Gametophytic competition games among relatives: When does spatial structure select for facilitativeness or competitiveness in pollination?

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Funding information
Natural Environment Research Council, Grant/Award Number: NE/K014617/1; RIKEN iTHEMS

Handling Editor: David Gibson

Abstract
1. Determining whether pollination occurs competitively or rather facilitatively among co-flowering plants is a central question in plant reproductive ecology. Kobayashi [2018; Journal of Ecology 107: 1433–1438] theoretically investigated the scenario in which intraspecific pollen tube competition (male–male competition) can lead to regulation of population growth due to reduced female success.
2. Kobayashi (2018) showed that evolutionary dynamics in intraspecific pollen tube competition can reduce female success and consequently generate negative density-dependence of population growth, which allows for numerous species to coexist in a spatially subdivided metacommunity. Kobayashi (2018) hypothesized that trait evolution driven by sexual selection may maintain biodiversity.
3. However, the models proposed by Kobayashi (2018) allow for the assumptions to be relaxed; he assumed: (i) fully global seed dispersal (instead of limited dispersal, albeit the spatial subdivision), (ii) fully local pollination (i.e., pollination occurred exclusively within patches), (iii) selfing rate was exactly proportionate (i.e., pollen grains distributed equally among all individuals within a patch, irrespective of their parental origins), (iv) haploid mode of inheritance, and most importantly, (v) each individual was mutually competitive, rather than facilitative for pollination.
4. Here, I extend the models of Kobayashi (2018) and show that when I relax assumptions (i)–(v), facilitativeness, as opposed to competitiveness, is more likely to be favoured by selection. The present results are attributed to kin selection in gametophytic competition among relatives in spatially subdivided populations.
5. If facilitativeness for pollination is favoured by kin selection, then the premise that the evolution of pollen traits can generate negative density-dependence does not necessarily follow. I also discuss the potential mechanisms by which pollen phenotypes can either strengthen or attenuate intraspecific and interspecific competition.

KEYWORDS
gametophytic interactions, inclusive fitness, kin competition, kin selection, plant mating system, pollen competition, pollination, sexual conflict, spatial structure
1 | INTRODUCTION

Understanding how adaptive changes in intraspecific competitive traits can affect the coexistence of multiple species is a central question in evolutionary community ecology. Competition occurs not only at the zygotic stage (i.e., among seeds and/or matured adults) but the gametic stage (i.e., among pollen grains for pollen tube growth) as well. According to the sexual conflict theory (Arnqvist & Rowe, 2005), male competitive traits (or pollen competitive traits) may be favored by selection even if they were costly to female success. How do such intraspecific competitive traits with a cost to female success foster species diversity? This question has never been addressed in the previous literature.

Kobayashi (2018) theoretically investigated the evolution of the pollen trait that increases siring probability yet reduces female fecundity (termed “selfishness” therein) and its subsequent ecological feedback to species coexistence in a spatially structured metacommunity. Using both analytical models and individual-based simulations, Kobayashi (2018) showed that the evolution of selfishness that is driven by intraspecific pollen tube competition is highly likely, which subsequently causes negative density-dependence, thereby allowing for the coexistence of 10 plant species in a spatially subdivided metacommunity. The resulting rank-abundance diagram (in which the abundance of each species on a logarithmic scale is plotted against the species from most abundant to least abundant) exhibited a S-shaped form (i.e., a steeper decrease in relative abundance among species of high rank and those of low rank compared to species of intermediate ranks), which is in agreement with classical studies (Hubbell, 2006; Whittaker, 1965; the description of the S-shape is cited from Poulin, 2007 with modifications). Kobayashi (2018) concluded that intraspecific pollen tube competition has the potential to regulate population growth and thus may allow for species coexistence in nature.

The idea that intraspecific pollen tube competition can regulate population growth has been unexplored thus far in the literature, and therefore Kobayashi (2018) offers new insight into the general question of how evolutionary dynamics of intraspecific competition can affect community dynamics. However, I raise several issues concerning the assumptions and subsequent analyses in Kobayashi (2018). First, Kobayashi (2018) assumed that seed dispersal is complete (despite the spatial subdivision), pollen dispersal is restricted to the local subpopulation and haploid is the mode of inheritance (despite the study’s primary focus being on sexual plants). Since the study by Tilman (1994), spatial subdivision and the role of colonization and competition in shaping succession have been of central interest to research on the maintenance of biodiversity; also, spatial subdivision may result in stronger kin competition, which may select for facilitative traits rather than selfishness. Therefore, incorporating spatial structure and dispersal in the model has the potential to change the results. Additionally, a more realistic description of sexual selection and conflict would be achieved if diploidy was assumed.

