufay, M., Anstett, M., 2003. Conflicts between plants and pollinators that reproduce within inflorescences: evolutionary variations on a theme. Oikos 100, 3–14.

Dunn, D.W., 2020. Stability in fig tree–fig wasp mutualisms: how to be a cooperative fig wasp. Biol. J. Linn. Soc. 130, 1–17.

Dunn, D.W., Jandér, K.C., Lamas, A.G., et al., 2015. Mortal combat and competition for oviposition sites in female pollinating fig wasps. Behav. Ecol. 26, 262–268.

Fishman, M.A., Hadany, L., 2010. Plant-pollinator population dynamics. Theor. Popul Biol. 78, 270–277.

Frederickson, M.E., 2013. Rethinking mutualism stability: cheaters and the evolution of sanctions. Q. Rev. Biol. 88, 269–295.

García-Algarra, J., Galeano, J., Pastor, J.M., et al., 2014. Rethinking the logistic approach for population dynamics of mutualistic interactions. J. Theor. Biol. 363, 332–343.

Grabowska, J., Zięba, G., Przybylski, M., et al., 2019. The role of intraspecific competition in the dispersal of an invasive fish. Freshwater Biol. 64, 933–941.

Gracia-Lázaro, C., Hernández, L., Borge-Holthoefer, J., et al., 2018. The joint influence of competition and mutualism on the biodiversity of mutualistic ecosystems. Sci. Rep. 8, 9253.

Gribbin, S.D., Thompson, D.J., 1990. Asymmetric intraspecific competition among larvae of the damselfly Ischnura elegans (Zygoptera:Coenagrionidae). Ecol. Entomol. 15, 37–42.

Gutiérrez, N.M., Stucchi, L., Galeano, J., et al., 2020. The role of intraspecific competition between plants in a nursery pollination system. Ecol. Evol. 10, 11869–11874.

Hardin, G., 1969. The tragedy of the commons. Science 162, 1243–1248.

Hastings, A., Gross, L.J., 2012. Encyclopedia of theoretical ecology California. University of California Press.

Heithaus, E.R., Culver, D.C., Beattie, A.J., 1980. Models of some ant-plant mutualisms. Am. Nat. 116, 347–361.

Herre, E.A., 1989. Coevolution of reproductive characteristics in 12 species of new world figs and their pollinator wasps. Experientia 45, 637–647.

Herre, E.A., West, S.A., 1997. Conflict of interest in a mutualism: documenting the elusive fig wasp-seed trade-off. Proc. R. Soc. B 264, 1501–1507.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398.

Huth, C.J., Pellmyr, O., 1999. Yucca moth oviposition and pollination behavior is affected by past flower visitors: evidence for a host-marking pheromone. Oecologia 119, 593–599.

Jandér, K.C., Herre, E.A., 2016. Host sanctions in panamanian ficus are likely based on selective resource allocation. Am. J. Bot. 103, 1753–1762.

Jandér, K.C., Herre, E.A., Simms, E.L., 2012. Precision of host sanctions in the fig tree–fig wasp mutualism: consequences for uncooperative symbionts. Ecol. Lett. 15, 1362–1369.

Johnson, C.A., Amarasekare, P., 2013. Competition for benefits can promote the persistence of mutualistic interactions. J. Theor. Biol. 328, 54–64.

Jones, A.W., Post, D.M., 2016. Does intraspecific competition promote variation? a test via synthesis. Ecol. Evol. 6, 1646–1655.

Jousselin, E., Van Noort, S., Rasplus, J.Y., et al., 2006. Patterns of diversification of Afrotropical Otiteselline fig wasps: phylogenetic study reveals a double radiation across host figs and conservatism of host association. J. Evol. Biol. 19, 253–266.

Kawata, S., Takimoto, G., 2022. Pollinator predation stabilizes plant–pollinator mutualisms through the modification of pollinator behavior. Ecol. Res. 38, 360–366.

Kerdelhue, C., Rossi, J.P., Rasplus, J.Y., 2000. Comparative community ecology studies on old world figs and fig wasps. Ecology 81, 2832–2849.

Kinoshita, M., Kasuya, E., Yahara, T., 2002. Effects of time-dependent competition for oviposition sites on clutch sizes and offspring sex ratios in a fig wasp. Oikos 96, 31–35.

Kleunen, M.V., Fischer, M., Schmid, B., 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. Oikos 94, 515–524.

Kulkarni, M., Naik, N.V., Borges, R.M., 2024. Who holds the reins? Context-dependent resource allocation in the mutualism between fig trees and their fig wasp pollinators. Oecologia 205, 215–227.

Li, Z.T., Peng, Y.Q., Wen, X.L., et al., 2016. Selective resource allocation may promote a sex ratio in pollinator fig wasps more beneficial for the host tree. Sci. Rep. 6, 35159.

Little, A.E.F., 2010. Parasitism is a strong force shaping the fungus-growing ant–microbe symbiosis. Springer, Netherlands 17, 245–264.

