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How do sessile dioecious species cope with their males?

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Abstract

In terrestrial plants the segregation of male and female reproductions on different individuals results in the seed-shadow handicap: males do not disperse any seed so that the number of local patches reached by seeds is potentially reduced in dioecious populations in comparison to hermaphrodite populations. An analytical model, incorporating a lottery-based recruitment and dispersal stochasticity, was built. The spatially mediated cost of the seed-shadow handicap has been assessed considering the criterions for the invasion of a resident hermaphrodite species by a dioecious species and the reverse invasion, both species having the same demographic parameters but assuming a likely higher fecundity for dioecious females. The reciprocal invasion of a dioecious and hermaphrodite species differing only by their fecundity is never possible. The seed-shadow handicap disappears when the dispersal or survival rate is high enough. This latter point is due to dispersal stochasticity, which allows for the existence of empty patches. A low fecundity and an aggregated seed distribution increase dispersal stochasticity and increase the positive impact of a low mortality rate on the relative competitivity of dioecy and hermaphroditism. Adding a dispersal cost has a comparable effect but also requires higher dispersal rates for the dioecious invasion.

Keywords: Dioecy; Seed dispersal; Invasion criterion; Competition for space; Sessile organisms; Lottery model; Dispersal stochasticity

1. Introduction

Dioecy is recognized to have evolved for two main reasons (Bawa, 1980; Thomson and Brunet, 1990). First, dioecy is a way to avoid auto-fecundation and the consequent inbreeding depression (Charlesworth and Charlesworth, 1978). Second, dioecy might lead to a more efficient use of resources when male and female reproductions use the same resources and do not share costs (Charnov and Maynard Smith, 1976). However, since terrestrial plants are sessile, dioecy also leads to the spatial segregation of female and male reproductions: males and females functions are achieved by different immobile individuals that may stand away from each other.

On the one hand, when female gametes are not dispersed before fecundation, as in flowering plants, females and males do not produce offspring unless pollen is dispersed far enough to reach females. On the other hand, all seeds are released by females. Considering two dioecious and hermaphrodite populations, having the same adult spatial pattern and the same seed dispersal distance distribution, the seed-shadow, i.e. the whole area to which a population disperses its seeds, is likely much wider for the hermaphrodite population than for the dioecious population. This confers higher dispersal ability to hermaphrodite species. Dioecious species can be considered to bear a seed-shadow handicap (Baker, 1955; Heilbuth et al., 2001). In particular, since some seeds are always expected to fall in their mother local patch, patches freed by the death of adults are more easily recolonized in hermaphrodite species than in dioecious species. In these species, recolonization of male patches requires, symmetrically to the dispersal of pollen from males to females, the uncertain dispersal of seeds from females that may stand far away. Consequently, dioecious species have to face the loss of two symmetric assurances: the "reproductive assurance" that ensures that all individuals of

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hermaphrodite self-compatible populations reproduce, and the "dispersal assurance" that ensures that all individuals of hermaphrodite populations disperse seeds. Demographic costs of dioecy have been recognized for a long time (Baker, 1955, 1967; Pannell and Barrett, 1998). Recently, the impact of the seed-shadow handicap has been emphasized using simulation models ([13]Heilbuth et al., 2001). We present here an analytical model analyzing this demographic cost. The model was derived from Gignoux's model of coexistence (Gignoux, 1994), to which the possibility of separated sexes has been added.

(1) We compared the necessary conditions for the persistence of hermaphrodite and dioecious species in isolation. (2) We derived the criterion for the invasion of resident hermaphrodite species by dioecious species introduced at low density as well as the criterion for the reverse invasion (Shmida and Ellner, 1984). (3) The invasion criterions were used to assess the seed shadow handicap. (4) The effect of a dispersal cost on the seed-shadow was determined. Establishing an invasion criterion is a very general way to assess the relative competitive ability of different species (Metz et al., 1992; Chesson, 2000). If the loss of dispersal assurance has no effect on the demography of a dioecious species, this species, provided a slight demographic advantage (for example in fecundity or survival), should be able to invade an equivalent hermaphrodite species. Deriving the criterion for the reverse invasion of an established dioecious population is important to assess the seed-shadow handicap but also to determine the outcome of an invasion by a dioecious species. If, and only if, both species are able to invade each other, they coexist in a stable way (Dieckmann, 1997).