Second, in the fecundity function (per capita), Kobayashi (2018) implicitly assumed that the efficiency of the phenotype of pollen grains for siring is predominantly high; therefore, pollen donors are necessarily competitive with one another. This premise may be rather restrictive because pollination facilitation in co-flowering plants has been shown in many previous studies (Brewbaker & Majumder, 1961; Chen, Matsubayashi, & Sakagami, 2000; Mitchell, Flanagan, Brown, Waser, & Karron, 2009; Moeller, 2004; Rathcke, 1983; Tur, Sáez, Traveset, & Alzen, 2016). For instance, Chen et al. (2000) demonstrated that proteins (phytosulfokine-α) stored in each pollen grain can diffuse on a stigma and induce the germination of pollen tubes of the surrounding pollen grains. It may thus be beneficial to consider facilitativeness in addition to competitiveness as a possible scenario of the biological reality.

Third, Kobayashi (2018) did not adequately evaluate the effects of the phenotype of other individuals sharing the same patch on female success. Therefore, the predicted evolutionary outcomes of competitiveness were underestimated, with discrepancies becoming more pronounced as the local subpopulation size increases.

All these assumptions can be jointly relaxed on the basis of kin selection theory (Ajar, 2003; Hamilton, 1963; Rousset, 2003, 2004; Rousset & Billiard, 2000; Taylor & Frank, 1996; Taylor, Wild, & Gardner, 2007) by explicitly taking competition for siring and resource among genetic relatives into account. Here, I present a reassessment of the models and consider a diploid plant species with spatially limited pollen and seed dispersal. In addition, I include the possibility of facilitativeness that increases female success at a cost to male success, as opposed to competitiveness (that increases male success at a cost to female success). I derive Hamilton’s rule (Hamilton, 1964) to assess the direction of selection on pollination-mediated interactions. In particular, I highlight how variation in the self-fertilization rate (selfing rate) can affect the results. The aim of the present Forum article is to extend the model in Kobayashi (2018) and show the importance of biological factors (including spatial structure and ploidy) that were missed in the original models, thereby stimulating future research in eco-evolutionary dynamics in spatially structured environments.

2 | MODELS AND RESULTS

2.1 | Model description

Similar to Kobayashi (2018), I consider a metapopulation of hermaphrodite, annual, self-compatible plant species. I restrict the present model to the evolutionary dynamics of a single species (see Discussion for a possible extension to the evolutionary dynamics of multiple species). In the metapopulation, the infinite number of patches, each comprising n microsites available to n seeds for germination, are connected by random seed and pollen dispersal (the islands model; Wright, 1931). At the beginning of a generation, each adult plant produces a large number, \( L_p \), of pollen grains (or \( J_p \), of ovules). These quantities are both implicit in Kobayashi (2018) but are useful for evaluating individual fecundity. Each pollen grain disperses to a distinct patch with a probability of \( d_p \), or else remains philopatric in the natal patch (i.e., does not disperse; Aguilée, Shaw, Rousset, Shaw, & Ronce, 2012); thus, \( d_p \) represents the pollen...
dispersal rate. In the original paper, \( d_p \) was assumed to be zero (no pollen dispersal between patches). Philopatric pollen grains are either potentially outcrossing or self-fertilizing, and I assume that philopatric and immigrating pollen grains are equally distributed across all ovules within the same patch, so that, given that a focal pollen grain has stayed philopatric (which occurs with a probability of \( 1 - d_p \)), it reaches a stigma of the same plant with a probability of \( 1/n \) (namely proportionate selfing; i.e., all the pollen grains available for siring are distributed equally among all the \( n \) individuals within the patch). The factor \( s = (1 - d_p) / n \) thus stands for the selfing rate. I will later generalize the models to \( s \neq (1 - d_p) / n \), which strongly affects the results. I assume that each pollen disperses between patches individually (i.e., does not disperse en masse or in a clump; Bawa, 2016) and assume that the same number of pollen grains available for outcrossing decreases exactly by the number of pollen grains for selfing (complete pollen discounting; Harder & Wilson, 1998). The produced seeds stay philopatric in the natal patch with a probability of \( 1 - d_s \); thus, \( d_s \) represents the seed dispersal rate. All adult plants then die simultaneously. Finally, competition for the n-microsites within each patch regulates the number of seeds that survive to adulthood, returning the metapopulation back to its original size. Therefore, I assume that the population size is constant across generations; more technically, I assume that ecological dynamics have reached an equilibrium state, by separating the time-scale for ecological and evolutionary dynamics (similar to the literature of adaptive dynamics theory; Dieckmann & Law, 1996; Hofbauer & Sigmund, 1990). Mathematical symbols used in the main text are summarized in Table 1.

2.2 Phenotype and fecundity

The character, \( x \), of a pollen grain (denoted by \( s \) in Kobayashi, 2018) is the evolving trait under scrutiny in the present study; in the original model by Kobayashi (2018), \( x \) represents selfishness (or "competitiveness" hereafter), which enhances the competitive ability of pollen grains but hampers the successful development of ovules into seeds. I extend the models to include the possibility that individuals can interact positively—termed "facilitativeness" here—through which pollen grains facilitate the fertilization of other pollen grains on the same stigma, thereby promoting the development of ovules into seeds (female success). Therefore, I will hereafter refer to \( x \) as a "phenotype." An important assumption (as in Kobayashi, 2018) is that the development of an ovule is determined by the expected phenotype of the pollen grains that the stigma received via pollination (either selfing or outcrossing). Additionally, I assume that the phenotype \( x \) is under the control of the parents, instead of the pollen grains themselves (i.e., the phenotype of the pollen grains is determined by the genotype of their parents).

