IDEA AND PERSPECTIVE

The population ecology of male gametophytes: the link between pollination and seed production

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Abstract

The fate of male gametophytes after pollen reaches stigmas links pollination to ovule fertilisation, governing subsequent siring success and seed production. Although male gametophyte performance primarily involves cellular processes, an ecological analogy may expose insights into the nature and implications of male gametophyte success. We elaborate this analogy theoretically and present empirical examples that illustrate associated insights. Specifically, we consider pollen loads on stigmas as localised populations subject to density-independent mortality and density-dependent processes as they traverse complex stylar environments. Different combinations of the timing of pollen-tube access to limiting stylar resources (simultaneous or sequential), the tube distribution among resources (repulsed or random) and the timing of density-independent mortality relative to competition (before or after) create signature relations of mean pollen-tube success and its variation among pistils to pollen receipt. Using novel nonlinear regression analyses (two-moment regression), we illustrate contrasting relations for two species, demonstrating that variety in these relations is a feature of reproductive diversity among angiosperms, rather than merely a theoretical curiosity. Thus, the details of male gametophyte ecology should shape sporophyte reproductive success and hence the dynamics and structure of angiosperm populations.

Keywords

density independence, facilitation, pollen tube, pollination, resource competition, style morphology, two-moment regression.

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INTRODUCTION

Flowering plants produce and sire seeds based on their ultimate success after ovule and pollen production, pollen dispersal, pollen-tube growth, ovule fertilisation and seed development. These processes occur sequentially, so the capacity for success during any stage depends on the outcomes of all prior stages. Nevertheless, until recently, consideration of the limits on seed production has focused on pollination and the resources available for seed production (Haig & Westoby 1988; Burd 2008). However, seed production and siring can be constrained despite adequate pollination and seed resources if relatively few pollen grains produce tubes that enter ovaries and fertilise ovules (Aizen & Harder 2007; Alonso *et al.* 2012, 2013). Indeed, pollen receipt must typically exceed ovule number five- to ten-fold to maximise seed production (e.g. Waser & Price 1991; Mitchell 1997; Aizen & Harder 2007). Thus, pollen germination and tube growth can impose a key filter on seed production and siring success. Surprisingly, although cellular aspects of the development of individual male gametophytes in pistils are subjects of intense research (e.g. Malhó 2006; Hiscock & Allen 2008; Dresselhaus & Franklin-Tong

2013; Sanati Nezhad & Geitmann 2013), the basic interactions that determine how many pollen tubes reach an ovary following pollination with a given number of pollen grains have received limited empirical attention and even less theoretical analysis (cf. Mulcahy 1983).

An ecological analogy may expose insights into the general consequences of pollen–pistil interactions for siring success and seed production (also see Cruzan 1986; Heslop-Harrison 2000; Herrera 2002). This analogy recognises angiosperm male gametophytes as independent haploid organisms that complete their lives in localised populations in the complex environments of the pistils of conspecific, diploid sporophytes. Such environments can be inhospitable to some male gametophytes (e.g. self- and heteromorphic incompatibility: de Nettancourt 2001) and variously permissive to others (Cruzan 1990, 1993; Herrero & Hormaza 1996), contributing to density-independent mortality. Furthermore, styles represent a competitive arena for compatible pollen-tube populations (Cruzan 1986) by providing resources that fuel growth (Haileselassie *et al.* 2005; Smith-Huerta *et al.* 2007; Rounds *et al.* 2011; Losada & Herrero 2014). If tubes deplete these resources faster than they are supplied (e.g. Herrero & Dickinson 1979), resource

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availability can limit the numbers of pollen tubes that can reach ovaries and fertilise ovules. According to this ecological analogy, the nature and magnitude of resource competition and density-independent processes in the style could influence the number and quality of the seeds in individual fruits. This perspective is implicit in some previous studies (e.g. Winsor & Stephenson 1995; Marshall *et al.* 1996), but we develop it explicitly by considering post-pollination pollen-tube success as the combined outcome of density-independent mortality and competition governed by the availability of resources and/or space and the dispersion of competitors.

In the absence of knowledge of the details of the post-pollination ecology of male gametophytes, we investigate theoretical consequences of the nature of resource competition and timing of density-independent (DI) survival for the relations of the mean and variation in pollen-tube success to pollen receipt. Our models are motivated by Brännström & Sumpter's (2005) recognition that most competition models can be characterised by whether organisms compete sequentially (contest) or simultaneously (scramble) and by their spatial distribution among resources. We specifically consider repulsed (i.e. evenly spaced) and random attempts to access resources as extremes of a spectrum of possibilities. We also investigate effects of the timing of DI relative to competition, because early DI mortality reduces the number of potential competitors, whereas late DI mortality depletes tubes that competed successfully. Furthermore, variation among pistils in early, but not late, DI survival can indirectly reduce mean tube success. Owing to the carrying capacity imposed by limited space/resources, prior DI survival of many pollen tubes will intensify their subsequent competition. Consequently, pistils with high DI survival will elevate the mean number of tubes entering ovaries proportionally less than poor DI survival depresses it, resulting in nonlinear averaging [Jensen's (1906) inequality]. This effect bears diverse consequences, including evolutionary effects on the allocation of reproductive resources (Schreiber *et al.* 2015) and the relative merits of alternative sexual systems (see Wilson & Harder 2003).

In this article, we elaborate the population ecology of male gametophytes and identify new hypotheses about the relation of ovule fertilisation to pollen receipt and its consequences for seed production and siring. We begin by developing eight models that illustrate the diversity of outcomes associated with all combinations of sequential vs. simultaneous competition that occurs randomly or evenly within stylar cross-sections and is either preceded or followed by DI mortality. These models focus on ecological interactions of pollen tubes with each other and the pistils they occupy, as they establish the capacity for subsequent seed production and siring. Next, we consider two empirical examples that illustrate patterns expected by sequential and simultaneous competition and the relative impacts of density-dependent and DI processes on pollen-tube survival. Finally, we consider ecological and evolutionary implications of male gametophyte ecology for traits that could influence post-pollination performance and sporophyte reproductive success. Variation in tube success among pistils features prominently in our theoretical and empirical analysis, because it arises naturally from competition and DI mortality and has manifold consequences. However, we do not examine specific causes of differential pollen-tube success (e.g. pollen or pistil genotype, stress), as we are concerned here with overall tube success, rather than the composition of the surviving gametophyte population.

MODELS OF POLLEN-TUBE ECOLOGY

Theoretical approach

What is the probability that n of the p pollen grains on a stigma produce a pollen tube that subsequently enters the ovary and can fertilise ovules, and how variable is this success among pistils? Suppose that pollen tubes compete in a single cross-section of the pistil, the 'competition zone', where resources and/or space are most limiting. In particular, the R 'resources' in the competition zone can support a carrying capacity of at most n_{max} pollen tubes. We assume that these resources are non-replenishing, distributed homogeneously and immobile. Resource immobility specifically allows us to model space occupancy by pollen tubes as a surrogate for their resource use without loss of generality. Specifically, a pollen tube survives competition only if it attempts to access space in the competition zone that is unoccupied by other tubes. These influences are summarised in the probability that s of the k tubes entering the competition zone survive competition, $C(s|k, R)$. We also propose that each pollen tube survives DI mortality (e.g. pollen inviability, effects of lethal alleles, incompatibility) with probability v. Therefore, the probability that y of x tubes survive DI mortality is $I(y|x, v)$. With a fixed v, DI survival generates a binomial distribution among pistils,

$$I(y|x, v) = \binom{x}{y} v^y (1 - v)^{x-y}.$$

Alternatively, v could vary among pistil-based populations of male gametophytes, accentuating overall variation in tube success. We represent this possibility by allowing v to vary among pistils around the mean, $\bar{v}$, according to the beta distribution, which is bounded to lie between 0 and 1 (Edwards 1960). The result is a beta-binomial distribution,

$$I(y|x, \bar{v}, \phi_v) = \frac{\Gamma(x + 1)\Gamma(a + b)\Gamma(y + a)\Gamma(x - y + b)}{\Gamma(y + 1)\Gamma(x - y + 1)\Gamma(a)\Gamma(b)\Gamma(x + a + b)},$$