2. Model hypotheses

Individuals of the different species (identified by subscripts) compete for space in an infinite spatially homogeneous regular lattice: only one adult can survive in each cell (local patch). Time is discrete (reproduction is seasonal). Although the model is not truly spatially explicit, the dispersal process is a source of spatial heterogeneity. In each cell deprived of adult, and in which some seeds have fallen (no dormancy has been considered), a new adult is recruited and its species is chosen according to a competitive lottery process (Chesson and Warner, 1981). No temporal or spatial environmental variability is considered. The system is described by P the proportion of cells occupied by no adult and by M_i and F_i the respective proportions of cells occupied by species i males and females (for a hermaphrodite species, F_i is the proportion of cells occupied by all adults). At each time step, and for each species i, (1) a proportion δ_i of adults dies (same mortality rate for males and females), (2) each adult female produces β_i seeds, (3) a proportion d_i (dispersal rate) of seeds is dispersed with an equal probability to any cell of the lattice but to the mother cell (global dispersal), while a proportion $1 - d_i$ of the seeds remains in the mother cell (no dispersal), (4) when there is no adult in a cell, a new one is recruited from the local seed pool and the probability that the recruited adult is of species i is the ratio of the number of species i seeds to the total number of seeds, (5) s_i is the proportion of adult individuals that produce seeds. For a dioecious species, it is the primary sex ratio of seeds, i.e. the proportion of female seeds. It is also the sex ratio of adults since male and female recruitment and mortality rates are supposed equal. Reproduction was never considered as limited by the availability of male gametes and was thus independent of both the sex ratio and the proportion of cells occupied by males. Thus, we only need to analyze the dynamics of females (F_i). When $s_i = 0.5$ the species can be considered as dioecious with an even sex ratio. When $s_i = 1$, all individuals produce seeds and the species can be considered as hermaphrodite. In this way, the same equations hold for both hermaphrodite and dioecious species.

Throughout the paper we consider two species, species 1 being dioecious ($s_1 = 0.5$), species 2 being hermaphrodite ($s_2 = 1$). To compare the dynamics of a hermaphrodite species to the dynamics of an "equivalent" dioecious species having the same survival and dispersal rates ($d_2 = d_1 = d$, $\delta_2 = \delta_1 = \delta$), as Wilson and Harder (2003) did, we consider that the fecundity of the dioecious species is ϕ times higher than the fecundity of the hermaphrodite species ($\beta_2 = \beta_1/\phi = \beta$). Throughout the article the term "equivalent dioecious and hermaphrodite species" is used for short and must be understood in his way. The increased fecundity is compatible with both (1) the sexual specialization theory (Charnov and Maynard Smith, 1976; Thomson and Brunet, 1990) and (2) the possible increase in realized fecundity due to the avoidance of inbreeding depression (Maynard Smith, 1989; Crawley, 1996). First, if hermaphrodite individuals invest the same amount of resource in male and female reproduction, dioecious females should have a fecundity twice as large as hermaphrodite females. If resource allocation to female reproduction is higher, dioecious females should have a fecundity lower than this doubled fecundity. Specialization into male or female reproduction may result in a more efficient use of resources, leading to higher fecundities. Second, the fecundity parameter used in the model is a realized fecundity, it is the number of viable seeds produced, released, and able to grow into new individuals. In this way, the parameter ϕ could also describe the increase in reproductive success resulting from the evolution of dioecy in a hermaphrodite species for which inbreeding avoidance cannot be neglected. The upper value for ϕ

was chosen arbitrarily in numerical calculations, but all ϕ values used are compatible with the observed effect of out-crossing in plants (Crawley, 1996).

On average, in a cell occupied by a female of species i, γ_i species i seeds are falling, while everywhere else (under a male of species i, under a male or a female of any other species) λ_i species i seeds are falling:

$$\lambda_i(t) = F_i(t)\beta_i d_i \text{ and } \gamma_i(t) = \lambda_i(t) + \beta_i(t)(1 - d_i(t)). \quad (1)$$

3. Dispersal stochasticity

Since dispersal is considered as stochastic, λ_i and γ_i are the mathematical expectations of the number of seeds falling in each type of cell. The real number of seeds falling in each cell (n_i) follows a probability law, i.e. stochasticity allows for variations in the number of seeds falling in each cell. The process allows for the existence of free cells where no seed has fallen, and where no adult is recruited. This hypothesis of stochastic dispersal is realistic since, especially at low densities of adult females or with low fecundities, important deviations from the expected numbers of seeds are likely to appear (Hurtt and Pacala, 1995; Schupp and Fuentes, 1995).

Assuming that there are 2 species, let $g(N_1,N_2)$ be the recruitment probability of a species 1 individual in a cell where there are on average N_1 and N_2 seeds of species 1 and 2:

$$g(N_1,\ N_2) = (1 - P(\text{no seed})) \times \sum_{\substack{i=0 \\ i+j>0}}^{+\infty} \sum_{j=0}^{+\infty} \frac{i}{i+j} P(n_1 = i)P(n_2 = j).$$

Using the hypothesis that the numbers of seeds, n_1 and n_2, follow 2 independent Poisson (P) laws of parameters N_1 and N_2 (modeling a random distribution of seeds) we get g_P after simplifications:

$$g_P(N_1, N_2) = (1 - e^{-N_1,-N_2})\frac{N_1}{N_1 + N_2}.$$

Similarly, if the numbers of seeds, n_1 and n_2, follow 2 independent binomial (B) laws of parameters (r_1, p) and (r_2, p) (modeling a regular, or over-dispersed, distribution of seeds) we get g_B using the same type of calculations:

$$g_B(r_1, r_2, p) = (1 - (1 - p)^{r_1 + r_2})\frac{r_1}{r_1 + r_2}.$$

Necessarily r_1, r_2 and p are chosen so that $E(n_1) = N_1 = r_1 p$ and $E(n_2) = N_2 = r_2 p$. Thus g_B can be rewritten as a function of N_1 and N_2:

$$g_B(N_1, N_2) = (1 - (1 - p)^{p^{-1}(N_1 + N_2)})\frac{N_1}{N_1 + N_2}.$$

We can also consider that the numbers of seeds, n_1 and n_2, follow 2 independent negative binomial (NB) laws of parameters (r_1, p) and (r_2, p) (modelling a clumped distribution of seeds). p is the probability of success and the random variables are the numbers of failures before getting r_i successes (and not the total numbers of trials as often assumed for NB distributions). Since $E(n_1) = N_1 = r_1(1 - p)/p$ and $E(n_2) = N_2 = r_2(1 - p)/p$ we get

$$g_{\text{NB}}(N_1, N_2) = (1 - p^{p(1-p)^{-1}(N_1 + N_2)})\frac{N_1}{N_1 + N_2}.$$

The three g functions can be rewritten in the same way:

$$g(N_1, N_2) = (1 - e^{k(p)(N_1 + N_2)})\frac{N_1}{N_1 + N_2}. \quad (2)$$

With $k(p)$ equal respectively to $\mathrm{In}(p)p/(1-p)$, -1 and $\ln(1 - p)/p$ for NB, P, and B distributions, p belonging to [0,1]. The second term of g is the probability of recruitment of a species 1 individual knowing that at least one seed has fallen in the considered cell. The first term is the probability of this event.

The P distribution ($k(p) = -1$), for which the mean is equal to the variance, is used to model random distributions (Cressie, 1993). For the B distribution $k(p)$ belongs to $]-\infty, -1]$ and the variance is equal to the product of $(1-p)$ by the mean, so that the variance is lower than the mean. This models regular seed distributions (Cressie, 1993). For the NB distribution $k(p)$ belongs to $]-1, 0]$ and the variance is equal to the product of $1/p$ by the mean, so that the variance is higher than the mean, which models aggregated seed distributions. $k(p)$ is always negative, and the smaller it is, the less likely it is that no seed falls in a cell: the effect of stochastic dispersal gets smaller. In this way, the type of the seed distribution and the value of p determine the strength of dispersal stochasticity. Whatever p, dispersal stochasticity is stronger for NB than for B, i.e. stronger for aggregated than for regular distributions and is intermediate for P, i.e random distribution. We have computed g for B and NB distributions in the simple (and analytically tractable) cases where seeds of the two species have the same p parameter. In our case this is realistic because we want to assess the invasion capability of equivalent species differing only by their reproduction mode (dioecious/hermaphrodite) and thus having the same level of dispersal stochasticity.

4. Persistence criterion

For any species in isolation we have at the equilibrium $P^* + F^* + M^* = 1$ and $P^* < 1$ is a necessary and sufficient condition for the persistence of this species.

Only one species is present, thus we have

$$P(t+1) = F(t)\delta[1-g(\gamma,0)] + M(t)\delta[1-g(\lambda,0)] + P(t)[1-g(\lambda,0)]. \quad (3)$$

The two first terms of this equation stand for the cells that are not recolonized after the death of a male or a female. The third term stands for the free cells that are not recolonized. At equilibrium, this leads to

$$P^* = s(1-P^*)\delta e^{k(p)(s(1-P^*)\beta d+\beta(1-d))} + [(1-s)(1-P^*)\delta + P^*]e^{k(p)s(1-P^*)\beta d}. \quad (4)$$

Computing the derivative of this expression as a function of P^*, we then get the following general persistence criterion:

$$-k(p)\beta\, ds > \delta\left(1-s+se^{k(p)\beta(1-d)}\right). \quad (5)$$

This leads to the following criterion for a hermaphrodite species ($s=1$):

$$-k(p)\beta d > \delta e^{k(p)\beta(1-d)}.$$

Eq. (4) can be used to derive numerically the value of P^*. For a P distribution ($k(p)=-1$), inequality (5) means that for a dioecious species to persist, the number of seeds produced and dispersed by the whole female population (left-hand side of the inequality), must be higher than the number of adults dying without recruiting locally any of their offspring (right-hand side of the inequality). This inequality takes into account the fact that dying individuals might be males (with a probability $1-s$), which by definition do not produce any seed, or females (with a probability s), which do not recruit locally any of their non-dispersed offspring, with a probability $1-g(\beta(1-d),0) = e^{-\beta(1-d)}$ (cf. Eq. (2) with only one species). If the species is hermaphrodite, dispersed seeds only have to make up for the cases where a dead hermaphrodite adult fails to recruit one of its non-dispersed seeds.

These equations are interpreted in the same way for the three types of seed distribution. When $k(p)$ decreases (its absolute value increases) the chances that no seed is locally recruited decrease (right-hand side of the inequality) and dispersed seeds reach more cells (left-hand side of the inequality). The condition for the persistence of a population is more severe for a NB ($0 > k(p) > -1$) than for a B ($-1 > k(p)$) distribution and is intermediate for a P distribution ($k(p) = -1$). Hence, the more aggregated seed distribution is, the more detrimental it is to the persistence of a population.