I write \( f(x,y) \) for the total number of seeds of a given individual each developed from the ovary that (i) is sired by a pollen grain of an individual whose phenotype is \( x \) and (ii) has received the pollen grains of individuals whose average phenotype is \( y \). Kobayashi (2018) used the following function:

\[
\bar{f}(x,y) = \frac{x}{y} \times (1-ny) \times J_{ov}
\]

where \( n \) represents the number of adult individuals within the patch and \( J_{ov} \) represents the number of ovules per capita. However, this formalism has a few issues. First, \( \bar{f}(x,y) \) is not well-defined for \( x = y = 0 \) (competitively neutral case), or competitively neutral pollen grains (\( x = 0 \) have no siring success despite their presence in a style (i.e., \( \bar{f}(0,y) = 0 \) for any \( y > 0 \); see Holsinger, 1991 for the formula for mass-action models of pollen tube competition). Heuristically, the effect of the pollen phenotype on siring is implicitly assumed to be extremely strong in Kobayashi (2018). Second, \( 1 - ny \) should be replaced with \( 1 - y \) (as detailed in Appendix S1A; see also Faria, Varela, & Gardner, 2015; Faria, Varela, & Gardner, 2017; Pizzari, Biernaskie, & Carazo, 2014 for a similar formalism). The correct calculation is as follows: within a patch after pollen dispersal, the total number of pollen grains available for fertilization equals \( n \times J_p \) (each potentially with different phenotypes), and such pollen grains are (unequally) shared among \( n \) individuals within the patch, so that the total number of pollen grains available per capita should read \( n \times J_p \), divided by \( n \), which cancels out the \( n \) factor (see also Figure 1). Below, I will more precisely evaluate the expected phenotypes of the pollen grains on the stigma of a given individual. Sex allocation theory uses the formula of the form \( f = x(1 - y) / y \) but does not necessarily apply here, as neither competitiveness nor facilitativeness are allocation strategies (but see Frank, 2006 for a review of allocation models for competitiveness, and Parker, 2000 for sperm competition among relatives).

I would suggest an alternative fecundity function, given by:

\[
f(x,y) = \frac{1+ax}{1+ay} \times (1-bky) \times J_{ov}
\]

where \( a > 0 \) represents the efficiency of phenotypes for siring, \( b \) represents the pollen-ovule ratio \( b = J_p/J_{ov} \) a P/O-ratio; Cruden, 1977; Cruden, 2000), and \( k > 0 \) is a scaling constant (which is typically small; see Appendix S1B for derivation). For convenience, I will rescale the phenotypic value \( x \) to a bounded range between \(-1 \) and \( 1 \), although this is an unessential assumption. In this expression, negative phenotypic values indicate that pollen competition is lowered and fertilization is increased; I refer to this evolutionary outcome as facilitativeness.

The present formalism has several advantages: one can first include the possibility of facilitativeness (\( x < 0 \)); second, one can recover the fecundity function in Kobayashi (2018) by taking \( a \rightarrow +\infty \) (see below); and finally, one can incorporate the P/O-ratio as an important quantity in plant reproductive ecology (Cruden, 1977, 2000). A final technical note is that both \( J_{ov} \) and \( J_p \) should be typically taken to a large value (ideally \( +\infty \)); otherwise the demographic stochasticity due to genetic drift can affect the evolutionary outcomes obtained with deterministic approximations.

2.3 Invasion fitness

I consider a single locus that encodes the phenotypic value \( x \) under additive gene actions and weak selection, with two alleles (one resident and the other a rare mutant) segregating in the locus. Given this,
we can use the selection differential (or fitness gradient) to assess the direction of selection within the adaptive dynamics framework (Dieckmann & Law, 1996; Hofbauer & Sigmund, 1990; Lehmann & Rousset, 2010). The reproductive success (per capita) occurs through male and female subcomponents (each with an equal weight of the class reproductive value, 1/2), via philopatric and dispersing seeds. The invasion fitness, defined as the expected number of adult offspring of the focal individual in a monomorphic population with a phenotype \( x \), is of the form (Appendix S1A; Rousset, 2004):

\[
W(x, x^p_0) = \frac{1}{2} W_m(x, x^p_0) + \frac{1}{2} W_f(x, x^p_0)
\]

