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Spatial seed and pollen games: dispersal, sex allocation, and the evolution of dioecy

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Abstract

The evolutionary forces shaping within- and across-species variation in the investment in male and female sex function are still incompletely understood. Despite earlier suggestions that in plants the evolution or cosexuality vs. dioecy, as well as sex allocation among cosexuals, is affected by seed and pollen dispersal, no formal model has explicitly used dispersal distances to address this problem. Here, we present a game-theory model as well as a simulation study that fills in this gap. Our model predicts that dioecy should evolve if seeds and pollen disperse widely and that sex allocation among cosexuals should be biased towards whichever sex function produces more widely dispersing units. Dispersal limitations stabilize cosexuality by reinforcing competition between spatially clumped dispersal units from the same source, leading to saturating fitness returns that render sexual specialization unprofitable. However, limited pollen dispersal can also increase the risk of selfing, thus potentially selecting for dioecy as an outbreeding mechanism. Finally, we refute a recent claim that cosexuals should always invest equally in both sex functions.

Introduction

Sex allocation theory aims at explaining within- and across-species variation in the investment in male and female function between individuals (Charnov, 1982; Schärer, 2009). Most plant species are cosexual, meaning that each individual fulfils both male and female sexual functions. This contrasts sharply with animals, in which only an estimated 5–6% of species are hermaphroditic (although this figure increases to about 30% if insects, which are never hermaphroditic, are excluded; Jarne & Auld, 2006). Despite this general trend, dioecy (the botanical term for the separation of sex functions in male and female individuals) has evolved many times throughout the plant kingdom (Bawa, 1980), and it occurs in ca. 6% of flowering plants (Renner & Ricklefs, 1995).

Why are plants so often cosexual? This question has a long history of attracting research attention by evolutionary biologists (e.g. Darwin, 1877; Charlesworth & Charlesworth, 1978; Charnov, 1982; Charlesworth, 2006). A central assumption in sexual allocation theory is that resources invested in one function are unavailable for the other; thus, there may often be a trade-off between male and female function (e.g. Ashman, 1999; Delph, 1990; Mazer *et al.*, 1999).

Theory suggests that the optimal sex allocation depends on how efficiently fitness can be gained by investing in either sex function (Charnov *et al.*, 1976). Altering mating opportunities thus can select for changed sex allocation, and support for this argument has been found in both animals (Baeza, 2007) and plants (Dorken & Pannell, 2008). The plant case (Dorken & Pannell, 2008, 2009) is of special interest because a follow-up paper documented microevolutionary change and not

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merely plastic allocation: hermaphrodites of *Mercurialis annua* mating in the absence of males evolved greater male allocation (Dorken & Pannell, 2009).

In general, optimal male and female allocations depend on the shape of the (sex-specific) mathematical curves mapping fitness gains on investment level. Saturating fitness gain curves make high investment less profitable, which selects against specialization in only one sex function. This makes cosexuality more likely (Charnov *et al.*, 1976). In contrast, when fitness gains are accelerating, high investment levels are required to gain the highest payoffs. This favours sexual specialization, i.e. dioecy. This theoretical framework also predicts that sex allocation among cosexuals should be biased towards whichever sex function has a steeper (less saturated) fitness gain curve (Charnov, 1982).

Although this theory can account for the evolution of both dioecy and cosexuality, the question of why fitness gain curves should be shaped in a certain way in the first place is surprisingly understudied. To explain the prevalence of cosexuality in plants, Maynard Smith (1978) suggested that saturating fitness gain curves may arise from dispersal limitations of both seeds and pollen. According to his argument, additional pollination success will be increasingly difficult to achieve once a focal plant's neighbours are pollinated already. Similarly, additional seeds produced will face reduced recruitment chances once a maternal parent plant's vicinity is already well stocked with seeds. These effects will be most notable when dispersal distances are short, leading to strong interference between the spatially clumped dispersal units from the same source.

Previous theoretical work suggests that this link between dispersal and sexual system may be of great general importance. Existing models fall into two categories: one class of models focuses exclusively on reproductive success via the female function (Heilbuth *et al.*, 2001; Wilson & Harder, 2003; Barot & Gignoux, 2004; Vamosi *et al.*, 2007), which provides no adequate framework for explaining the evolution and maintenance of dioecy. Another set of models accounts for both male function and female function, but treats dispersal rather implicitly, by considering, on the one hand, the numbers of seed-producing individuals whose seeds compete locally, and, on the other hand, the numbers of individual seed-producers that each pollen-producer can reach and fertilize (Lloyd & Bawa, 1984; see also Charnov, 1982). Although these models have lent analytical support to Maynard Smith's (1978) verbal arguments, their simplicity does not wholly capture the role of dispersal for the evolution of sexual systems. First, it is difficult to relate their assumption of fixed competitor numbers to a realistic view of dispersal in terms of dispersal kernels. Second, they do not account for a possible feedback between sexual system and spatial configuration, which arises from the fact that cosexuality implies a greater density of seed and pollen sources for a given population density. Third, none of these models has accounted for the possibility that the risk of selfing, which may be an important cost of cosexuality, may also depend on dispersal patterns.

Here, we present a game-theory model, backed up with individual-based simulations, that fills in these gaps. We derive specific predictions that we then contrast with known across-species patterns. First, we investigate the effect of seed and pollen dispersal distances on optimal sex allocation among cosexuals. Second, we examine the evolutionary stability of cosexuality vs. dioecy under different dispersal regimes.

The model

We consider an infinitely large population where each individual produces many dispersal units (seeds and pollen) that become distributed in space centred around its own location. Individuals invest X resources in seed production, and $1 - X$ resources in pollen production, which defines cosexuality as $0 < X < 1$. Reproductive success is gained when opportunities for germination and fertilization arise, which happens at a low rate throughout the habitat. Because fertilization events without subsequent germination do not yield reproductive success, such 'failed fertilizations' can be neglected for our purposes. Therefore, we consider that successful fertilization and germination events occur at the same rate.