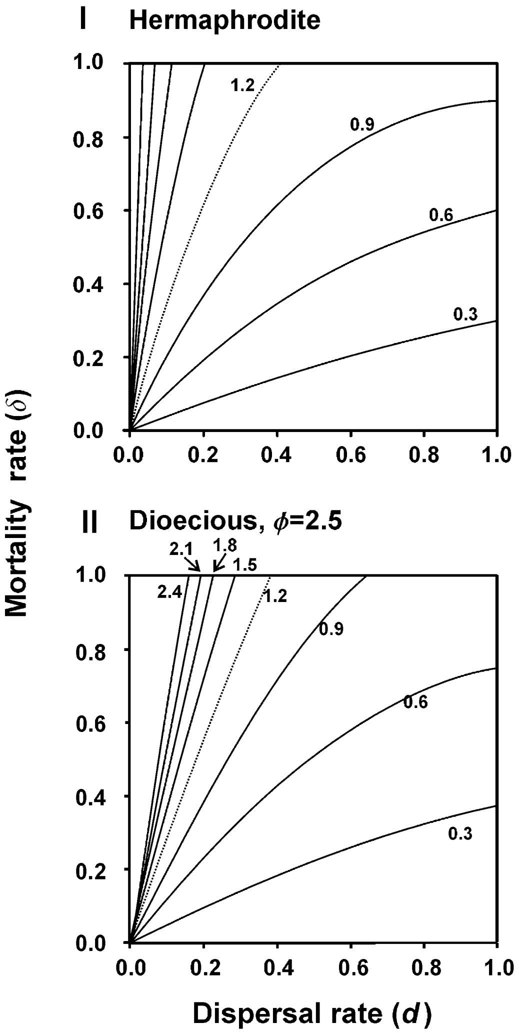

Fig. 1. Limit condition for the persistence of an isolated population in the dispersal-mortality plane. The Poisson law has been used for the number of seeds dispersed to each cell. Numbers on the curves denote fecundities. A species must lie below and on the right-hand side of the corresponding curve to persist. Panel I corresponds to a hermaphrodite species, while panel II corresponds to a dioecious species with $\phi = 2.5$ and an even sex-ratio: the basic fecundity (displayed on the curves) has then been multiplied by 2.5 to take into account the likely increase in fecundity induced by the specialization of individuals into male or female reproduction (see text). Inequality (5) was solved numerically using Mathematica (Wolfram, 1996) to draw the figure. As landmarks, the curve corresponding to a fecundity of 1.2 is displayed with a special line type: ······.

From Fig. 1, three patterns of persistence arise: (A) For low fecundities, the constraint on survival and dispersal is stronger for the persistence of hermaphrodite populations than for the persistence of dioecious populations (the dioecious persistence curve is above the hermaphrodite persistence curve). (B) For high fecundities the persistence constraint is more benign for the hermaphrodite species than for the dioecious species. (C) There are intermediate fecundities for which the corresponding dioecious and hermaphrodite persistence curves cross each other (see Fig. 1 for $\beta = 1.2$, see also explanations of Figs. 2 and 3 and the different types of invasion limit). In these cases the persistence curve of the dioecious species is above the one for the hermaphrodite species for the higher dispersal rates: the persistence criterion becomes more benign for the dioecious species when dispersal rate increases. Because these three cases

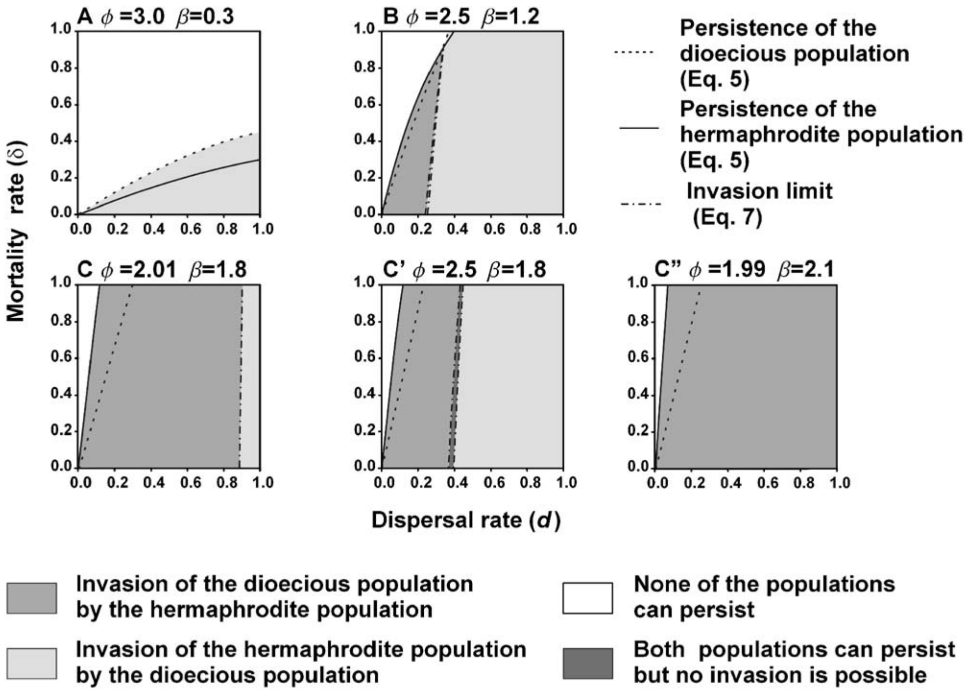

Fig. 2. Reciprocal invasion and persistence limits for equivalent dioecious and hermaphrodite populations. Each panel displays these limits for a different combination of ϕ (increase in fecundity due to the reproductive specialization of dioecious individuals) and β (fecundity). In all cases a Poisson law was used for the number of seeds per cell and the dioecious species had an even sex-ratio. Panel names correspond to the relative position of the persistence limits.