where, \( x \) represents the expected phenotype of the focal individual (supposedly bearing at least one mutant allele), and \( x^p_0 \) represents the average phenotype of the parents of the pollen grains received.
**Figure 1** A schematic illustration for paternal success via pollen export (a) and maternal success via pollen receipt (b). For simplicity, this depiction assumes that a single individual (of hermaphrodite) is characterized by a single flower. In each panel, PP abbreviates pollen phenotype; each color represents a genotype; and the individual $i$ is the focal adult in a pollination season. (a) A representative individual with individual label and phenotype $(i, x_i)$ produces an amount, $J_p$, of pollen grains and export them. Each pollen grain is either (i) dispersing to an alternative patch with a probability of $d_p$, (ii) exported to a random patchmate (say $j 
eq i$, out of $n - 1$) with a probability of $1 - d_p - s$, and thus the total number of pollen grains of $i$ exported to $j$ is $(1 - d_p - s)J_p/(n - 1)$, or (iii) selfing with a probability of $s$. (b) A representative receiver (again $(i, x_i)$) receives pollen grains from other patches, the patchmates, or itself. In total, $d_p J_p \times n$ pollen grains (each with a phenotype $x$) are imported from other patches, and are distributed equally among $n$ individuals (top row). Thus, the factor $n$ is cancelled by dividing $d_p J_p \times n$ by $n$ and the effect that the individual $i$ receives from the other individuals in different patches is $d_p J_p x_i$. Similarly, the pollen grains from the $n - 1$ patchmates (excluding the focal individual) are distributed equally among $n - 1$ individuals. Thus the effect that the individual $i$ receives from the other patchmates is $(1 - d - s) \frac{n}{n-1} \sum_{j \neq i} x_j / (n - 1)$. Finally, the effect the individual $i$ receives from itself is $s J_p x_i$. Collectively, the individual $i$ is subject to the average pollen phenotype $(x_i + (1 - d_p - s) \frac{n}{n-1} \sum_{j \neq i} x_j / (n - 1) + d_p x) J_p$ [Colour figure can be viewed at wileyonlinelibrary.com].

by the focal individual, defined by $x_{(o)}^p = (1 - d_p) x_{(o)}^e + d_p x$ with the average phenotype $x_{(o)}^e$ of the $n$ patchmates including the focal individual (i.e., all individuals sharing the same patch). $W_e$ or $W_w$ represents the success via male (or female, respectively; Taylor, 1988), given by (Appendix S1B):

\[
W_e(x, x_{(o)}^e) = \left(1 - d_e\right) \frac{1 - d_e}{f(x, x_{(o)}^e)} + \frac{d_e}{f(x, x_{(o)}^e)}
\]

An important assumption is that the ecological dynamics have reached a steady state (separation of time-scales); therefore, the patch size $n$ does not vary similar to the analytical model in Kobayashi (2018).

### 2.4 Evolutionary invasion analysis

I apply the neighbour-modulated fitness approach to kin selection analysis (Frank, 1998; Rousset, 2003, 2004; Rousset & Billiard, 2000; Taylor & Frank, 1996; Taylor et al., 2007). To analyse the model, I evaluate the probability measures of identity by descent (IBD) within a patch, by applying a population-genetic approach (similar to a number of theoretical studies, reviewed in Lehmann & Rousset, 2010). I write $Q_w$ for the IBD probability between two homologous genes randomly sampled with replacement from the same individual; $Q_{wo}$ for the IBD probability between two distinct homologous genes within an individual; $Q_{w0}$ for the IBD probability between two homologous genes randomly sampled from two distinct patchmates; and $Q_{w0}^R = Q_{w0} / n + (1 - (1/n)) Q_{o0}$ for the IBD probability between two homologous genes randomly sampled with replacement from patchmates. I evaluate these quantities at equilibrium using recursive equations shown in Taylor (1992) and Rousset (2004) (see Appendix S1C), assuming that the patch size $n$ is at equilibrium (the separation of time-scales). The fitness gradient along $x$ is given by:

\[
\mathbf{g}(x) = \frac{\partial W}{\partial x} Q_w + \frac{\partial W}{\partial p} Q_{wo} (5)
\]

with each partial derivative evaluated at neutrality, $x_0 = x_{(o)}^p = x_{(o)}^e = x$. The first factor represents the effect of the mutant phenotype on its
own reproductive success multiplied by the probability of consanguinity between the mutant allele and the mutant individual (either homozygotic or heterozygotic), and the second factor represents the average effects of the phenotype of a mating partner (patchmate or non-patchmate) on the reproductive success of the mutant. When the fitness gradient is positive at $x$, i.e., $g(x) > 0$ (or negative, $g(x) < 0$), a higher (or lower) phenotypic value than $x$ is likely favoured by selection (respectively), until a convergently stable phenotype is reached: $g(x) = 0$ at $x = x^*$. That is, $x^*$ is a candidate evolutionarily stable strategy (cESS; Maynard Smith & Price, 1973). As $a$ and $b$ are both positive in Equation 2, one can categorize the biological meanings of the cESS based on its sign: $x^* > 0$ indicates that the cESS represents competitiveness (with a cost to female success), whereas $x^* < 0$ indicates that the cESS represents facilitativeness (with a cost to male success).