Because kin competition is known to influence sex allocation (Hamilton, 1967) and dispersal (Hamilton & May, 1977; Gandon, 1999; Ronce *et al.*, 2000), and we are primarily interested in effects of competition at the fertilization and recruitment stage (as opposed to the long-term consequences of growing close to kin), we define that to count as an 'opportunity' a location has to be a large enough vacancy that one individual can grow in it without harming kin. This does not harm the generality of the model but strengthens the reasoning that opportunities should occur at a low rate. In the Discussion, we will comment on the likely effects of relaxing our assumption of no post-recruitment competition.

Our assumption of a low rate of opportunity formation means that most dispersal units fail to contribute to reproductive success. When a reproductive opportunity arises in a given area, the probability that a certain individual can reap this opportunity depends on the density of its relevant dispersal units in that area, relative to the total density of such dispersal units in the same local area. This means that an individual's dispersal units, if poorly spread out, compete mostly with each other, whereas if widely spread they compete mostly with those of other individuals.

We consider a spatial scale such that there is on average one individual per unit of space, implying that there are πr^2 individuals per circular area of radius r. We envisage a population where almost all individuals use the same sex allocation strategy, which we refer to as the resident strategy. We assume that dispersal distances r are drawn from probability density function $D(r, d_\mathrm{i})$ with mean distance d_i, which takes values d_s and d_p, for seeds and pollen, respectively. Although we develop our model for a general form of $D(r, d_\mathrm{i})$, our computational examples are based on either of two possible forms (Fig. 1): a half-normal distribution, $D(r,d_i) = \frac{2e}{d_i\pi}^{-\frac{r^2}{d_i^2\pi}}$, which is appropriate when movement arises from small independent steps in random directions; and a negative exponential distribution, $D(r,d_i) = \frac{e^{\frac{-r}{d_i}}}{d_i}$, which is appropriate if each dispersal movement has a constant speed and direction until terminated at a constant rate.

Letting the functions $f(X)$ and $g(1–X)$ denote the numbers of viable seeds and pollen produced per unit of investment, respectively, we consider two cases: in case 1, we assume that a fixed 'start-up' cost C has to be paid for providing and maintaining a 'machinery' for producing both seeds and pollen before further investment translates into the production of gametes. Accordingly, we let

$$f(X) = \begin{cases} 0 & \text{if} \quad X \le C \\ X - C & \text{if} \quad X > C \end{cases}$$

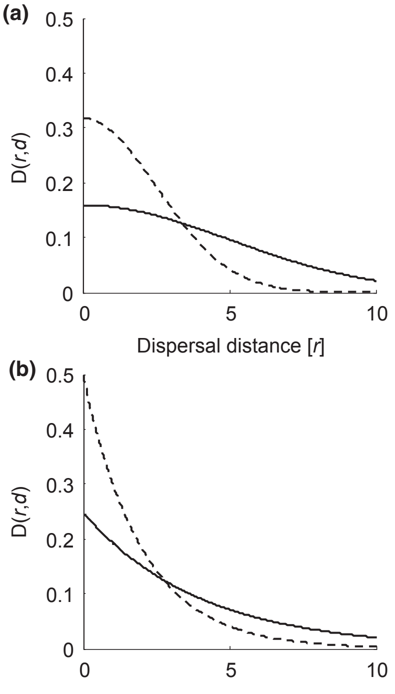

Fig. 1 Half-normal (a) and negative exponential (b) shape of dispersal kernels with mean distances: $d_\mathrm{i} = 2$ (dashed) and $d_\mathrm{i} = 4$ (solid). Kernels specify the proportion of dispersal units settling at a given distance from the source.

and

$$g(1-X) = \begin{cases} 0 & \text{if} \quad 1 - X \le C \\ 1 - X - C & \text{if} \quad 1 - X > C \end{cases},$$

so that f and g remain 0 up to a threshold before beginning to increase. This formulation implies that unisexuals can produce gametes more efficiently by paying only one type of start-up cost. In case 1 we assume no selfing.

In case 2, there is no start-up cost; functions f and g increase in the entire range from 0 onwards, so that any small investment results in a small number of gametes being produced. Nonlinearity in f arises because of selfing. Selfing generally leads to reduced seed viability (Lloyd, 1979; Charlesworth & Charlesworth, 1990; Porcher *et al.*, 2009). Because the risk of selfing likely depends on the relative numbers of self- vs. allopollen surrounding each ovule, we let the proportion of selfed seeds be $\mathit{selfed}(\hat{X}, X) = \frac{\mathit{selfpollen}}{\mathit{selfpollen}+\mathit{allopollen}}$. Here, $\mathit{selfpollen} = g(1-\hat{X})D(0, d_p)$ is the focal individual's number of nondispersed pollen, and $\mathit{allopollen} = g(1 - X)b_p$ is the adjusted density $g(1–X)$ of competitors' pollen, where the coefficient b_p adjusts for spatial clumping. We assume that selfed seeds are unviable with probability k, so that the production of viable seeds is given by $f(X) = X(1 - k \cdot \mathit{selfed})$.

Similar modifications to $f(X)$ could also be caused by mechanisms other than selfing. For example, if seed-dispersing animals are disproportionally attracted to high-yield plants (Vamosi *et al.*, 2007), seeds on low-yield plants may perish because of dispersal failure. As perished seeds do not yield any fitness to their mother, this effectively reduces the value of $f(X)$ at the low end of X.

We let the pollen available for export follow a linear function, $g(1 - X) = 1 - X$, implying that selfing uses up a negligible amount of pollen (no pollen discounting).

It is important to note that the linearity or nonlinearity in f refers to the stage of seed production and is thus independent of our central question which is to analyse the pathway to nonlinearity envisaged by Maynard Smith (1978): whatever the scaling rules that determine the numbers of seeds and pollen, they subsequently will have to compete locally over germination or fertilization opportunities, and this can yield saturating fitness gains depending on competitor numbers.