Maloof, J.E., Inouye, D.W., 2000. Are nectar robbers cheaters or mutualists? Ecology 81, 2651–2661.

Miao, B.G., Liu, M.X., Wang, B., et al., 2023. Active pollination in a functionally dioecious Ficus species: an interplay between pollinator behaviour and floral morphology. Flora 302, 1–9.

Moore, J.C., Loggenberg, A., Greeff, J.M., 2005. Kin competition promotes dispersal in a male pollinating fig wasp. Biol. Lett. 2, 17–19.

Pellmyr, O., 1989. The cost of mutualism: interactions between Trollius europaeus and its pollinating parasites. Oecologia 78, 53–59.

Pellmyr, O., Huth, C.J., 1994. Evolutionary stability of mutualism between yuccas and yucca moths. Nature 372, 257–260.

Pellmyr, O., Kjellberg, F., Herre, E.A., et al., 2020. Active pollination drives selection for reduced pollen-ovule ratios. Am. J. Bot. 107, 164–170.

Pellmyr, O., Leebens-Mack, J., Huth, C.J., 1996a. Non-mutualistic yucca moths and their evolutionary consequences. Nature 380, 155–156.

Pellmyr, O., Thompson, J.N., Brown, J.M., et al., 1996b. Evolution of pollination and mutualism in the yucca moth lineage. Am. Nat. 148, 827–847.

Rankin, D.J., Bargum, K., Kokko, H., 2007. The tragedy of the commons in evolutionary biology. Trends Ecol. Evol. 22, 643–651.

Rosa-Conroy, L.D.L., Arteaga, M.C., Bullock, S.H., et al., 2019. Population variation in the intensity of fruit infestation and pre-dispersal seed predation in Yucca shoddier (Asparagaceaes) by its obligate pollinator. Plant Ecol. 220, 711–720.

Rosenzweig, M.L., 1978. Competitive speciation. Biol. J. Linn. Soc. 10, 275–289.

Roughgarden, J., 1972. Evolution of niche width. Am. Nat. 106, 683–718.

Sachs, J.L., Simms, E.L., 2006. Pathways to mutualism breakdown. Trends Ecol. Evol. 21, 585–592.

Sakhalkar, S.P., Janeček, S., Klomberg, Y., 2023. Cheaters among pollinators: nectar robbing and thieving vary spatiotemporally with floral traits in Afrotropical forests. Ecosphere 14, e4696.

Segar, S.T., Pereira, R.A., Compton, S.G., et al., 2013. Convergent structure of multitrophic communities over three continents. Ecol. Lett. 16, 1436–1444.

Smith, T.B., Skulason, S., 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annu. Rev. Ecol. Evol. Syst. 27, 111–133.

Stone, L., 2020. The Stability of Mutualism. Nat. Commun. 11, 1–7.

Svanbck, R., Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc. R. Soc. B 274, 839–844.

Thompson, A.R., 2003. Population ecology of marine mutualists. University of California, Santa Barbara.

Wang, L., Wang, R.W., 2022. Host regulation and seasonality generate population chaos in a fig-wasp mutualism. Chaos Solitons Fract. 165, 112811.

Wang, R.W., Derek, W., Sun, B.F., 2014. Discriminative host sanctions in a fig–wasp mutualism. Ecology 95, 1384–1393.

Wang, R.W., Ridley, J., Sun, B.F., et al., 2009. Interference competition and high temperatures reduce the virulence of fig wasps and stabilize a fig-wasp mutualism. PLoS One 4, e7802.

Wang, R.W., Sun, B.F., Zheng, Q., et al., 2011. Asymmetric interaction and indeterminate fitness correlation between cooperative partners in the fig–fig wasp mutualism. J. R. Soc. Interface 8, 1487–1496.

Wang, W.R., Shi, A.N., Zhang, X.W., et al., 2024. Asymmetric and uncertain interactions within mutualisms. J. Plant Ecol. 17, 1–15.

West, S.A., Kiers, E.T., Pen, I., et al., 2002. Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? J. Evolution. Biol. 15, 830–837.

Wu, B.L., Umer, M., Guo, Y., et al., 2023. Positive responses of soil nutrients and enzyme activities to AM fungus under interspecific and intraspecific competitions when associated with litter addition. Rhizosphere 27, 100728.

Zhang, F., Cang, H., Terblanche, J.S., 2011. An interaction switch predicts the nested architecture of mutualistic networks. Ecol. Lett. 14, 797–803.

Zhang, T., Jandér, K.C., Huang, F.J., et al., 2021. The evolution of parasitism from mutualism in wasps pollinating the fig, Ficus microcarpa, in Yunnan Province, China. P. Natl. A. Sci. 118, e2021148118.

Zhang, X.W., Dunn, D.W., Wen, X.L., et al., 2019. Differential deployment of sanctioning mechanisms by male and female host trees in a gynodioecious fig–wasp mutualism. Ecology 100, e02597.