(1)

where $\phi_v > 0$ depicts the variation in v and $a = \bar{v}/\phi_v$, $b = (1 - \bar{v})/\phi_v$ (Richards 2008). We also consider effects of the timing of density independence relative to competition on the probability that n pollen tubes represent the p pollen grains on a stigma in the associated ovary, $T(n|p)$. If DI mortality occurs before tubes reach the competition zone (early DI), then

$$T(n|p) = \sum_{y=n}^{p} I(y|p, v) \cdot C(n|y, R), \tag{2a}$$

whereas if it occurs after the competition zone (late DI), then

$$T(n|p) = \sum_{s=n}^{p} C(s|p, R) \cdot I(n|s, v) \tag{2b}$$

(v in eqn 2a refers generically to the constant probability of DI survival for the binomial distribution, or $\bar{v}$ for the beta-

binomial distribution). Given eqn 2b, the mean number of pollen tubes entering the ovary following stigmatic receipt of p pollen grains for many pistils is

$$\bar{n} = \sum_{n=0}^{p} T(n|p) \cdot n$$

and the variance is

$$\mathrm{var}(n) = \sum_{n=0}^{p} T(n|p) \cdot n^2 - \bar{n}^2.$$

The details of competition (i.e. $C[s|k, R]$) depend on whether the k competing tubes enter the competition zone sequentially or simultaneously and their use of the space/resources within it. We consider two distributions of attempts by pollen tubes to access the stylar cross-section of the competition zone. A repulsed distribution arises if pollen tubes actively avoid space occupied by other tubes and instead grow alongside each other. Such avoidance generates a deterministic outcome, so $\bar{n}$ and $\mathrm{var}(n)$ can be determined analytically if density independence occurs after competition, or numerically if it occurs before competition. Alternatively, a random distribution of attempts arises if pollen tubes try to grow regardless of the locations of other tubes. This behaviour introduces stochasticity for two reasons. Random attempts to occupy space leave unoccupied areas that are too small to support a pollen tube. Consequently, the realised maximum number of tubes that could survive competition ($n_{\max}$) varies among otherwise identical pistils. In addition, with random attempts to use space/resource as few as two tubes can compete, even though considerable space/resource remains unclaimed. Not surprisingly, with random space use the details of $C(s|k, R)$ depend in a complicated manner on the sizes and shapes of the competition zone and pollen-tube cross-sections, and for sequential competition on whether space used by earlier tubes is blocked or available for growth of a later tube. Consequently, simulations are needed to characterise the distribution of $T(n|p)$ and estimate $\bar{n}$ and $\mathrm{var}(n)$ for random space use.

These simulations considered competition by pollen tubes with circular cross-sections of area 1 for resources in a circular competition zone with area $R = 82.5$. This geometry accommodates an average of $n_{\max} \approx 40$ successful tubes after 1000 randomly distributed, sequential attempts at space use (range = 35–46 tubes, based on 10 000 simulations). With such sequential random competition, a pollen tube survives and continues growing past the competition zone if the site it attempts to occupy is currently completely unoccupied; otherwise it fails. We present results for simulations based on the assumption that prior failed tubes block subsequent tubes. If instead, prior failed tubes do not affect occupancy by subsequent tubes, more tubes pass through the competition zone (with more variation among pistils), but the shapes of the relations of mean and standard deviation (SD) to pollen receipt resemble those presented here (results not shown). To simulate simultaneous random competition, all k pollen tubes were assigned random locations and those that occupied space alone succeeded, whereas those with over-lapping cross-sections failed. DI survival was implemented by drawing a random number of either the original p tubes (early DI) or the s tubes surviving competition (late DI) from a binomial or beta-binomial distribution. For pollen receipt ranging from $p = 1$ to 300 grains, we conducted 10 000 simulations and calculated the mean and SD of the number of surviving tubes, n. Simulations were implemented in the data step of SAS 9.4 (SAS Institute Inc. 2014a, see Appendix S1 in Supporting Information).

Theoretical results

The ecological conditions experienced by male gametophytes within pistils can generate distinctive relations of both the mean and SD number of pollen tubes entering ovaries to pollen receipt by associated stigmas (Fig. 1). Most obviously, sequential vs. simultaneous competition creates asymptotic (Fig. 1a, d) vs. peaked (humped) relations (Fig. 1g, j) of the mean number of successful tubes to pollen receipt. Repulsed use of space/resources within the competition zone imposes a relatively abrupt transition from non-competitive, increasing relations (within grey areas in Fig. 1a–c, g–i) to competitive relations (within unshaded areas in Fig. 1a–c, g–i) that either vary little (Fig. 1a–c, dashed lines) or decline (Fig. 1g–i) with increasing pollen receipt. In contrast, such a transition is not a feature of random space/resource use, as competition is possible as long as >1 tube accesses the competition zone. Thus, the mean and SD of tube success change less abruptly with pollen receipt (Fig. 1d–e, j–l). Early DI allows relatively high mean tube success (Fig. 1a, d, g, j, solid lines), because only high-quality tubes compete for resources, whereas late DI mortality (Fig. 1a, d, g, j, dashed lines) claims some of the limited number of tubes that survive competition, aggravating its effect. In addition, with abundant pollen receipt and sequential competition, early DI creates less variable tube success than late DI (Fig. 1b, c, f, g), whereas the opposite is true for simultaneous competition (Fig. 1h, i, k, l). We now summarise the details and causes of these diverse relations when all styles provide identical environments (i.e. $\phi_v = 0$). Variation among stylar environments (i.e. $\phi_v > 0$) tends to smooth mean dose–response relations and increases overall variation in tube success (see Empirical results).

With sequential competition, each successive tube incrementally depletes the unused space/resources, ultimately imposing an asymptotic carrying capacity of n_a tubes (Figs 1a, d, 2a). If tubes adopt a repulsed distribution, the transition from a linear (non-competitive) increase in tube success to the carrying capacity occurs discontinuously within individual pistils when the first $n_{\max}$ tubes have exhausted the available resources (Fig. 2a, grey line),

$$s = \begin{cases} k & \text{if } k < n_{\max} \\ n_a = n_{\max} & \text{if } k \geq n_{\max} \end{cases}$$