Sex allocation in a purely cosexual population

An individual's fitness gains through seed or pollen production can be partitioned according to the success of its dispersal units at any given distance from the individual's location. We first consider seeds. Dispersal kernels in our model are continuous (as outlined in Fig. 2) but, for the sake of argument, we will divide

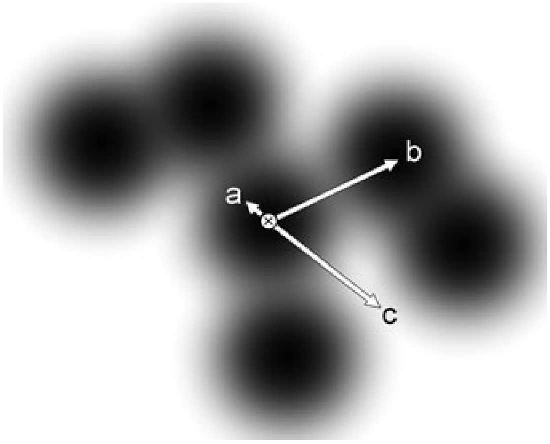

Fig. 2 Outline of the spatial situation envisioned in our model. Dark blotches represent areas of high seed density (seed shadows) around individual plants. If dispersal distances from the focal individual (marked x) are short (a), seeds compete mostly with sibling seeds, making high investment in seed production unprofitable. If dispersal distances are long (b, c), any competition faced is likely from nonsiblings, making seed success chances nearly independent of their mother's total investment. An analogous argument applies to pollen.

space into narrow concentric rings with the parent plant in the centre. The narrower the rings the better the approximation, and the analysis below makes the calculation accurate by deriving the success of plants by letting the rings become infinitesimally narrow. A mutant allocating $\hat{X}(0<\hat{X}<1)$ resources to seed production transfers $\int_{r_1}^{r_2} D(r,d_s)f(\hat{X})dr$ seeds to any ring-shaped area between the distances r_1 and r_2, where on average they compete against $b_s f(X)\cdot\pi(r_2^2-r_1^2)$ seeds produced by resident strategists ('resident seeds'). Here, the coefficient b_s adjusts for spatial clumping of resident seeds.

If we consider a narrow ring-shaped area (such that $r_1 \approx r_2$), all mutant seeds within this area have approximately the same chances of success (i.e. we can neglect the effect that mutant seeds face somewhat stronger competition from each other on the inner part of the ring). The relative success of mutant seeds in this area is then $\int_{r_1}^{r_2} D(r,d_s)f(\hat{X})\cdot dr \Big/ \left(\int_{r_1}^{r_2} D(r,d_s)f(\hat{X})\cdot dr + b_s f(X)\cdot\pi(r_2^2-r_1^2)\right)$.

In the limit, where $r_2 \to r_1$, we obtain the distance-dependent seed success rate

$$v_s(\hat{S},S,d_s,b_s,r)=\frac{D(r,d_s)f(\hat{X})}{D(r,d_s)f(\hat{X})+2\pi r b_s f(X).} \tag{1}$$

Taking into account that reproductive opportunities available at distance r increase in proportion to the circumference $2\pi r$ of a correspondingly sized circle, the mutant's fitness gain from seed production is

$$F_s(\hat{X},X,d_s,b_s)=\int_{r=0}^{\infty} 2\pi r\cdot v_s(\hat{X},X,d_s,b_s,r)dr. \tag{2}$$

The success of outbreeding pollen is developed exactly analogously. The mutant's distance-dependent pollen success rate is thus

$$v_p(\hat{X},X,d_p,b_p,r)=\frac{D(r,d_p)g(1-\hat{X})}{D(r,d_p)g(1-\hat{X})+2\pi r b_p g(1-X),} \tag{3}$$

and its fitness gained from outbreeding pollen is proportional to $\int_{r=0}^{\infty} 2\pi r\cdot v_p(\hat{X},X,d_p,b_p,r)dr$. Selfing affects fitness gains from the male function in two ways. First, the focal mutant gains a fitness component $selfed(\hat{X},X)(1-k)F_s$ from selfing. Second, because a proportion *selfed* (X, X) $(1-k)$ of residents' offspring are produced by selfing, the number of offspring produced by outbreeding is correspondingly reduced. Thus, the mutant's total fitness via the male function is given by

$$\begin{aligned} F_p(\hat{X},X,d_p,b_p) &= selfed(\hat{X},X)(1-k)F_s \\ &\quad + (1-selfed(X,X)(1-k)) \\ &\quad \int_{r=0}^{\infty} 2\pi r\cdot v_p(\hat{X},X,d_p,b_p,r)dr. \end{aligned} \tag{4}$$

To ensure internal consistency of our model, we must now implement two logical constraints. First, in a population at density dependent equilibrium, average fitness is independent of the strategies being adopted. Second, in a sexually reproducing population, the population-wide total fitness gained through the male function must equal the population-wide total fitness gained through the female function (the so-called Fisher condition, Houston & McNamara, 2005). These constraints are met when

$$F_s(X,X,d_s,b_s)=F_p(X,X,d_p,b_p)=1. \tag{5}$$

In other words, any cosexual strategy, when competing against itself, attains unity fitness from seed production and unity fitness from pollen production. Because the F_i functions are monotonously decreasing in b_i and are independent of X given that $\hat{X}=X$, there is a unique pair of $\{b_s,b_p\}$ values satisfying eqn (5) for given parameter values. These 'clumping coefficients' b_i lie in the range $0 < b_i < 1$, are easily found numerically, and take lower values as the degree of spatial clumping increases. This means that for a focal resident, competing against a background of clumped dispersal units is equivalent in effect to competing against a smaller number of homogeneously distributed units, as adjusted by b_i. Based on the assumption that a focal mutant is similarly affected by its surrounding spatial configuration, the coefficients b_i can be used to approximately account for the effect of spatial clumping. Essentially, this approach amounts to comparing the performance of mutants and residents against the same simplified background.