Using a marginal cost and benefit, $-C(x) := \partial \log (f(z, y)) / \partial z|_{z=x^*}$, and $B(x) := \partial \log (f(z, y)) / \partial y|_{y=x^*}$ (see Frank, 1998; Lehmann, 2007; Rousset, 2004), one can show that $g(x) > 0$ equals to:

\[
\frac{1}{2} \left( 1 - (d_f^*)^2 \right) (B(x) - C(x)) Q_w
\]

\[
+ \frac{1}{2} \left( 1 - (d_s^*)^2 \right) Q_{ov}^R B(x) - \frac{1}{2} \left( Q_{ov} - Q_{ov}^R \right) \left( 1 - d_s^* \right)^2 \left( 1 - d_p^* \right)^2 \frac{C(x)}{x} > 0
\]

where each value of the IBDs is evaluated at equilibrium (see Appendices S1D and S1E for details). The decomposition into female and male subcomponent is more useful when traits under selection are potentially under paternal and/or maternal control (e.g., as in dioecy species). Note that I have defined $C(x)$ with a minus sign placed so as to make the argument consistent with the previous literature on the evolution of altruism and spite (Rousset, 2004).

One can conceptualize the results using Hamilton’s rule and the scaled version of genetic relatedness (a scaled relatedness) advocated in social evolution theory (Frank, 1998; Gardner, Arce, & Alpedrinha, 2009; Gardner & West, 2004, 2006; Lehmann & Rousset, 2010; Rodrigues & Gardner, 2012, 2013). The above invasion condition ($g(x) > 0$) simplifies down to $H(x) = \rho B(x) - C(x) > 0$ in terms of Hamilton’s (1964) rule, where:

\[
\rho = \frac{\left( 1 - d_s^* \right)^2 Q_{ov}^R + Q_w}{2 - \left( 1 - d_s^* \right)^2 (1 - d_p^*) Q_{ov}^R / 2} - \frac{1}{2} \left( 1 - d_s^* \right)^2 (1 - d_p^*) Q_{ov}^R / 2
\]

where $Q_w$ is re-interpreted as $\left( 1 - d_p^* \right)^2 Q_{ov}^R$. In Equation 7, $\rho$ represents the scaled relatedness, as a measure of relatedness between gametes and zygotes (pollen grains and seeds) from the perspective of adults (taking into account the increased kin competition; Frank, 1998; Gardner et al., 2009; Gardner & West, 2004; Lehmann & Rousset, 2010; Rodrigues & Gardner, 2013; see Appendix S1F for a more precise interpretation). An elementary analysis shows that $\rho < 1$ (Appendix S1E) but may be negative when selfing rate is very small ($\delta \ll (1 - d_p^*) / \pi$). Previous studies (especially Rodrigues & Gardner, 2013) have presented the full account of the meaning of the scaled relatedness (see also Tarnita & Taylor, 2014).

The CESS is determined by nullifying the Hamilton’s rule $H(x) = 0$, which, with $B(x)$ and $C(x)$ both substituted, is given as a function of model parameters; namely,

\[
x^* = \frac{1}{bk} \left( 1 - \frac{a + bk}{a} \rho \right)
\]

insofar as the feasibility condition $-1 \leq x^* \leq 1$ is satisfied (otherwise the cESS is determined by $x^* = 1$ if $H(1) > 0$ or $x^* = -1$ if $H(-1) < 0$). When $a$ is large (which is set as 0.2 in Figure 2, top panels), competitiveness is likely; however, decreasing $a$ (to 0.08 in Figure 2, bottom panels) leads to facilitativeness. Hence, a careful choice of $a$ is beneficial to offer broader insight.

To assess when selection favours competitiveness versus facilitativeness $x^* < 0$, we solve $x^* = 0$ in Equation 8; the threshold value of $\rho = \tilde{\rho}$ at which facilitativeness and competitiveness switch with one another ($x^* = 0$) is given by:

\[
\tilde{\rho} = \frac{a}{a + bk} \frac{C(0)}{B(0)}
\]

The realized fecundity ($F^*$, defined by $f(x^*, x^*)$), the fecundity per capita at the intermediate cESS) reads:

\[
F^* = J_{ov} x^* = \rho \frac{C(0)}{B(0)}
\]

which monotonically decreases with $a$ (and when $\rho < 0$, $F^*$ is re-interpreted as $f(x^*, x^*) = f(1, 1) = (1 - bk) J_{ov}$). Notably, the realized fecundity linearly increases with the scaled genetic relatedness $\rho$, indicating that genetic structure monotonically increases the population growth (per capita).