lead to different types of invasion limit (see text below and Figs. 2 and 3) we keep their denomination (A, B, C) throughout the paper. When ϕ increases, dioecy becomes more favorable than hermaphroditism for increasing fecundity values (graphic results not displayed).

These are evidences of the impact of the seed-shadow handicap and the fact that this handicap disappears when ϕ or d increases. The whole pattern is due to the nonlinearity of Eq. (5). When β or $|k(p)|$ decreases, the probability that a hermaphrodite individual recruits at its death one of its non-dispersed offspring decreases due to dispersal stochasticity, and goes to zero, which is the probability that a male produce seeds. Consequently, when β or $|k(p)|$decreases, hermaphrodite species and their equivalent dioecious species become more similar, as regards the recruitment of conspecific offspring in the patches freed by the death of adults. Hence, a small fecundity advantage (ϕ) makes the persistence of the dioecious species easier than the persistence of its equivalent hermaphrodite species.

5. Invasion criterion

To derive a general criterion for the invasion of species 2 by species 1, we derive the limit (r_1) of the growth rate of a species 1 population, when the proportion of cells occupied by this invading species goes to 0 and when the proportion of free cells is P_2^* (Eq. (4)). Since fecundity does not depend on males, and since the sex ratio is constant we only need to study female dynamics:

$$\begin{aligned}F_1(t+1) = {} & F_1(t)(1-\delta_1) + s_1F_1(t)\delta_1 g(\gamma_1,\lambda_2)\\ & + s_1M_1(t)\delta_1 g(\lambda_1,\lambda_2) + s_1F_2(t)\delta_2 g(\lambda_1,\gamma_2)\\ & + s_1M_2(t)\delta_2 g(\lambda_1,\lambda_2) + s_1P(t)g(\lambda_1,\lambda_2), \qquad (6)\end{aligned}$$

(1) The first term stands for the survival of species 1 females, (2, 3) the second and third terms for the death of species and the recolonization of the corresponding cells by species 1 females, (4, 5) the fourth and fifth terms for the death of species 2 females and males, and the recolonization by species 1 females, (6) the last term for the colonization of free cells by species 1 females.

We considered two equivalent species ($d_2 = d_1 = d$, $\delta_2 = \delta_1 = \delta$, $\beta_2 = \beta_1/\phi = \beta$). Dividing all terms by $F_1(t)$ and replacing λ_i and γ_i by their expressions (Eq. (1)), we get:

$$\begin{aligned}\lim_{F_1(t)\to 0} \frac{F_1(t+1)}{F_1(t)} = {} & r_1 = 1-\delta_1\\ & + s_1\delta g\big(\beta\phi(1-d), s_2(1-P_2^*)\beta d\big)\\ & + s_1\delta\phi g\big(s_2\big(1-P_2^*\big)\beta d,\ \beta(1-d)\big)\\ & + \frac{s_1\phi}{s_2} g(s_2(1-P_2^*)\beta d, 0)\left((1-s_2)\delta + \frac{P_2^*}{1-P_2^*}\right).\end{aligned}$$