A mutant's total fitness gain from both seed and pollen production is given by:

$$W(\hat{X},X,d_s,d_p)=F_s(\hat{X},X,d_s,b_s)+F_p(\hat{X},X,d_s,b_s,d_p,b_p). \quad (6)$$

We can find a stationary point in this function by setting

$$\left.\frac{\partial W(\hat{X},X,d_s,d_p)}{\partial \hat{X}}\right|_{\hat{X}=X}=0 \quad (7)$$

and solving for X. This is a fitness maximum and hence a candidate evolutionary stable strategy (ESS) (Maynard Smith, 1982) to which we refer as X^*, if

$$\left.\frac{\partial^2 W(\hat{X},X,d_s,d_p)}{\partial^2 \hat{X}}\right|_{\hat{X}=X}<0. \quad (8)$$

Evolutionary stability

Now a population may contain three types of individuals: a proportion p of cosexuals using sex allocation X, a proportion $(1 - R)$ $(1 - p)$ of females, and a proportion R $(1 - p)$ of males. Here, R is the sex ratio among unisexuals, i.e. the proportion of dioecious individuals that are males. To find the best cosexual strategy X^* in this population, we generalize eqn (1) to

$$v_s(\hat{X},X,d_s,b_s,r,p,R) = \frac{D(r,d_s)f(\hat{X})}{D(r,d_s)f(\hat{X})+2\pi r b_s(pf(X)+(1-R)(1-p)f(1))} \quad (9)$$

which has in its denominator the contribution of the $(1 - R)$ $(1 - p)$ females to seed production. Note that females, producing no pollen, do not incur a cost of selfing. Similarly, eqn (3) generalizes to

$$v_p(\hat{X},X,d_p,b_p,r,p,R) = \frac{D(r,d_p)(1-\hat{X})}{D(r,d_p)(1-\hat{X})+2\pi r b_p(p(1-X)+(1-p)R)} \quad (10)$$

taking into account the contribution of the $(1 - p)$ R males to pollen production. To ensure that population-wide per capita fitness gain from each the female and the male function is unity, we choose coefficients $\{b_s, b_p\}$ satisfying

$$\begin{aligned} &pF_s(X,X,d_s,b_s,p,R)+(1-p)RF_s(1,X,d_s,b_s,p,R)= \\ &pF_p(X,X,d_p,b_p,p,R)+(1-p)(1-R)F_p(0,X,d_p,b_p,p,R)=1. \end{aligned} \quad (11)$$

Using these $\{b_s, b_p\}$ values, eqns (9) and (10) allow us to derive a fitness function analogous to eqn (6). For a given sex ratio R among dioecious individuals and for a given strategy X of resident cosexuals, the best cosexual mutant strategy achieves fitness

$$W_{\mathrm{cosex}}=\max_{\hat{X}}\left(W(\hat{X},X,d_s,d_p,k,p,R)\right), \quad (12)$$

which we can approximate numerically by computing solutions at $\hat{X}=\{0.01,0.02,\ldots,0.99\}$. Note that mutant fitness becomes independent of X when cosexuals are very rare. Assuming that unisexuals occur at their optimal sex ratio $R = R^*$, their fitness is given by

$$\begin{aligned} W_{\mathrm{dioecy}}=\max_{R}\big(&RW(1,X,d_\mathrm{s},d_\mathrm{p},k,p,R) \\ &+(1-R)W(0,X,d_\mathrm{s},d_\mathrm{p},k,p,R)\big). \end{aligned} \quad (13)$$

Note that this optimum R^* will depend on the sex allocation X of cosexuals. We can numerically approximate R^*, and hence W_{dioecy}, by computing solutions at $R=\{0.00,0.01,\ldots,1.00\}$.

Cosexuality is evolutionarily stable if

$$W_{\mathrm{cosex}} > \left.W_{\mathrm{dioecy}}\right|_{\substack{X=X* \\ p=1}}. \quad (14)$$

Dioecy is evolutionarily stable if

$$W_{\mathrm{dioecy}} > \left.W_{\mathrm{cosex}}\right|_{p=0}. \quad (15)$$

Although our game-theory model is flexible in certain respects (e.g. it can be derived for any shape of a dispersal kernel), it does not account for some other aspects, such as stochasticity, and kin competition after the stage of germination. To account for such processes, we have also performed individual-based simulations to examine the robustness of our results. The details of these simulations are given in the Electronic Appendix S1 – Figs S1–S4.

Results

Gain functions

Our model produces fitness gain curves for each sex that are saturating for short dispersal distances but are approximately linear for long dispersal distances (Fig. 3a, b). This pattern is robust to the shape of dispersal kernel (Appendix S1 – Fig. S5). Selfing costs, however, can change the shape of the female gain function from saturating to accelerating, especially if dispersal distances are long (Fig. 3c).