Notably, there has been an established classification of phenotypes in social evolution theory. Specifically, Hamilton (1964) proposed that whether a given phenotype (or typically a type of social behaviours) represents altruism, spite, selfishness, or mutual benefit should be defined on the basis of (a) the lifetime consequences of the phenotype for the interactants (actors and recipients) and (b) fitness effects (not fecundity effects as in the present model; West, Griffin, & Gardner, 2007). Here, I intentionally avoid following that classification scheme to simplify the argument; for further details, see Rousset (2004), West et al. (2007), and Lehmann and Rousset (2010).

## 3 | KOBAYASHI (2018) REVISITED: EXTREMELY EFFICIENT PHENOTYPES

### 3.1 | Evolution of competitiveness: haploidy

One can recover the analytical result in Kobayashi (2018) (but with a slight discrepancy; see below) by assuming (a) a haploid system (and thus $Q_w = 1$, with $Q_w$ regarded as $(1 - d_p) Q_{ov}^R$), (b) the pollen dispersal rate is zero ($d_p = 0$), (c) selfing is proportionate ($s = (1 - d_p) / n = 1 / n$), and (d) phenotypic efficiency for siring is
which decreases as the population becomes more panmixia (i.e., with $d_s$ and $n$). Setting $d_s = 1$ yields $x^* = (n-1)/(n+1)$, which differs from that obtained in Kobayashi (Equation 3 therein) by a factor of $1/n$; in Kobayashi’s (2018) model, the average phenotypic effect (“the total effect of selfishness”) on a single ovule was not divided by $n$, which is incorrect (as I showed above, Section 2.3; see Faria et al., 2015; Faria et al., 2017 for the formulation of the fecundity functions under male-harm and female-resistance in spatially structured populations; see also Figure 1). As $n$ increases, the present cESS $x^*$ approaches 1 (i.e., extremely high competitiveness; Figure 3a), whereas Kobayashi’s (2018) $x^* = (n-1)/(n(n+1))$ approaches 0. Incidentally, the value of realized fecundity $F^* = f(x^*, x^*)$ at the cESS obtained in Kobayashi (2018) is not affected by the error, but this is because of the linearity of $f(x, x)$ in $x$ in Kobayashi (2018). If one assumes a nonlinear relationship, say $f(x, y) = (1+ax)/(1+ay) \times \exp(-bxy)$, then the expression of $F^*$ does change.

### 3.2 Evolution of competitiveness: diploidy

The same approach gives the cESS for diploidy (assuming $a \to +\infty$ and $d_p = 0$, with $d_s$ left unspecified, which yields $\rho = 2/(n+1)$), and the resulting cESS is given by $x^* = (n-1)/(n+1)$ regardless of the seed dispersal rate (“Taylor’s, 1992 cancelling result”, Figure 3b; reviewed in Lehmann & Roussè, 2010), which is similar to the limiting case for $d_s \to 1$ for haploidy. Hence, at least when pollen dispersal is fully restricted to the local patch, haploid and diploid
models yield qualitatively different results, suggesting that the ploidy is critical to evolutionary outcomes.

3.3 Facilitation is never favoured by selection

Formally, Kobayashi (2018) studied one limiting case for $a \rightarrow +\infty$. Here show that this limiting condition always favours competitiveness as opposed to facilitativeness, regardless of the pollen dispersal, seed dispersal, selfing rate, and patch size. To see this, plug $x = 0$ into Hamilton’s rule, $H(x) = PB(x) - C(x)$, with $H(0) < 0$ specifying the necessary condition that at least some extent of facilitativeness is favoured by selection. Taking $a \rightarrow +\infty$ after solving $H(0) < 0$ supplies $\rho \geq 1$ (Appendix S1E), which is never fulfilled because $\rho$ is smaller than 1 (Appendix S1E). Hence, selection a priori favours competitiveness whenever $a \gg 0$.

4 Illustrative generalization: Biased selfing

I here examine the effects of disproportionate selfing $s \neq (1 - d_p)/n$ on the above prediction (i.e., I look at the case in which philopatric pollen grains are distributed unequally within a patch). Examining this situation is important because in the presence of a mechanistic function for self-fertilization, pollen grains are likely in competition for siring with genetic relatives or even full copies of self at the locus of interest (Bawa, 2016). I introduce a scaled selfing parameter defined by $\sigma = s/(1 - d_p)$ (with the extreme case $d_p = 1$ excluded) and a “selfing bias” defined by $r := (\sigma - 1/n)/(1 - 1/n)$, which measures the deviation of selfing rate from the case in which philopatric pollen grains are distributed equally $(1/n)$. $r$ is zero when selfing is proportionate (i.e., when $s = (1 - d_p)/n$). I varied $\sigma$ from 0 to 1 and evaluated $r$ with different values of patch size $n = 4, 16$ and 64. A general trend is that a large patch size favours competitiveness (Figure 4, right panels; Appendices S1D and S1E), which is because siring competition among relatives is less likely with $n$ larger. Similarly, higher selfing favours facilitativeness (Figure 4a–c) by increasing kin competition for siring (the local mate competition; Hamilton, 1967). Hence, these illustrative analyses show that a higher selfing rate can favour facilitativeness due to kin selection.