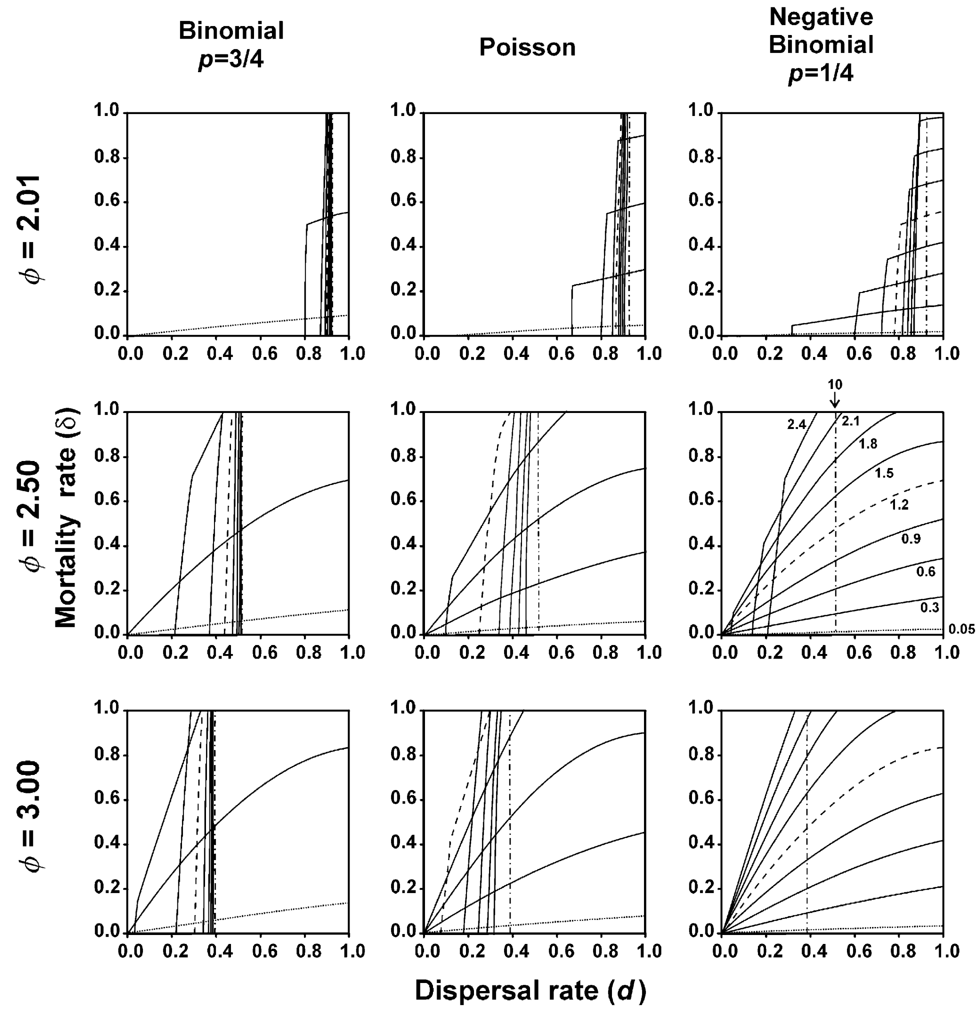

Fig. 3. Limit curves for the invasion of a hermaphrodite species ($s_2 = 1$) by a dioecious species ($s_1 = 0.5$) taking the same dispersal and mortality rates (Eq. (7)). Each curve corresponds to a different fecundity for the hermaphrodite population (as indicated on one panel). As landmarks, 3 curves are displayed with special line type: ······, 0.05; — — —, 1.2; ——, 10. A given hermaphrodite species is invaded by its equivalent dioecious species if it lies under and on the right hand side of the corresponding curve. Each panel displays the limit invasion curve for a different combination of ϕ (the increase in fecundity, 2.01, 2.5, 3.0) and the statistical law for the number of seeds falling in each cell. The 2.01 value has been chosen as the minimal value since $\phi > 2$ is a necessary condition for the invasion. For the Poisson law (*P*) the variance is equal to the mean. For the binomial law (*B*) with $p = 3/4$ the variance is four times as small as the mean. For the negative binomial law (NB) with $p = 1/4$ the variance is four times as high as the mean.

This leads, after some algebraic manipulations using Eq. (4), to the general condition for the successful invasion of a resident population by individuals of an equivalent species introduced at low density, both species differing only by their sex ratio (hermaphrodite species, $s_i = 1$; dioecious species, $s_i > 0$) and fecundity (ϕ):

$$\frac{\phi s_1}{s_2} > \frac{1 - s_1 g\big(\beta\phi(1-d), \big(1-P_2^*\big)s_2\beta d\big)}{1 - s_2 g\big(\beta(1-d), \big(1-P_2^*\big)s_2\beta d\big)}. \tag{7}$$

The denominator of the right-hand side of this inequality is the probability that an individual of the established population ($\big(1-P_2^*\big)s_2\beta d$ dispersed seeds) does not recruit in its cell, at its death, any of its non-dispersed $\beta(1-d)$ seeds. The numerator is the probability that an individual of the invading population does not recruit in its cell, at its death, any of its non-dispersed $\beta\phi(1-d)$ seeds while invading an established population of an equivalent species ($\big(1-P_2^*\big)s_2\beta d$ seeds). Since individuals of the two species only produce seeds with a probability s_i, g is multiplied by s_i to get the probability of recruiting a non-dispersed offspring. Taken together, this ratio (Eq. (7)) is a measure of the relative difficulty for adults of two species to recruit, at their death, one of their non-dispersed offspring during the invasion of one species by the other. This recruitment difficulty for the invading species can be made up by an increase in its relative fecundity at the population scale, i.e. the left-hand side of the inequality, $\phi s_1/s_2$.