Sex allocation

In the absence of selfing, cosexuals invest more in whichever sex function produces more widely dispersing units (Fig. 4a). Selfing modifies this pattern towards greater investment in seed production (Fig. 4b). These patterns, shown for a negative exponential dispersal kernel in Fig. 4, look very similar for a half-normal

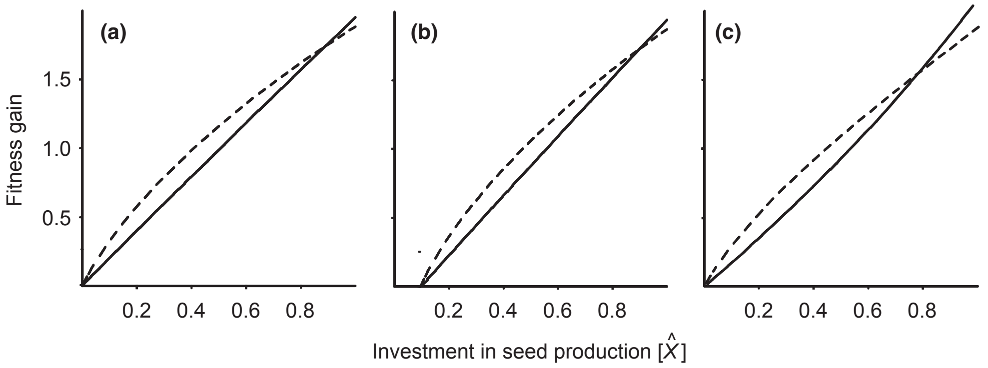

Fig. 3 Fitness gain from investment in seed production (eqn 2) by a cosexual individual, assuming (a) neither start-up costs nor selfing costs; (b) start-up costs for seed production ($C = 0.1$) that are independent of the amount produced; or (c) selfing costs ($k = 0.7$). Dispersal follows a negative exponential kernel with mean $d_s = 0.5$ (broken line) or $d_s = 5$ (solid line), respectively. Pollen dispersal is $d_p = 5$.

kernel (Appendix S1 – Fig S6). The magnitude of any start-up costs has no influence on how the remaining resources are allocated to either sex function.

Evolution of dioecy

Dioecy requires for its evolution a suitable nonlinearity in the fitness functions. In our model, such nonlinearity can arise either because of start-up costs associated with each sex function (case 1) or because of costs of selfing (case 2). Dioecy readily evolves if start-up costs (Fig. 5) or selfing costs (Fig. 6) are high, and if both seeds and pollen disperse far (Figs 5 and 6; Appendix S1 – Figs S1–S4). However, under selfing costs, the required dispersal distance is much less for pollen than for seeds (Fig. 6; Appendix S1 – Figs S3 and S4). If selfing costs coincide with low seed dispersal, far-dispersing pollen can also have the opposite effect of stabilizing cosexuality (Fig. 6).

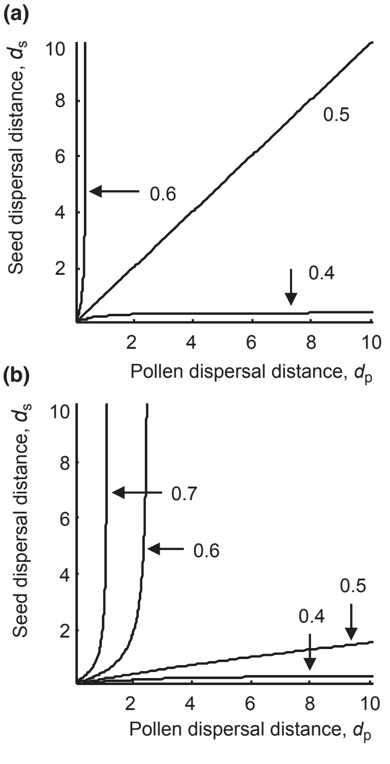

Fig. 4 Isoclines of optimal allocation X^* to seed production in a cosexual population, assuming a negative exponential dispersal kernel and (a) no selfing or (b) selfing with costs of magnitude $k = 0.65$.

The regions in parameter space where cosexuality and dioecy are ESSs, respectively, are separated by a narrow area where either or neither pure strategy is an ESS. This area is further subdivided into areas where cosexuality can be invaded only by males, only by females, or by both sexes (Figs 5 and 6). These results are qualitatively robust with respect to the type of dispersal kernel assumed. However, the stability conditions of dioecy are slightly broader if a half-normal rather than a negative exponential dispersal kernel is assumed (Figs 5 and 6; Appendix S1 – Figs S1–S4).

Discussion

Confirming and expanding on previous arguments (Maynard Smith, 1978; Lloyd & Bawa, 1984), our model shows that dioecy evolves more easily in plant species with widely dispersing seeds and pollen. Conversely, dispersal limitations tend to stabilize cosexuality. This is because limited dispersal makes 'sibling' dispersal units (seeds or pollen) compete for the same germination and fertilization opportunities, such that increasing seed or pollen production gives diminishing returns (Fig. 3) and a better strategy is to invest some effort in producing both.

Another prediction from our model is that cosexuals should bias their investment towards the sex function associated with wider dispersal (cf. Lloyd & Bawa, 1984), which is typically the male function (Levin & Kerster,

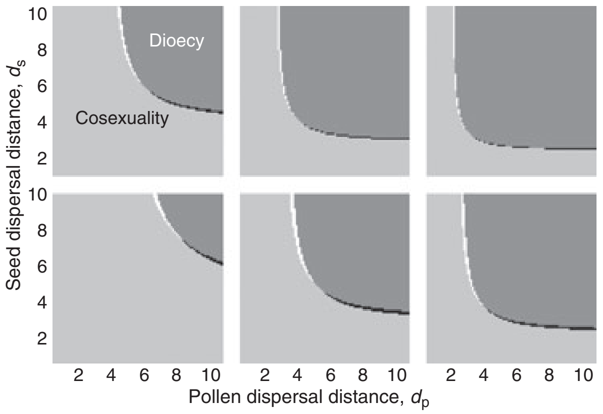

Fig. 5 Areas of evolutionary stability when a fixed start-up cost (panels from left to right: $C = 0.01$; $C = 0.02$; $C = 0.03$) has to be paid for each sex function before any further investment translates into gametes. Dispersal kernels (cf. Fig. 1) follow a half-normal (upper row) or negative exponential (lower row) distribution. Outcomes include dioecy (dark grey) cosexuality (light grey), and areas where neither pure strategy is stable, and where cosexuality can be invaded by male mutants (white), or female mutants (black).