(ramp model, Brännström & Sumpter 2005). With late DI, this segmented relation is also evident for the mean and SD in tube number among pistils, although DI mortality lowers the average asymptote below the carrying capacity (i.e. to $\bar{v}n_{\max}$, rather than $n_{\max}$: Fig. 1a–c, dashed line). In this case, the SD varies with the mean as expected for a (beta-)binomial distribution with the maximum number of tubes equal to p for
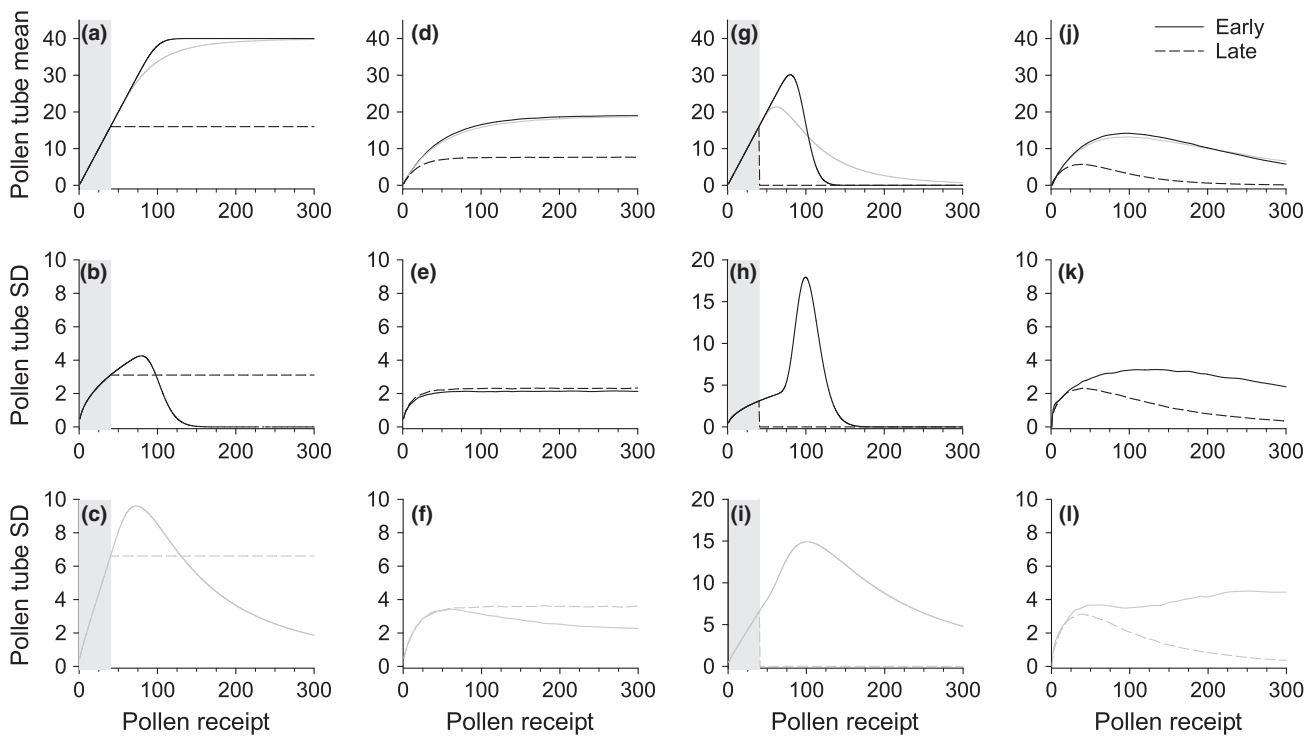
Figure 1 Theoretical effects of pollen receipt (p) on the mean and standard deviation of the number of pollen tubes entering the ovary when tubes compete sequentially (a–f) or simultaneously (g–l) with a repulsed (a–c, g–i) or random distribution (d-f, j-l) of attempted resource use in the competition zone and either early (solid lines) or late DI mortality (dashed lines: mean survival, $\bar{v}$ = 0.4). Results are depicted for binomial (black curves in a–b, d–e, g–h, j–k) and beta-binomial variation (ϕ_v = 0.1: grey curves in a, c, d, f, g, i, j, l) in DI mortality among pistils. Conditions allow an average carrying capacity of 40 tubes in the absence of DI mortality. Shaded areas in a–c and g–i indicate intensities of pollen receipt that do not impose resource competition. Based on analytic solutions (late DI) or numerical solutions (early DI) for repulsed tubes, and 10 000 simulations for random competition.
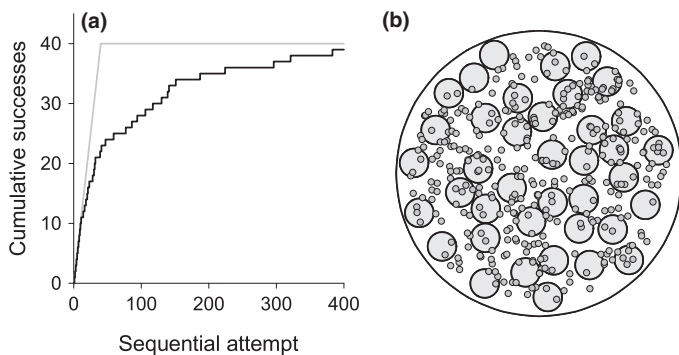

Figure 2 Single realisations of sequential competition, including (a) the relation of the cumulative number of successful pollen tubes during sequential attempts to access space/resources in the competition zone, and (b) an illustration of an outcome of 400 random attempts. In (a), the grey and black lines, respectively, illustrate sample results for repulsed and random attempts to access space. In (b), the large white circle depicts a stylar cross-section of area 100 in which 39 tubes with cross-sectional area 1 (light grey circles) successfully accessed free space/resources and 361 tubes failed to access free space (centres indicated by dark grey spots). Given the geometry of this example, a mean maximum of 48.6 tubes can survive random, sequential competition. Note that successful tubes are distributed more regularly than the random distribution of attempts.

$p \le n_{max}$, or to n_{max} otherwise. In contrast, early DI smoothes the transition to the carrying capacity for mean tube number (Fig. 1a, solid lines), because in styles that receive $p > n_{max}$

pollen grains stochastic survival results in $k < n_{max}$ tubes in some styles but $k > n_{max}$ tubes in other styles. The nonlinear averaging associated with such situations reduces mean tube number compared to the deterministic expectation. Furthermore, with early DI the SD in tube number declines progressively with increasing pollen receipt as more than n_{max} tubes enter the competition zone in an increasing fraction of pistils. Thus, the distribution of successful tube number is increasingly under-dispersed compared to a binomial distribution. Regardless of the timing of DI mortality, the slope of the initial, non-competitive relation of tube success to pollen receipt (e.g. within the shaded area in Fig. 1a) equals the average fraction of viable male gametophytes, $\bar{v}$.

When randomly distributed pollen tubes compete sequentially, the average probability of surviving competition declines steadily for successive tubes (Fig. 2a, black line), so the carrying capacity ($n_{max} < R$) is approached more gradually than for a repulsed tube distribution (Fig. 1d). In particular, if failed tubes block later tubes (e.g. Fig. 2b), the mean density-dependent (DD) survival probability is approximately $\exp(-p/n_{max})$, so the expected number of tubes surviving competition is

$$\bar{s} \approx n_{max}\left(1 - e^{-p/n_{max}}\right)$$

(Fig. 1d, black and grey lines: Skellam model, Brännström & Sumpter 2005). If instead, failed tubes do not block later tubes, tube number accumulates more gradually to a higher carrying capacity (not shown). Similarly, a higher asymptotic

mean is approached more gradually with early DI (Fig. 1d, solid lines) than with late DI (Fig. 1d, dashed lines). The SD in tube number also increases asymptotically with pollen receipt for late DI (Fig. 1e, f, dashed lines). In contrast, for early DI the SD initially increases to a level dominated by DI stochasticity and then declines to a level determined by the variability in the maximum number of randomly distributed tubes that the competition zone can support (Fig. 1e, f, solid lines). Despite random attempts to access space/resources, successful tubes are relatively evenly spaced (Fig. 2b), because only tubes with exclusive access continue growing, causing 'self-thinning'.