Using Eq. (7), we determine in which cases a dioecious species with an even sex-ratio is able to invade a resident equivalent hermaphrodite species and in which cases the reverse invasion is possible. First, this inequality depends on mortality through P_2^* (Eq. (4)). Second, and obviously, for an even sex ratio, a necessary condition for a dioecious invasion is $\phi > 2$, and when $\phi < 2$ the hermaphrodite species always invade its equivalent dioecious species. Because inequality (7) cannot be solved analytically, numerical computations using Mathematica (Wolfram, 1996) were used to display graphically invasion limits (Fig. 2). (A) If the persistence curve of the dioecious species is above that of the equivalent hermaphrodite species, the latter cannot invade and is always invaded by the other one. (B) If the two persistence curves cross each other the limit invasion curves are partially composed of the persistence curves of the dioecious and hermaphrodite species, (Eq. (5)) and their respective invasion criterions (Eq. (7)). This inequality leads to two different invasion limits, for the dioecious and hermaphrodite invasions, which define a thin area in which the two species can persist alone but are not able to invade each other. The dioecious (hermaphrodite) species can invade the hermaphrodite (dioecious) species in the parameter domain corresponding to the higher (lower) dispersal rate values. (C and C′) If the persistence curve for the hermaphrodite species is above that of the equivalent dioecious species and if $\phi > 2$, the invasion domains are only defined by the invasion criterion (Eq. (7)). Again the dioecious (hermaphrodite) species can invade the hermaphrodite (dioecious) species in the parameter domain corresponding to the higher (lower) dispersal rate values. (C″) If the persistence curve of the hermaphrodite species is above that of the equivalent dioecious species and $\phi < 2$, the hermaphrodite species always invades the dioecious species and the reverse is never possible.

The key point (which can only be shown numerically) is that invasion limits may only cross each other at the intersection of the persistence curves (Fig. 2, panel B). In other words, the invasion is never reciprocal and the two considered species can never coexist in a stable way. To determine invasion limits in Fig. 2 the P distribution was used for the number of seeds falling in each cell. The NB and B distributions lead qualitatively to the same patterns (graphical results not displayed) and do not enable reciprocal invasion. In all cases, the parameter domain on which both species can persist but not invade each other is very small. Due to this result, it is valid to focus on the criterion for the invasion of a hermaphrodite population by an equivalent dioecious population (discarding the criterion for the reverse invasion) to assess their relative competitivity.

6. Assessment of the seed-shadow handicap

The comparison of the persistence criterion of hermaphrodite and dioecious species gives first clues on the seed-shadow handicap: it is more difficult for dioecious than for hermaphrodite species (having the same mortality, and dispersal rate) to persist unless the dioecious species has a higher fecundity than the hermaphrodite species, the dispersal rate is sufficiently high and fecundity is sufficiently low. To analyze further the seed-shadow handicap invasion criterions must be used, and it is valid to focus on the criterion for the invasion by the dioecious species (see above). Each panel of Fig. 3 displays the same pattern. For low fecundity values, only species with low mortality can persist and a dioecious species always invade its equivalent hermaphrodite species (case (A)). For intermediate fecundity, (B) cases appear: dioecious invasion depend clearly on both mortality and dispersal. For high fecundity values only hermaphrodite populations with high dispersal rates will be invaded (case (C)). When fecundity increases further the limit invasion curve goes progressively to a vertical line (as shown by the curve corresponding to a fecundity of 10, Fig. 3). The invasion by a dioecious species is then only possible if the dispersal rate is higher than a fixed value $d_{\mathrm{lim,D}}$ that does not depend on the mortality rate (see below). The smaller ϕ the more frequent the intermediate (B) case which leads to composite invasion curves (Fig. 3). The higher ϕ, the more likely the invasion by a dioecious species: from the first to the third row of panels (Fig. 3), the limit condition moves towards lower values of the dispersal rate and higher values of the mortality rate.

The general pattern described above is valid for the three statistical laws used for the number of seeds falling in each cell. However, the NB distribution leads more often to intermediate (B) cases and to (A) cases than the P distribution: limit curves correspond mostly to the persistence limit of the dioecious species. The B distribution has the opposite effect, i.e. invasion limit curves are mostly composed of nearly vertical lines corresponding to the invasion criterion (case (C)). Switching from a B distribution to a P distribution and then to a NB distribution has the same effect as increasing ϕ so that there is a gradient from the upper left panel of Fig. 3 (mostly (C) cases) towards its lower right panel (mostly (A) cases).

The limit dispersal rate value ($d_{\mathrm{lim,D}}$) is found deriving the limit of both terms of inequality (7), when β goes to infinity. When fecundity increases, all cells are reached by more and more seeds and consequences of recruitment stochasticity disappear (P_2^* goes to 0). This leads to a second-order equation for d with only ϕ as parameter and which is valid for the three types of seed distribution (BN, P, B) whatever $k(p)$. The only solution of this

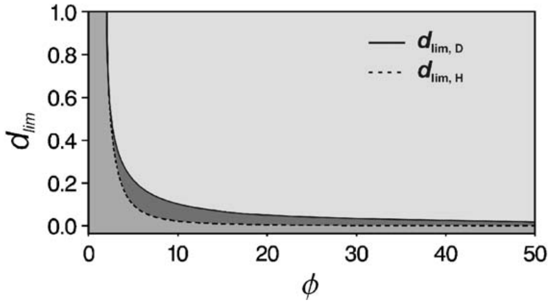

Fig. 4. Variations of the limit dispersal rates for the invasion of equivalent dioecious ($s_1 = 0.5$) and hermaphrodite species ($s_2 = 1$), when fecundity goes to infinity. These limit values only depends on ϕ, the increase in fecundity in the dioecious species. Grey shades denoting invasion domains are the same as in Fig. 2. A wide and unrealistic range was used for ϕ to show the convergence of the two invasion curves.