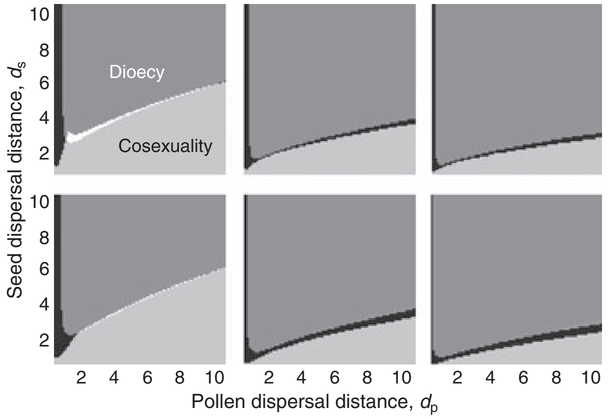

Fig. 6 Areas of evolutionary stability when cosexuality is associated with a cost of selfing that increases from left to right panels (left: $k = 0.6$; middle: $k = 0.7$; right: $k = 0.8$), assuming that dispersal follows a half-normal (upper row) or negative exponential (lower row) distribution. Outcomes include dioecy (dark grey) cosexuality (light grey), and areas where either (white) or neither pure strategy is stable, and where cosexuality can be invaded by female mutants (black), or both male and female mutants (striped).

1974; Hu & Ennos, 1997; Latta *et al.*, 1998). As with the evolution of dioecy, such an allocation bias can be interpreted as a strategy to reduce self-competition, i.e., competition among dispersal units from the same parent. This finding contradicts Iyer & Roughgarden's (2008) recent claim that cosexual individuals should always invest equally in both sex functions. As detailed in Appendix A, Iyer and Roughgarden reached this (incorrect) conclusion by re-evaluating a model by Charnov (1982), but in doing so failed to recognize how competition via male and female function occurs at different scales.

In addition to spatial clumping, the net benefits of dioecy vs. cosexuality are also influenced by any 'start-up' costs of possessing the machinery for producing both seeds and pollen and by the cost of selfing. High start-up costs and selfing costs both select for dioecy (Figs 5 and 6). Cosexuals respond to selfing costs by investing less in pollen (Fig. 4), which reduces the extent of selfing. Moreover, because selfing interferes especially with cosexuals' female function, it facilitates the invasion of females (Fig. 6) who can avoid these costs. The effect of pollen dispersal in our model depends on the type of cost assumed. Low pollen dispersal increases self-competition of the male function, thus potentially stabilizing cosexuality (Fig. 5). On the other hand, low pollen dispersal may increase the risk of selfing, thus selecting for dioecy as an outbreeding mechanism (Fig. 6).

According to our model, high population density has an effect equivalent to wide dispersal in facilitating the evolution of dioecy. This is because our results are governed by the relative strengths of competition at two levels: first, between the same plant's dispersal units; second, between dispersal units from different plants. Between-plant competition becomes relatively more important when more competitors are 'within reach', which may be the case either because they are nearby, or because their seeds and pollen disperse widely. This argument can also be used to extend the results to dispersal kernels that we did not explicitly consider. Fat-tailed kernels, for example, are likely to have a similar effect as wide dispersal in general, because they similarly increase the number of competitors 'within reach'.

An interesting feedback between sexual system and spatial configuration arises from the fact that, for a given population density, cosexuality implies a greater density of seed and pollen sources. If (say) pollen is distributed by twice as many individuals under cosexuality than under dioecy, this causes a more even pollen distribution across the habitat. Reduced spatial clumping relaxes self-competition, leading to less saturating fitness gains from each sex function. This association between cosexuality and less saturating gains, combined with the result that saturating gains stabilize cosexuality, can lead to negative frequency-dependent selection. For example, if cosexual mutants invade a dioecious population, this may change the sex-specific fitness gain functions such that it eliminates their initial advantage. This negative frequency-dependence is reflected by narrow areas of parameter space where cosexuality and dioecy can mutually invade each other (Fig. 6). The possibility of such mutual invasibility contradicts earlier findings of a nonspatial model (Wolf & Takebayashi, 2004) and suggests a novel explanation for the rare maintenance of all three sex morphs (trioecy) in some species (Geber *et al.*, 1999).

Consistent with Charlesworth & Charlesworth (1978), selfing costs in our model facilitate the invasion of female (rather than male) mutants (Fig. 6), which may explain the more frequent occurrence of gynodioecy as compared to androdioecy in nature.

Another possible feedback, not accounted for here, may exist between sexual system and inbreeding depression (e.g. Lande *et al.*, 1994). Frequent selfing in cosexual populations may facilitate purging of deleterious recessive alleles, thus limiting the strength of inbreeding depression. On the other hand, less effective purging may lead to higher degrees of inbreeding depression under dioecy. In the light of the present model, this effect would stabilize dioecy once evolved.

As we derive very similar results from a game-theory approach (that necessitates some approximations) as well as from an individual-based simulation (electronic Appendix A), the predictions appear robust with respect to the modelling approach used. We will therefore now turn to examining how well these predictions hold in nature. Dispersal and dioecy have been linked by various lines of empirical evidence. Dioecious plants often have fleshy fruits dispersed by birds (Bawa, 1980; Vamosi *et al.*, 2003). This is thought to be a particularly effective dispersal mode (Hubbell, 1979), which may also explain why dioecious species are overrepresented in island floras (Bawa, 1982; Lloyd, 1982). In terms of our model, this pattern could be interpreted such that bird dispersal facilitated the evolution of dioecy by relaxing competition between maternal siblings. An alternative (but not mutually exclusive) explanation for the same pattern has been proposed by Bawa (1980) and Givnish (1980): if birds are disproportionally attracted to high-yield plants, this will generate an incentive for plants to maximize their fruit yield, thus favouring the evolution of specialized females. In other words, there will be an accelerating fitness gain curve for the female function as a direct result of bird behaviour. However, such disproportional bird attraction lacks empirical support (Howe, 1980, 1981; Russo, 2003).