5 Discussion

5.1 Comparison with the original results

Reanalysing the model of Kobayashi (2018), I found that facilitativeness is likely favoured by selection when the patch size $n$ is small, selfing rate is high, pollen dispersal rate is small, and $a$ is small (low efficiency of phenotypes for siring). A heuristic interpretation is that, if pollen grains are in competition with genetically related pollen grains, selection then favours lower competitiveness and higher facilitativeness, i.e., $x^* < 0$. This prediction is highly sensitive to the choice of the value of $a$ (Equations 9 and 11; Figure 2). Therefore, the occurrence of negative density-dependence may be a by-product in Kobayashi (2018); positive density-dependence through siring facilitation among genetically related individuals can also occur, with a potential consequence for competitive exclusion and community dynamics (but also note that facilitation is more likely when the patch size is smaller).

The present approach is somewhat more complicated than, but generally consistent with, that in Kobayashi (2018), with the quantitative differences attributed to the phenotypic efficiency parameter $a$ (the phenotype becomes more efficient for fertilization as $a$ increases). If a competitively neutral phenotype $x = 0$ has no siring success in the extreme case of $a \rightarrow +\infty$ as in Kobayashi (2018), selection necessarily favours higher pollen-competitiveness for greater siring success.

5.2 Mechanisms of pollen-mediated interactions

In Kobayashi (2018), pollen-mediated interactions occur exclusively within species; Rathcke (1983) postulated, however, that pollen-mediated interspecific interactions can occur through “improper pollen

FIGURE 3 Comparison of the candidate ESS (cESS, $x^*$; which is competitiveness here) plotted against the seed dispersal rate $(d_s)$ for haploid and diploid cases with $a \rightarrow +\infty$, $d_p = 0$, and $s = (1 - d_p)/n$ as in Kobayashi (2018). Black curves: the present results; grey curves: analytical results in Kobayashi (2018). In haploid case (a), the level of competitiveness decreases with the seed dispersal rate ($d_s$, abscissa); in diploid case (b), in contrast, competitiveness is unchanged with $d_s$. A larger patch size, $n$, leads to a higher level of competitiveness [Colour figure can be viewed at wileyonlinelibrary.com]}
transfer,” in which simultaneously transferred heterospecific pollen grains result in the loss of siring success of conspecific pollen grains. In addition, competition for pollinators is also likely, with a consequence for selection favouring self-fertilization (Bell, Karron, & Mitchell, 2005; Buide, Valle, Pissatto, & Narbona, 2015; Fishman & Wyatt, 1999; Katsuura & Ushimaru, 2019; Kudo & Kasagi, 2005; Mitchell et al., 2009; Randall & Hlu, 1990; Schweiger et al., 2010; Smith & Rausher, 2008; Stucky, 1985; Van Kleunen, Manning,
There is thus more room for extending the models to explore the consequences of improper pollen transfer for community dynamics, and I believe that Kobayashi’s (2018) approach offers a benchmark to further study the intersection between plant reproductive ecology and community ecology. Although competition is certainly a fundamental representative of pollen interactions (Delph & Havens, 1998; Frank, 2010), facilitation can also occur even among different co-flowering species (Brewbaker & Majumder, 1961; Chen et al., 2000; Ghazoul, 2006; Moeller, 2004; Rathcke, 1983; Tur et al., 2016). Mechanisms of facilitativeness include pollinator attraction strategy (e.g., Torices, Gómez, & Pannell, 2018). Appendix S1F presents an example of the evolution of dimorphism in anthers (one type for rewarding pollinators and the other for fertilization; heteranthery), and showed that the present modelling framework is applicable to the evolutionary dynamics of costly pollinator attraction (motivated by Biernaskie & Elle, 2006; Vallejo-Marin, Manson, Thomson, & Barrett, 2009, but see also Klinkhamer & de Jong, 1993 for the hypothesis of the dilemma of pollinator attraction). If the consequences of pollinator attraction can lead to higher population growth of different species and this mutualistic interaction is stronger than resource competition, the prediction of pollen-mediated negative density-dependence in Kobayashi (2018) may fundamentally change. It would be highly interesting to investigate pollination processes at the community level based on Kobayashi’s models.

Although Kobayashi (2018) cited Brandvain and Haig (2005) and Lankinen and Karlsson Green (2015) as evidence for the role of chemical interference against pollen tube growth, I found these citations problematic: Brandvain and Haig (2005) showed no evidence of chemical interference, and Lankinen and Karlsson Green (2015) is a review article citing two studies (Marshall, Hatfield, & Bennett, 1996; Varis, Reininharju, Santanen, Ranta, & Pulkkinen, 2010) for potential, chemical interference between pollen grains. However, I found neither Marshall et al. (1996) nor Varis et al. (2010) showed chemically based interference. Identifying the likely traits that mediate facilitativeness (e.g., pollen size; McCallum & Chang, 2016) versus facilitativeness is required in future studies.