Simultaneous competition introduces the possibility of catastrophic tube failure if no tube has exclusive access to resources, creating a peaked relation of the number of successful tubes to pollen receipt (Fig. 1g, j). Specifically, with repulsed tubes all tubes survive if $k \leq n_{max}$, but none survive otherwise, so

$$s = \begin{cases} k & \text{if } k \leq n_{max} \\ 0 & \text{if } k > n_{max} \end{cases} \qquad (3)$$

(tent model; Brännström & Sumpter 2005). Late DI mortality further depresses mean tube number, but it does not alter the shape of the relation (Fig. 1g, dashed line). The SD in this case is as expected for a (beta-)binomial distribution with a maximum of p or 0 tubes, for $k \leq n_{max}$ or $k > n_{max}$ respectively (Fig. 1h, i, dashed line). With early DI mortality, nonlinear averaging extends the range of pollen receipt associated with positive mean tube numbers and slows the descent to complete failure in all tubes as an increasing proportion of pistils have zero tube success (Fig. 1g, solid lines). This combination of pistils with positive or zero tube success creates a peak in the among-pistil SD in tube numbers for intermediate pollen receipt (Fig. 1h, i, solid lines). As with sequential competition of repulsed tubes, the initial slope of the relation of tube success to pollen receipt equals the average fraction of viable male gametophytes, $\bar{v}$.

Random attempts to access resources greatly enhance the chance that some tubes will survive simultaneous competition, even with abundant pollen receipt, reducing the risk of complete tube failure in individual pistils. In this case, mean tube number varies in a broadly hump-shaped manner with pollen receipt (Fig. 1j), which is approximated by

$$\bar{s} \approx p e^{-p/n_{max}}$$

(Ricker model; Brännström & Sumpter 2005) if competition occurs prior to DI mortality (Fig. 1j, dashed line). The SD of tube success generally varies similarly to the mean with increasing pollen receipt (Fig. 1k, l). Exceptions arise with highly variable, early DI, for which two modes become evident: the lower dominated by the stochasticity of space use and the upper dominated by the stochasticity in DI survival (Fig. 1l, solid line).

EMPIRICAL EVIDENCE

The theoretical diversity of male gametophyte ecology identified above is biologically relevant only to the extent that the modelled conditions actually occur in angiosperm pistils. Thorough assessment of this diversity requires a survey of the dose–response relations for species that likely differ in pollen and pistil characteristics, which is beyond the scope of this study. The following two examples illustrate a statistical approach to such empirical analysis and reveal contrasting dose–response relations. These examples were selected because they involve large data sets, facilitating characterisation of effects on the mean and variation in tube success; and they demonstrate predicted diversity of dose–response relations (see Harder *et al.* 2016 for additional examples). These examples involve previously published data for *Parkinsonia praecox* (Ruiz & Pav.) Hawkins (=*Cercidium australe*: Fabaceae, Caesalpinioideae) (Aizen & Feinsinger 1994: sites COS, IMH and VIP combined: 2956 pistils) and *Tristerix corymbosus* (L.) Kuijt (Loranthaceae) (Aizen 2003: open-pollinated and pollen-supplemented flowers: 1276 pistils). Briefly, epifluorescence microscopy was used to count both pollen grains on the stigma and pollen tubes at the base of the style in *Parkinsonia* flowers, and pollen tubes penetrating the stigma (an estimate of effective pollen load) and about two thirds of the way along the style (2 cm) in *Tristerix* flowers (see Aizen & Feinsinger 1994 and Aizen 2003 for further sampling and methodological details).

Statistical methods

Most mechanistic details incorporated in the theoretical models (especially those related to random space/resource use) are too complex to be explicit subjects of data analysis; however, the general theoretical relations of the mean and SD of tube success among pistils to pollen receipt are amenable to analysis. The theoretical results (Fig. 1) indicate that all relations of the mean and SD could be represented by either an asymptotic or a peaked relation to pollen receipt (p). Therefore, we used the following asymptotic function (model A),

$$f_A(p) = \alpha\left(1 - \exp\left[-\beta\left(\frac{p}{\alpha}\right)^\gamma\right]\right), \qquad (4a)$$

and peaked function (model P),

$$f_P(p) = \beta p \exp\left(-\left[\frac{p}{\alpha}\right]^\gamma\right), \qquad (4b)$$

to characterise pollen-tube dose–response relations (see Fig. 3). Model A involves an asymptote of α, whereas model P reaches a peak of $\alpha\beta\gamma^{-1/\gamma}e^{-1/\gamma}$ at $p^* = \alpha\exp\left(-\frac{\ln(\gamma)}{\gamma}\right)$. Despite being phenomenological, models A and P for the mean simplify to the Skellam and Ricker models, respectively, when $\beta = \gamma = 1$ (equating $\alpha = n_{max}$), and they approximate the ramp and tent models, respectively, if $\gamma > 1$ (see Fig. 3). They also allow additional flexibility that is not a feature of our theoretical models, but may be evident in actual data. Parameters of models for mean tube number also provide estimates of mean DI survival. Most straightforwardly, $\bar{v}$ is estimated by the predicted mean number of tubes following pollination with a single pollen grain, or $\hat{v} = \alpha\left(1 - e^{-\beta\alpha^{-\gamma}}\right)$ for model A and $\hat{v} = \beta e^{-\alpha^{-\gamma}}$ for model P. However, if $\gamma > 1$ for model A this estimate includes the effects of positive density
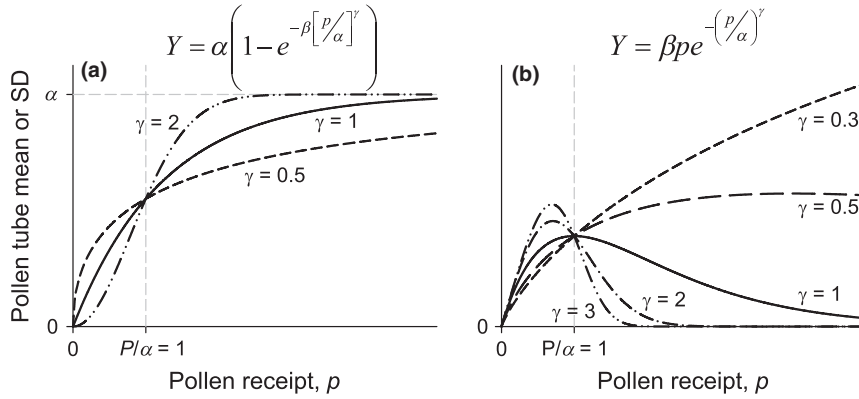
$$Y = \alpha\left(1 - e^{-\beta\left[\frac{p}{\alpha}\right]^{\gamma}}\right)$$

$$Y = \beta p e^{-\left(\frac{p}{\alpha}\right)^{\gamma}}$$

Figure 3 Examples of possible relations that can be represented by the (a) asymptotic model (a: eqn 4a) and the (b) intermediate peak model (P: eqn 4b) used to fit variation in the mean and standard deviation of the number of pollen tubes entering ovaries. $\beta = 0.4$ in all cases.

dependence (facilitation), so $\bar{v}$ is better estimated at the inflection point (at which negative and positive density dependence are equal), namely $\hat{v} = (\gamma - 1)\exp\left(\frac{1 - \gamma - \ln(\gamma - 1) + \ln(\beta) + \ln(\gamma)}{\gamma}\right)$.