Correlations between dioecy and certain pollination modes have also been reported. Dioecious plants often have small, inconspicuous, greenish flowers pollinated by small generalist bees and flies (Thomson & Brunet, 1990). Although such insects have been suggested to be highly responsive to flower number, potentially leading to accelerating returns from male function (Bawa, 1980), there appears to be no evidence to support this view. Neither do these small insects typically cover distances large enough to greatly reduce competition between pollen from the same plant (Bawa, 1980). However, as already speculated by Lloyd (1982), the habit of small generalist insects to visit the same plant repeatedly may create a high risk of selfing, potentially selecting for dioecy as an outbreeding mechanism.

Dioecy is also associated with wind pollination and with a woody growth form (Vamosi *et al.*, 2003). These features may favour the evolution of dioecy as follows. Our model predicts that conditions where selfing costs are likely to arise will favour dioecy as such conditions select against the production of both seed and pollen in the same area. The undirected movement of pollen by wind, and the spatial concentration of flowers on a (typically large) woody plant, may both elevate the risk of selfing, which then favours the evolution of dioecy as an outbreeding mechanism. On the other hand, both wind dispersal and large size of adult plants may facilitate long-distance pollen movement (Klinkhamer *et al.*, 1997; De Jong & Klinkhamer, 2005), and, as shown in our model, this makes saturating gain functions less likely. Indeed, there is accumulating evidence for wind pollination yielding less saturating gain curves than biotic pollination (De Jong & Klinkhamer, 2005). It could also be argued that woody, large plants, with their typically long generation times, are under increased pressure to produce varied, outbred offspring that present new challenges to their faster-evolving parasites. This would effectively increase the viability cost k of selfing for woody plants. Although this last hypothesis is rather speculative, the net effect of woody growth form on fitness gain functions clearly deserves much more attention.

One limitation of our game-theory model is that it accounts for population kin structure only up to the point of germination. It is therefore reassuring to note that the results of our individual-based simulations (electronic Appendix A) are in good qualitative agreement with the game-theory model. In individual-based simulations, kin structure and kin competition can arise automatically, without any need to formulate its action explicitly.

To conclude, and contrasting with some other recent work (Iyer & Roughgarden, 2008), we have shown that sex allocation can respond to unequal dispersal distances of seeds and pollen. There is some support for the predictions, e.g. that sex allocation is biased towards the longer dispersing sex. However, the precise shape of the gain curves has rarely been measured in nature. It is clearly a future challenge to do so.

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References

Ashman, T.L. 1999. Determinants of sex allocation in a gynodioecious wild strawberry: implications for the evolution of dioecy and sexual dimorphism. *J. Evol. Biol.* **12**: 648–661.

Baeza, J.A. 2007. Male mating opportunities affect sex allocation in a protrandric-simultaneous hermaphroditic shrimp. *Behav. Ecol. Sociobiol.* **61**: 365–370.

Barot, S. & Gignoux, J. 2004. How do sessile dioecious species cope with their males? *Theor. Popul. Biol.* **66**: 163–173.

Bawa, K.S. 1980. Evolution of dioecy in flowering plants. *Annu. Rev. Ecol. Syst.* **11**: 15–39.

Bawa, K.S. 1982. Outcrossing and the incidence of dioecism in island floras. *Am. Nat.* **119**: 866–871.

Charlesworth, D. 2006. Evolution of plant breeding systems. *Curr. Biol.* **16**: R726–R735.

Charlesworth, B. & Charlesworth, D. 1978. Model for evolution of dioecy and gynodioecy. *Am. Nat.* **112**: 975–997.

Charlesworth, D. & Charlesworth, B. 1990. Inbreeding depression with heterozygote advantage and its effect on selection for modifiers changing the outcrossing rate. *Evolution* **44**: 870–888.

Charnov, E.L. 1982. *The Theory of Sex Allocation*. Princeon University Presss, Princeton, NJ.

Charnov, E.L., Smith, J.M. & Bull, J.J. 1976. Why be an hermaphrodite. *Nature* **263**: 125–126.

Darwin, C. 1877. *The Different Forms of Flowers on Plants of the Same Species*. John Murray, London.

De Jong, T.J. & Klinkhamer, P.G.L. 2005. *Evolutionary Ecology of Plant Reproductive Strategies*. Cambridge University Press, Cambridge.

Delph, L.F. 1990. Sex-differential resource-allocation patterns in the subdioecious shrub *Hebe subalpina*. *Ecology* **71**: 1342–1351.

Dorken, M.E. & Pannell, J.R. 2008. Density-dependent regulation of the sex ratio in an annual plant. *Am. Nat.* **171**: 824–830.

Dorken, M.E. & Pannell, J.R. 2009. Hermaphroditic sex allocation evolves when mating opportunities change. *Curr. Biol.* **19**: 514–517.

Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**: 345–364.

Geber, M.A., Dawson, T.E. & Delph, L.F. 1999. *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, Heidelberg.

Givnish, T.J. 1980. Ecological constraints on the evolution of breeding systems in seed plants – dioecy and dispersal in gymnosperms. *Evolution* **34**: 959–972.

Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* **156**: 477.

Hamilton, W.D. & May, R.M. 1977. Dispersal in stable habitats. *Nature* **269**: 578–581.

Heilbuth, J.C., Ilves, K.L. & Otto, S.P. 2001. The consequences of dioecy for seed dispersal: modeling the seed-shadow handicap. *Evolution* **55**: 880–888.

Houston, A.I. & McNamara, J.M. 2005. John Maynard Smith and the importance of consistency in evolutionary game theory. *Biol. Philos.* **20**: 933–950.

Howe, H.F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* **61**: 944–959.

Howe, H.F. 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *Auk* **98**: 88–98.

Hu, X.S. & Ennos, R.A. 1997. On estimation of the ratio of pollen to seed flow among plant populations. *Heredity* **79**: 541–552.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**: 1299–1309.