5.3 | Sexual conflict and parent-pollen conflict

Selective advantage of facilitativeness (costly to male) versus competitiveness (costly to female) may differ between the perspectives of paternal versus maternal plants (sexual conflict; Arnqvist & Rowe, 2005; Delph & Havens, 1998). Possible outcomes of such conflicts can be sensitive to the degree of self-fertilization, as suggested in both empirical (Brandvain & Haig, 2005; Cailleau, Grimanelli, Blanchet, Cheptou, & Lenormand, 2018; Raunsgard et al., 2018) and theoretical studies (Jordan & Connallon, 2014; Peters & Weis, 2018). Especially in the context of intersexual interactions in spatially subdivided plant populations, I would propose that the interplay between the reproductive system (or mating system) and sexual conflict are of critical importance, although these are relatively unexplored in previous studies.

Pollens grains and adult plants are also subject to a conflict (parent-offspring conflict), depending on whether the phenotypes of pollen grains are determined by themselves or by their parents (Walsh & Charlesworth, 1992). For instance, the reproductive success of adult plants occurs through its own male and female functions, whereas the success from the perspective of pollen grains occurs only through siring (male subcomponent); therefore, natural selection may favour differential pollen phenotypes depending on whether zygote or gamete controls the pollen phenotype. This conflict is clearly captured in the fitness gradient in (Equation 6), in which the cESS nullifies the total component: $\phi^*(x) = 0$ but does not nullify the male subcomponent. Therefore, although the present results may change if one assumes self-controlled pollen phenotypes, the framework built upon Kobayashi (2018) can allow for studying the conflicts over zygotic and gametic expression of phenotypes.

Finally, it is likely that pistils have mechanisms for facilitating pollination and reducing competition. Shimizu and Okada (2000) found that female gametophytes produce attractive as well as repulsive factors, resulting in higher fertilization and preventing polyspermy. How micro-scale female traits (at diploid pistils and/or haploid gametophyte) can affect community-wide dynamics poses cross-disciplinary questions that link community dynamics and cell–cell interactions.

5.4 | Kin selection, mating system and community

In Kobayashi (2018), competition and pollination both occur within patches but seed dispersal is fully global. Although these simplifying assumptions allowed for the analytical exploration of cESS in Kobayashi (2018), they can be relaxed in the individual-based simulations. This modification may be of great importance because pollen and seed dispersal qualitatively affected the results. This discrepancy is more pronounced with higher selfing and lower pollen dispersal because of stronger kin selection and kin competition (Bawa, 2016; Cheplick, 1992, 1993; Ehlers & Bilde, 2019; Lloyd & Lively, 1993). For instance, what happens if competing species differ in selfing rate, seed dispersal rate, pollen-dispersal rate or in any other lifehistory traits, especially in light of the “limited similarity” concept (Tilman, 1994)? Kobayashi’s (2018) model has the potential to reveal an interesting relationship between the extinction rate and selfing lineages in spatially structured communities.

Although I restricted myself to the evolutionary dynamics of a single species, investigation for species-coexistence driven by evolution in spatially structured communities deserves further study, especially considering the effects of limited dispersal on community dynamics. A recent study by Mullon and Lehmann (2018) developed a theoretical device to study eco-evolutionary outcomes in spatially structured communities. The key prediction in Mullon and Lehmann (2018) is that the changes in the abundance distributions of species within patches can induce selection for intra-specific facilitation and inter-specific competition, which in turn affects the future, local community dynamics.
6 | CONCLUSIONS

To conclude, revisiting Kobayashi's (2018) model, I would suggest that the community dynamics outcomes should be reanalysed, particularly by considering spatial structure, self-fertilization and the diploid mode of genetic inheritance in stochastic simulations. Implementing these factors would lead to a richer understanding of the roles of spatial structure, kin competition, genomic imprinting, sexual conflict and/or self-fertilization in plant-community dynamics. I believe we can bridge the gaps between evolutionary biology and community ecology, and thereby understand how the evolution of traits driven by conspecific interactions can influence species coexistence and vice versa—namely eco-evolutionary community dynamics.

ACKNOWLEDGEMENTS

I thank Takashi Tsuchimatsu, Associate Editor, and two anonymous reviewers for helpful comments. I thank Natural Environment Research Council (NERC; NE/K014617/1, to Mike Boots) and RIKEN iTHEMS for funding (report number: RIKEN-iTHEMS-Report-19). The title of this article is inspired by Parker (2000). The author declares no conflict of interest.

AUTHORS’ CONTRIBUTIONS

R.I. carried out mathematical modelling and analyses, drafted the manuscript and produced graphic figures.

DATA AVAILABILITY STATEMENT

No data are used for this study.

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**How to cite this article:** Iritani R. Gametophytic competition games among relatives: When does spatial structure select for facilitativeness or competitiveness in pollination? *J Ecol.* 2020;108:1–13. https://doi.org/10.1111/1365-2745.13282