To characterise the relation of tube success to pollen receipt, we devised a maximum-likelihood approach, two-moment regression, that simultaneously models the effects of an independent variable on both the mean and SD of a dependent variable. Standard regression methods model variation in the first moment, or mean, of a dependent variable, based on an assumption that the second moment, or variance, is constant or varies according to a specific fixed relation to the mean (e.g. Stroup 2013). In contrast, our theoretical models propose that the mean and variance (or SD) of tube success can vary somewhat independently (Fig. 1). To accommodate this effect, we capitalised on the joint dependence of the variance of a beta-binomial distribution on both the mean and among-flower dispersion parameter, ϕ_f (Richards 2008). Given pollen receipt, p, the mean for this distribution is $\mu(p) = \bar{t}p$ and the variance among flowers is

$$\sigma^2(p) = \mu(p)\left(1 - \frac{\mu(p)}{p}\right)\left(1 + \frac{[p-1]\phi_f}{1 + \phi_f}\right). \tag{5}$$

The last term in eqn 5 represents inflation of the variance compared to that of a binomial distribution, which is represented by the first two terms. Either eqn 4a or 4b can be used straightforwardly to model the relation of mean pollen-tube number to pollen receipt (i.e. $\mu(p) = f_A(p)$ or $\mu(p) = f_P(p)$). To relate the SD of tube success to pollen receipt we also allowed ϕ_f to vary as a function of pollen receipt. Specifically, we rearranged eqn 5 to characterise $\phi_f(p)$ in terms of the mean and variance,

$$\phi_f(p) = \frac{\sigma^2(p) - \mu(p)\left(1 - \frac{\mu(p)}{p}\right)}{\mu(p)(p - \mu(p)) - \sigma^2(p)}, \tag{6}$$

with $\sigma(p)$ given by either eqn 4a (model A) or 4b (model P). We considered all four possible combinations of models A and P for mean pollen-tube number and models A and P for the SD in pollen-tube number, denoted by two-letter codes (e.g. model AP depicts the mean and SD by models A and P

respectively). Implementation of models A and P for the SD requires a safeguard that $\phi_f(p) > 0$.

Both data sets included replicate observations from individual plants, which also allowed us to isolate among-plant variation in pollen-tube number from within-plant variation. For these analyses, the fit of eqn 4a or 4b for the SD represents within-plant variation and the estimated mean pollen-tube number was allowed to vary among plants, with the mean for plant i represented as

$$\mu_i(p) = \frac{p\mu(p)e^{z_i}}{p - \mu(p) + \mu(p)e^{z_i}},$$

where z_i is a normally distributed deviate (mean = 0, variance = σ_I^2). This expression is a logistic function of p, which assures that $0 \le \mu_i(p) \le p$. These mean deviates were used to calculate plant-specific $\bar{t}_i = \mu_i(p)/p$, which in turn were incorporated in plant-specific $a_i = \bar{t}_i/\phi_f(p)$ and $b_i = (1 - \bar{t}_i)/\phi_f(p)$ parameters of the beta-binomial distribution (cf. eqn 1: note the use of a common $\phi_f(p)$ for all plants). Given an estimate of $\hat{\sigma}_I^2$, the among-plant variance of $\mu_i(p)$ can be calculated (by numerical integration) as

$$\hat{\sigma}_A^2(p) = \int f_N(z|0, \sigma_I^2)\mu_i^2(p, z)dz - \hat{\mu}_G^2(p),$$

where $f_N(z|0,\sigma_I^2)$ is the probability density of the normal distribution and

$$\hat{\mu}_G(p) = \int f_N(z|0, \sigma_I^2)\mu_i(p, z)dz$$

is the estimated grand mean pollen-tube number. Among-plant variation causes $\hat{\mu}_G(p)$ to differ slightly from the estimate of mean tube success provided by fits of eqn 4a or 4b (< 2% for the cases presented here).

We fit these two-moment regression models with the nlmixed procedure of SAS/STAT 13.2 (SAS Institute Inc. 2014b) and used Akaike's information criterion (AIC) to select which of the four model(s) provided the most parsimonious explanation of the data. In particular, retained models had either the lowest AIC (AIC_{min}), or their AIC differed from AIC_{min} by no more than six units (Richards 2005). Given this decision criterion, we present the difference

between a model's AIC and AIC_{min} (Δ_{AIC}), rather than the AIC values themselves. Note that if the peak for eqn 4b (model P) lies beyond the maximum observed pollen receipt (Fig. 3) it describes a seemingly asymptotic relation of pollen-tube number to pollen receipt like that of eqn 4a (model A). In this case, models A and P with $\Delta_{AIC} < 6$ represent equivalent, rather than alternative, explanations of the data. Appendix S2 in Supporting Information provides sample SAS and R routines for implementing these analyses and Appendix S3 presents a tutorial for implementing the R program.

Empirical results

The relations of the mean and SD of pollen-tube number to variation in natural pollen receipt for *Parkinsonia* and *Tristerix* (Fig. 4) suggest contrasting population ecology of male gametophytes. Two models provide acceptable fits to the *Parkinsonia* data, AP and AA (Table 1). Both models identify that mean tube number approaches an average asymptote ($\hat{\alpha}$) of about 11 tubes (Table 2; Fig. 4a), suggesting sequential competition. The likely distribution of attempted resource access and timing of DI survival are somewhat obscured by
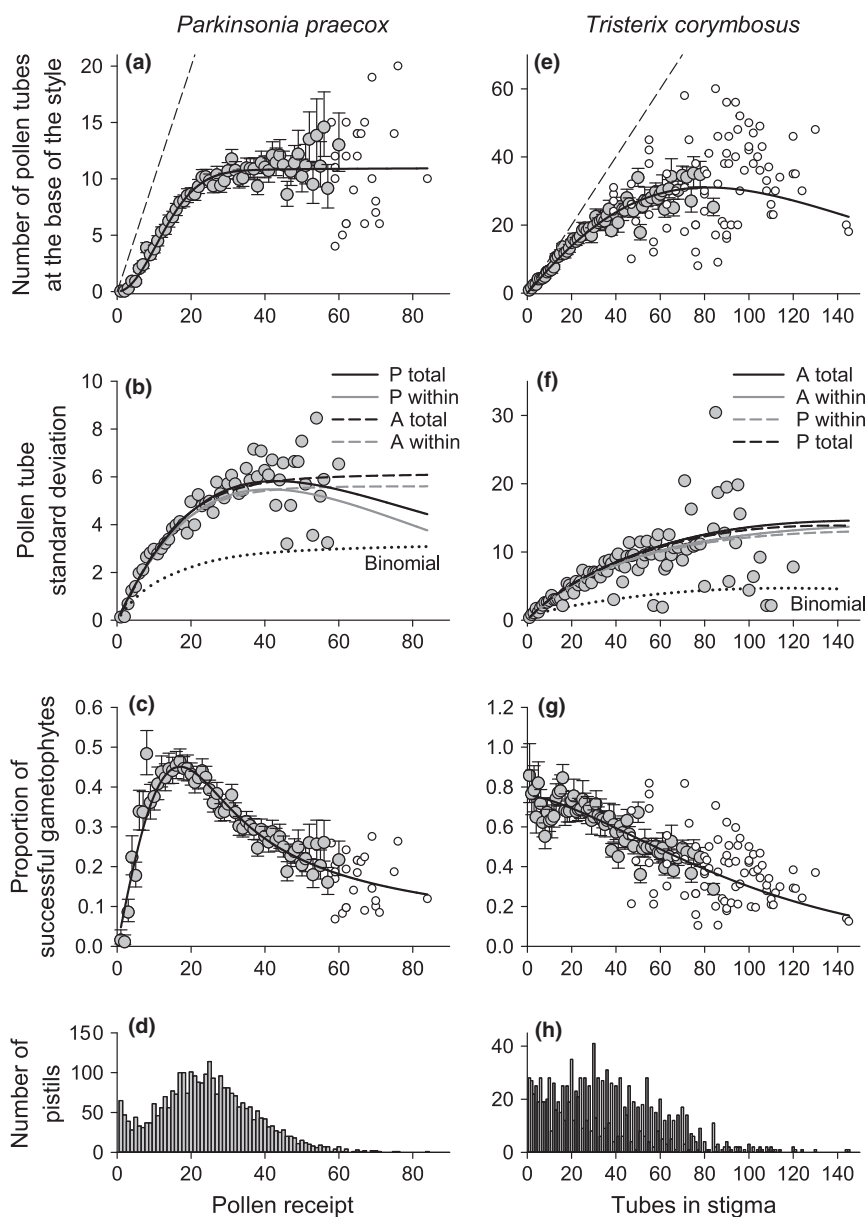