Iyer, P. & Roughgarden, J. 2008. Dioecy as a specialization promoting sperm delivery. *Evol. Ecol. Res.* **10**: 867–892.

Jarne, P. & Auld, J.R. 2006. Animals mix it up too: The distribution of self-fertilization among hermaphroditic animals. *Evolution* **60**: 1816–1824.

Klinkhamer, P.G.L., deJong, T.J. & Metz, H. 1997. Sex and size in cosexual plants. *Trends Ecol. Evol.* **12**: 260–265.

Lande, R., Schemske, D.W. & Schultz, S.T. 1994. High inbreeding depression, selective interference among loci, and the threshold selfing rate for purging recessive lethal mutations. *Evolution* **48**: 965–978.

Latta, R.G., Linhart, Y.B., Fleck, D. & Elliot, M. 1998. Direct and indirect estimates of seed versus pollen movement within a population of ponderosa pine. *Evolution* **52**: 61–67.

Levin, D.A. & Kerster, H.W. 1974. Gene flow in seed plants. *Evol. Biol.* **7**: 139–220.

Lloyd, D.G. 1979. Some reproductive factors affecting the selection of self-fertilization in plants. *Am. Nat.* **113**: 67–79.

Lloyd, D.G. 1982. Selection of combined versus separate sexes in seed plants. *Am. Nat.* **120**: 571–585.

Lloyd, D.G. & Bawa, K.S. 1984. Modification of the gender of seed plants in varying conditions. *Evol. Biol.* **17**: 255–338.

Maynard Smith, J. 1978. *The Evolution of Sex*. Alden Press, Oxford.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Mazer, S.J., Delesalle, V.A. & Neal, P.R. 1999. Responses of floral traits to selection on primary sexual investment in Spergularia marina: the battle between the sexes. *Evolution* **53**: 717–731.

Porcher, E., Kelly, J.K., Cheptou, P.O., Eckert, C.G., Johnston, M.O. & Kalisz, S. 2009. The genetic consequences of fluctuating inbreeding depression and the evolution of plant selfing rates. *J. Evol. Biol.* **22**: 708–717.

Renner, S.S. & Ricklefs, R.E. 1995. Dioecy and its correlates in the flowering plants. *Am. J. Bot.* **82**: 596–606.

Ronce, O., Gandon, S. & Rousset, F. 2000. Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* **58**: 143–159.

Russo, S.E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* **136**: 80–87.

Schärer, L. 2009. Tests of sex allocation theory in simultaneously hermaphroditic animals. *Evolution* **63**: 1377–1405.

Thomson, J.D. & Brunet, J. 1990. Hypotheses for the evolution of dioecy in seed plants. *Trends Ecol. Evol.* **5**: 11–16.

Vamosi, J.C., Otto, S.P. & Barrett, S.C.H. 2003. Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *J. Evol. Biol.* **16**: 1006–1018.

Vamosi, J.C., Zhang, Y. & Wilson, W.G. 2007. Animal dispersal dynamics promoting dioecy over Hermaphroditism. *Am. Nat.* **170**: 485–491.

Wilson, W.G. & Harder, L.D. 2003. Reproductive uncertainty and the relative competitiveness of simultaneous hermaphroditism versus dioecy. *Am. Nat.* **162**: 220–241.

Wolf, D.E. & Takebayashi, N. 2004. Pollen limitation and the evolution of androdioecy from dioecy. *Am. Nat.* **163**: 122–137.

Appendix A

Iyer & Roughgarden (2008) (henceforth referred to as IR) reject the idea that the ESS sex allocation depends on mating patterns, claiming that ‘in any group with sperm competition between individuals, the ESS sex allocation is 50:50, as is the ESS sex ratio for dioecious species’. To develop their argument, IR consider the following model by Charnov (1982): among outbreeding hermaphrodites that mate with k individuals each, individuals allocate a fraction r of their reproductive resources to sperm production, the remaining $1 - r$ being allocated to egg production. All eggs are fertilized, so that fitness from the female function is proportional to investment in egg production. The fitness of a mutant allocating $\hat{r}$ to sperm production is then

$$w(\hat{r}) = 1 - \hat{r} + k(1 - r)\frac{\hat{r}}{\hat{r} + (k-1)r}. \tag{A1}$$

Finding the maximum of this function and setting $\hat{r} = r$ gives $r* = \frac{k-1}{2k-1}$, to which Charnov refers as the ESS sex allocation. For finite k, this implies female-biased sex allocation, $r^* < 1/2$.

IR challenge the view that r^* represents an ESS by pointing out that residents using sex allocation $r = 0.5$ always have higher fitness than any mutant in the same 'mating group' of size k. A critical question in this context is what exactly is meant by 'mating group'. IR, by comparing fitness between mating group members, implicitly interpret 'mating group' to mean 'a population in which each individual mates with all other individuals'. Charnov, in contrast, used the term 'mating group' to refer to a focal individual and its k mates, which together constitute a subset of a much larger population. This definition includes situations where these k mates also mate with each other, or each mate with a different set of mates. Thus, competition occurs at two different scales. Via the male function, competition occurs among sperm within 'females' (the mating group scale), leading to diminishing fitness returns. Via the female function, competition occurs among offspring that are unlikely to compete with sibs (the population scale), leading to linear fitness returns.

In summary, Charnov's insight that competition via male and female function may occur at different scales was missed by IR, who assumed that both scales (mating group and population) are the same. We, therefore, conclude that IR's criticism of Charnov's work is misguided.

Although tangential to the above argument, it is worth noting that IR create further potential for confusion by deviating from Charnov's model in two ways that they do not explicitly acknowledge: first, they allow for self-fertilization, thus negating the assumption of outbreeding; second, they refer to groups of size k rather than $(k + 1)$ as in the original model.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Individual-based simulations.

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