Figure 4 Effects of natural pollen receipt on the mean (a, e) and standard deviation (b, f) number of pollen tubes at style bases and the mean proportion of gametophytes with successful pollen tubes (c, g) for *Parkinsonia praecox* (a–d) and *Tristerix corymbosus* (e–h). Solid curves represent the best-fitting model (AP for a–c; PA for e–g), dashed curves in b and f represent the alternate model (PA and AP respectively). (d) and (h) show pollen-receipt (i.e. sample size) distributions. Grey symbols ($\pm$ SE for means) depict summary statistics for pollen counts represented by ≥ 5 pistils. Open symbols in (a) and (e) represent observed tube numbers for pollen counts represented by < 5 pistils. In (b) and (f), total and within signify the overall and within-plant standard deviations respectively. The dashed lines in (a) and (e) represent 1 : 1 relations of tube number to pollen receipt.

an unexpected initially accelerating dose–response relation ($\gamma > 1$, see Table 2: Fig. 4a, c, < 11 grains). This relation indicates facilitation, rather than competition, at low tube densities. With greater pollen receipt (> 11 grains), the proportion of pollen grains represented by successful tubes declined steadily with increasing pollen receipt (Fig. 4c), which is indicative of random attempts to access stylar resources. The best-fitting model, AP, identifies a peaked relation for the SD (maximum at 41.2 grains, 95% CI = 5.39 grains: Fig. 4b), which is expected for random tube distributions only if DI mortality acts before competition (Fig. 1f). Both models AP and AA indicate that about 60% of male gametophytes survived DI mortality (Table 2, $\hat{v}$). In addition, both models identified significant among-recipient variation in overall pollen-tube performance (Δ_{AIC} for model AP without among-plant variation = 117), although it represented a minor component of overall variation in tube success (compare black and solid grey lines in Fig. 4b).

For *Tristerix*, both models PA and PP satisfied the model-retention criterion, supporting a peaked relation for the mean (Table 1, Fig. 4e: this conclusion does not depend on the inclusion of the two observations with greatest pollen receipt). Proportional tube success declines continuously with increasing pollen receipt (Fig. 4g), as expected for a random distribution of attempted space/resource access. The predicted mean peaks well within the range of the observed pollen receipt (81.5 grains, 95% CI = 10.62 grains), as is expected for simultaneous competition. Models PA and PP both identify that the SD increases asymptotically with increasing pollen receipt, as the peak SD predicted by Model PP (166.7 pollen grains, 95% CI = 129.7) exceeds the maximum observed receipt (see Fig. 4f). For random competition, such a relation is indicative of early DI mortality. The estimated $\hat{v}$ indicates average DI survival of about 76% of pollen tubes (Table 2); however, this is probably an overestimate for all male gametophytes, because loss during pollen germination is not represented. Fits of both models detected significant among-recipient variation in overall pollen-tube performance (Δ_{AIC} = 56.6), although again it represented a minor component of overall variation in tube success (compare black and solid grey lines in Fig. 4f).

DISCUSSION

Our analyses reveal considerable potential and actual diversity in the population ecology of male gametophytes. The theoretical analysis demonstrates that both the mean dose–response relation and variation in tube success among pistils can depend on the timing of DI mortality and the nature of competition for limited space/resources (Fig. 1). The two empirical examples further illustrate that this variety is likely a feature of the diversity of reproductive systems among angiosperms (also see Harder *et al.* 2016), rather than a theoretical curiosity. The *Parkinsonia* example additionally identifies facilitation as an aspect of DD interactions. We now briefly review published evidence germane to the population ecology of male gametophytes and consider some implications of this ecology.

Density-independent processes

In addition to generally depressing average pollen-tube success, DI mortality can modify relations of the mean and variation in success to pollen receipt, depending on whether it acts before or after DD processes. Our estimates ($\hat{v}$ in Table 2) and those for other species (e.g. Cruzan 1989; Waser & Price 1991; Alonso *et al.* 2012; Harder *et al.* 2016) indicate that DI failure typically claims > 25% of male gametophytes that reach stigmas. Much of this loss may occur prior to pollen-tube competition if some pollen deposited on stigmas fails to germinate owing to inviability or physical/physiological causes (e.g. Dafni & Firmage 2000; Murphy 2000; Németh & Smith-Huerta 2002), stigmatic or stylar self-incompatibility mechanisms halt gametophyte growth (de Nettancourt 2001), or tubes of binucleate species fail during the transition from autotrophic to heterotrophic growth before consuming appreciable stylar resources (Cruzan 1986; Stephenson *et al.* 2003). DI loss could also occur during tube growth because of poor genetic quality of individual male gametophytes (e.g. Losdat *et al.* 2014) and/or tubes growing into constricted intercellular gaps in stylar transmitting tissue that either block further growth or cause tubes to rupture once emerging into less-confined space (see Sanati Nezhad *et al.* 2013). The latter mechanisms could act anywhere along a pollen-tube's journey to the ovary, rather than necessarily before or after competition. Finally, late-acting (ovarian) incompatibility (Gibbs 2014) would impose DI mortality after competition.

Interestingly, the same DI event should have more impact on average pollen-tube success if it acts after competition, rather than before (compare solid and dashed lines in Fig. 1a, d, g, j). Of particular relevance, early DI should winnow intrinsically inferior male gametophytes, so that only superior male gametophytes compete for access to ovules, whereas with late DI some inferior male gametophytes could survive competition only to succumb later, despite having blocked superior male gametophytes during competition. Because of the latter effect, late DI depresses the asymptotic tube number below the stylar carrying capacity, risking incomplete ovule fertilisation, which seems maladaptive.

We assumed that DI mortality differs among pistils owing to variation in male gametophyte quality, stylar environments and the vagaries of tube growth. Such variation modifies the shape of the average dose–response relation only if it arises before competition. This influence is most evident for repulsed tubes, for which increasing pollen receipt causes a distinct

Table 1 Fits of models of the joint effects of pollen receipt by stigmas on the mean and standard deviation (SD) of the number of pollen tubes at the bases of styles for *Parkinsonia praecox* and *Tristerix corymbosus* based on Δ_{AIC}. The fitted models include combinations of an asymptotic relation (model A: eqn 4a) or a relation with an intermediate peak (model P: eqn 4b) for the mean and SD. Bold values identify models warranting interpretation ($\Delta_{AIC} \leq 6$)

Mean model	SD model	*Parkinsonia praecox*	*Tristerix corymbosus*
A	A	**1.21**	7.42
A	P	**0**	12.25
P	A	255.47	**0**
P	P	256.15	**2.54**

Table 2 Parameter estimates ($\pm$ SE) for the best-fitting two-moment regression models for the analyses of *Parkinsonia praecox* (model AP) and *Tristerix corymbosus* (model PA)

Species	Mean				Standard deviation		
	α	β	γ	ν	α	β	γ
P. praecox	10.71 ± 0.27	0.500 ± 0.023	2.000 ± 0.063	0.605 ± 0.019	45.52 ± 2.46	0.325 ± 0.019	1.117 ± 0.128
T. corymbosus	105.4 ± 4.44	0.758 ± 0.020	1.454 ± 0.127	0.757 ± 0.019	14.68 ± 1.94	0.317 ± 0.017	0.938 ± 0.040

transition from non-competitive to competitive conditions with increasing pollen receipt. This transition has less impact on mean tube success, but amplifies variation among pistils, for early DI mortality compared to late DI mortality (Fig. 1a–c, g–i: compare solid and dashed lines). Even if pollen receipt exceeds the competition threshold, variation in early DI mortality can leave fewer surviving pollen tubes than the threshold number for competition in some pistils. Thus, average success of repulsed tubes reflects the (weighted) combination of tube success under non-competitive and competitive conditions. The effect of this nonlinear averaging is accentuated with increased variation (Fig. 1a–c, g–i: compare black and grey solid lines), but diminishes as mean pollen receipt increases above the competition threshold. As pollen inviability likely influences the mean and variation in early-DI failure universally, the catastrophic failure that is theoretically possible for simultaneous competition among repulsed pollen tubes (eqn 3; Fig. 1g–i, dashed lines) is probably rarely evident for mean tube success.

Density-dependent processes

As for competition in general (Brännström & Sumpter 2005), our theoretical results illustrate that both the spatial and temporal nature of pollen-tube interactions should govern the incidence and outcomes of competition among male gametophytes. Our conception of male gametophyte competition included two relevant spatial characteristics: the assumption that space/resources are limiting in a localised competition zone; and the distribution of pollen tubes within that zone. A stylar region in which competition is especially intense is probably realistic (see photographs in Modlibowska 1942), as styles commonly constrict, often either immediately after the stigma or just before the ovary, restricting access by pollen tubes (Cruzan 1986; Castro *et al.* 2009; Losada & Herrero 2014). More speculative are repulsed or random tube distributions within stylar cross-sections. Relatively repulsed distributions would arise if developing pollen tubes detect and follow gradients of resources or stylar signals (see Dresselhaus & Franklin-Tong 2013; Higashiyama & Takeuchi 2015), reducing the chance of growing into regions depleted by other tubes. However, variation in gradients and/or local increases in tube density imposed by the structure of the transmitting tissue or stylar canal would tend to increase the probability of tube interaction, adding a random component to attempted resource access. That both empirical examples suggest random resource access implies that such perturbations may occur commonly, although such generalisation requires more cases. An important feature of random space/resource access is that competition can occur if > 1 pollen tube occupies a style, contrary to the intuition that male gametophytes compete only when pollen receipt exceeds ovule number (e.g. Haldane 1932; Németh & Smith-Huerta 2003; Marshall *et al.* 2007). Thus, opportunities for competition probably depend on local conditions adjacent to the tips of growing tubes, rather than on global conditions within the competition zone.

Whether male gametophytes compete sequentially or simultaneously likely depends on the timing of pollen arrival on stigmas and pollen germination (Modlibowska 1942; Thomson 1989), and variation in tube growth rate (e.g. Herrero & Dickinson 1980; Cruzan 1986, 1990; Winsor & Stephenson 1995; Skogsmyr & Lankinen 1999). Sequential competition should be common for wind-pollinated species (see Bochenek & Eriksen 2011), animal-pollinated species in which individual flowers typically receive multiple pollen-depositing visits (e.g. Burkhardt *et al.* 2009), and species with binucleate pollen (e.g. Thomson 1989), which is quiescent during dispersal and germinates slowly (see Hoekstra 1979). In contrast, simultaneous competition should be promoted by receipt of abundant, metabolically active pollen during a single pollinator visit (e.g. receipt of aggregated pollen, Harder & Johnson 2008), or stigmatic or stylar mechanisms that delay pollen germination or tube growth (see Lankinen *et al.* 2007 and references therein). However, a strict dichotomy between sequential and simultaneous competition is probably unrealistic, as germination and growth rates likely always differ among male gametophytes in a pistil (e.g. Herrero & Dickinson 1980; Cruzan 1986, 1990; Winsor & Stephenson 1995; Skogsmyr & Lankinen 1999). Thus, despite a staggered start of the race along the style, promoting sequential competition, late-germinating, fast-growing gametophytes could catch earlier, slower gametophytes, temporarily imposing local simultaneous competition. Conversely, simultaneous competition induced by a synchronised start should grade relatively quickly into sequential competition as faster growing tubes outdistance slower tubes. Given these possibilities, strictly simultaneous competition seems most likely if competition is intense close to the stigma; otherwise sequential competition should predominate.

Simultaneous competition is particularly interesting from several perspectives. Most obviously, such competition is risky, because high pollen receipt reduces the number of surviving tubes (Figs 1g, j and 4e). This risk should promote mechanisms that guard against excess pollination (e.g. brief stigma receptivity, small stigmas). It may also explain cases of surplus hand pollination causing lower seed production than natural pollination (Young & Young 1992), as the latter should typically involve sequential accumulation of smaller pollen loads. Stylar mechanisms that impose simultaneous pollen germination have been proposed as a means intensifying competition to filter poor-quality pollen (Willson & Burley

1983; Lankinen *et al.* 2007 and references therein); however, our results identify important conditions for such mechanisms to be effective. These mechanisms would be detrimental if tubes adopt repulsed distributions, because receipt of enough pollen to cause competition leads to catastrophic failure of all tubes (Fig. 1g). If instead tubes attempt to access space/resource randomly, competition is possible with just two gametophytes. Thus, any qualitative improvements in zygote quality would have to outweigh the quantitative losses. This problem is compounded by the randomness of the process, as failed tubes could be high-quality gametophytes. These difficulties suggest that simultaneous competition, like that inferred for *Tristerix* (Fig. 4e), exists primarily for reasons other than qualitative filtering.

The dose–response relation for *Parkinsonia praecox* revealed positive density dependence following limited pollen receipt (Fig. 4c), which was not incorporated in our theoretical analysis. This relation probably reflects facilitation during pollen germination, as has been reported for other species (e.g. Cruzan 1986 and references therein, Harder *et al.* 2016). From a population ecology perspective, such a relation represents an Allee effect (Taylor & Hastings 2005), with pollen in very sparse populations on stigmas having lower establishment probabilities than in denser populations. An appreciable fraction of flowers in the *Parkinsonia* sample experienced such limited pollination (Fig. 4d), so Allee effects could commonly contribute to pollen limitation in this species.

Our models did not include all DI and DD processes that impinge on the lives of successful male gametophytes, as ovule fertilisation was omitted. The most likely DI process during this stage is late-acting self-incompatibility, which not only kills male gametophytes, but can also disable affected ovules (Gibbs 2014). The relevant DD process occurs if pollen tubes in the ovary outnumber ovules. The resulting competition likely occurs sequentially among repulsed pollen tubes, because of events associated with ovule fertilisation. Specifically, the synergid cells of female gametophytes signal the location of receptive ovules to pollen tubes, but signalling stops once one synergid ruptures during interaction with a pollen tube (Dresselhaus & Franklin-Tong 2013). Thus, pollen tubes should pair individually with ovules, as long as receptive ovules remain. This interpretation suggests that ovule fertilisation introduces additional, but not novel, features of male gametophyte ecology.

Variation in male gametophyte performance

Our consideration of the relation of pollen-tube success to pollen receipt differs from previous studies (e.g. Cruzan 1989; Waser & Price 1991; Alonso *et al.* 2012, 2013) in the attention paid to characterising the nature and sources of variation. Such attention is warranted statistically and biologically. From a statistical perspective, correct characterisation of the sampling distribution and identification of the sources of variation improves parameter estimation (including associated reliability estimation: Richards 2008). This feature is especially relevant for model selection, as it enhances the chance of identifying an appropriate representation of the influences on a dependent variable (Richards 2008). For example, had we

assumed a constant ϕ for the beta-binomial distribution, regardless of pollen receipt, regression analysis of the *Tristerix* data would have found that both models A (AIC = 7749.85) and P (AIC = 7752.08) for the mean to warrant consideration, whereas allowing ϕ to vary with pollen receipt identified clear preference for model P (Table 1). As nonlinear regression techniques that account for both non-normal sampling distributions and random effects are now readily available (e.g. see Appendix S2), they should be the methods of choice.

From a biological perspective, the sources and magnitude of variation in tube success should influence its effects on reproductive outcomes. Most observed variation in tube success for *Parkinsonia* and *Tristerix* occurred among flowers within individual plants (Fig. 4b, f). According to our models, within-plant variation in tube success should arise from DI mortality and random attempts to access space/resources (Fig. 1). To appreciate the effects of within-plant variation, consider seed production by two plants on which each flower has 5 ovules and receives 10 pollen grains, with 50% average tube success. On one plant, pollen-tube success does not vary among flowers, so 5 tubes survive per flower, allowing complete ovule fertilisation. On the other plant, binomial variation could result in 0–10 tubes surviving per flower. Flowers in which < 5 tubes survive experience incomplete ovule fertilisation: in this specific case reducing expected seed production by 12.3% compared to the case without variation in tube success. Conversely, survival of > 5 tubes represents missed opportunities from both female and male perspectives. Beta-binomial variation of the type observed for both *Parkinsonia* and *Tristerix* would aggravate both problems. Richards *et al.* (2009) referred to such depression of realised reproductive success compared to the expectation based on average pollen receipt as variance limitation. The consequences of within-plant variation in pollen-tube success should select for diverse traits that either reduce the variation or mitigate its effects (see Richards *et al.* 2009; Schreiber *et al.* 2015).

Our empirical analysis also detected limited variation in tube success among recipient plants (Fig. 4b, f: also see Cruzan 1990; Cruzan & Barrett 1993; Kerwin & Smith-Huerta 2000). Such effects could reflect the genetic and physiological states of recipient plants (Haileselassie *et al.* 2005; Hedhly *et al.* 2005) and/or pollen characteristics of pollen donors in the mating neighbourhood (Stehlik *et al.* 2006; Gauzere *et al.* 2013). Genetic causes should be targets of selection for stylar traits that govern male gametophyte performance (see Herrero & Hormaza 1996). In contrast, stochastic causes should select for traits that enhance pollen receipt, even if investment in ovule production and seed development are reduced (see Schreiber *et al.* 2015).

Effects of pollen quality

Sequestration of female gametophytes within sporophytic pistil tissue distinguishes angiosperms from gymnosperms. In addition to enhancing protection of ovules and seeds, this feature imposes a filter on the quality of male gametophytes that fertilise ovules (Mulcahy 1979). Indeed, when multiple donors contribute pollen to stigma, the relative representation of fathers among seeds in the associated ovary seldom matches

that of the potential fathers in the pollen (Ruane 2009), at least in part because of differential success of male gametophytes (e.g. Skogsmyr & Lankinen 1999; Haileselassie *et al.* 2005; Carlson *et al.* 2009). This filter should similarly act among gametophytes from individual pollen donors, to the extent that they differ qualitatively. Relevant aspects of gametophyte quality should affect both DI survival, including viability (Dafni & Firmage 2000), genotype (Cruzan 1993; Charlesworth *et al.* 2005; Losdat *et al.* 2014), pollen size and autotrophic performance (Cruzan 1990), and DD success, including the rates of pollen germination and tube growth (Cruzan 1986). Thus, pollen quality should pervasively affect gametophyte success within and among pistils, although the relative influence of DD vs. DI aspects of gametophyte quality likely varies with pollen receipt.

This expectation contrasts with those of Mitchell (1997) and Alonso *et al.* (2012). For example, Alonso *et al.* (2012) hypothesised that 'as pollen receipt increases the quantity effect (on pollen-tube success) . . . is expected to decline. At the same time, however, the importance of pollen quality . . . is expected to increase' (p. 533; parenthetical clarification added). The suggestion that quantitative effects decline with increasing pollen receipt is inconsistent with the general ecological expectation of intensified negative DD interactions (see Fig. 4c, g). That qualitative effects on male gametophyte success vary positively with pollen receipt seems reasonable, as the universal effects on DI success should be augmented by effects associated with DD success. However, for pollen quality to not affect tube success in stigmas that receive few grains (see Alonso *et al.*'s Fig. 1) would require no qualitative effects on DI performance, which seems unlikely. Thus, both qualitative and quantitative aspects of tube success should vary positively with increasing pollen receipt.

Based on their perspective, Alonso *et al.* (2012) proposed 'that a change in the relative importance of . . . the quantity and quality of pollen receipt . . . underlies the shape of natural pollen grain-pollen tube dose–response curves, and that this can be deduced by use of breakpoint/piecewise regression analysis' (p. 533). Qualitative influences can affect the shapes of these relations; however, Fig. 2a illustrates that contrasting shapes can also arise solely because of the details of DD interactions among identical male gametophytes. Therefore, individual dose–response relations, like those depicted in Fig. 4a, e, or analyzed by Alonso *et al.* (2012, 2013), provide no explicit information about the relative influences of gametophyte quality vs. quantity. Instead, discrimination between these effects requires one of two types of information: characterisation of changes in the composition of the population of gametophytes from stigma to ovary; or comparison of dose–response relations among pistils that received pollen of differing quality (e.g. Aizen *et al.* 1990; Cruzan 1990; Losdat *et al.* 2014; Harder *et al.* 2016).

CONCLUSION

The male gametophytes occupying a stigma constitute an ecological population. A group of immigrants arrives at a vacant site, either sequentially or simultaneously, and may establish a population, possibly subject to an Allee effect. Subsequent DI

mortality and competition for space and/or resources further diminish the population. Thus, the relation of final population size to the number of immigrants depends on basic ecological processes. Furthermore, these processes and environmental heterogeneity generate extensive variation in abundance (and composition) among populations.

Of course, the collective fates of male gametophytes in a pistil are ecologically and evolutionarily relevant in a larger context, as they establish potential siring success of source sporophytes and seed production of the recipient sporophyte (e.g. Aizen & Feinsinger 1994; Németh & Smith-Huerta 2003; Burkhardt *et al.* 2009; Bochenek & Eriksen 2011). Our theoretical analysis illustrates that the specific timing of DI processes and the spatial and temporal details of DD interactions create signature relations of the mean and variation of tube success to pollen receipt (Fig. 1). Consequently, details of the population ecology of male gametophytes should leave an imprint on sporophyte reproductive success and hence on the structure and dynamics of angiosperm populations.

AUTHORSHIP

MA and LH conceived the project and developed initial models, LH designed and implemented the simulations, MA provided the data, SR and LH developed and implemented the statistical analysis, LH wrote the first draft and all authors contributed substantially to the final manuscript.

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