equation in the interval [0,1] is:

$$d_{\text{lim,D}}(\phi) = \frac{1}{2}\left[\frac{2+\phi}{\phi} - \sqrt{\left(\frac{2+\phi}{\phi}\right)^2 - \frac{4}{\phi-1}}\right].$$

As already suggested by Fig. 3, $d_{\text{lim,D}}$ is a decreasing function of ϕ and goes to 0 when ϕ goes to infinity, and $d_{\text{lim,D}}(2) = 1$ (Fig. 4). First, this confirms that the increase in female fecundity due to the switch from hermaphroditism to dioecy is critical to determine the success of an invasion by a dioecious species. Second, when the fecundity of the hermaphrodite population is high and when $\phi = 2$, dioecious species are never able to invade unless they have very high dispersal rates ($d \approx 1$), which might not be realistic.

When fecundity goes to infinity, the limit for the invasion of a dioecious species by an equivalent hermaphrodite species also goes to a vertical line which only depends on ϕ (equation not given but calculated as for $d_{\text{lim,D}}$). The corresponding limit dispersal rate, $d_{\text{lim,H}}$, goes to 0 when ϕ goes to infinity, and $d_{\text{lim,H}}(2) = 1$ (Fig. 4). $d_{\text{lim,H}} - d_{\text{lim,D}}$ goes to 0 when ϕ goes to infinity or to 2. Hence the limit invasion curves defined by inequality (7) converge when fecundity goes to infinity and ϕ goes to infinity or to 2. It can be shown numerically that this convergence holds whatever the fecundity when ϕ goes to 2 or to infinity. The convergence is quicker when ϕ goes to 2 than when ϕ goes to infinity (comparison between Fig. 3 (C) and (C′), see also Fig. 4 for the case where β goes to infinity). These results confirm that the parameter domain on which equivalent dioecious and hermaphrodite species can persist but not invade each other is small, especially for realistic ϕ values (probably not much higher than 3).

7. Effect of a dispersal cost on the seed-shadow handicap

Dispersed seeds might suffer an extra mortality (δ_d), for example because they are dispersed by animals which eat the fruits and destroy some of the seeds or eat the seeds but scatter some of them (Howe and Smallwood, 1982). We get general persistence and invasion criterions as previously:

$$-k(p)(1-\delta_d)\beta d s > \delta\left(1 - s + s e^{k(p)\beta(1-d)}\right)$$

and

$$\frac{\phi s_1}{s_2} > \frac{1 - s_1 g\left(\beta\phi(1-d), \left(1-P_2^*\right)s_2\beta d(1-\delta_d)\right)}{1 - s_2 g\left(\beta(1-d), \left(1-P_2^*\right)s_2\beta d(1-\delta_d)\right)}.$$

Fig. 4 gives graphical examples of the effect of a dispersal cost on the limit for the invasion of a hermaphrodite population by an equivalent dioecious population. The trends shown are valid for the three laws used for seed distribution and the whole range of parameters used in Fig. 3. The dispersal cost has four effects: (1) It bends persistence curves, i.e. when the dispersal rate increases the mortality rate must decrease for a population to persist (Fig. 5 panel I, $\delta_d = 0.9$ or $\delta_d = 0.7$). (2) Due to the dispersal cost, persistence curves of equivalent dioecious and hermaphrodite species are more likely to cross each other, so that case (C) invasion limits are often turned into case (B) (Fig. 5 panel I, see also Fig. 2 and explanations above). (3) It pushes whole persistence curves downwards (Fig. 5

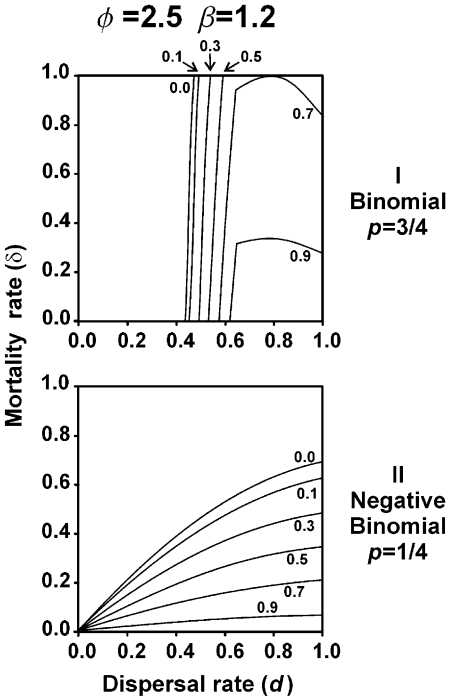

Fig. 5. Effect of a dispersal cost on the limit for the invasion of a hermaphrodite ($s_2 = 1$) population by an equivalent dioecious species ($s_1 = 0.5$). As an example two combinations of the law for the number of seeds by cell, ϕ (increase in fecundity due to the reproductive specialization of dioecious individuals) and β (fecundity) were chosen. Each curve corresponds to a different dispersal cost, i.e. an extra mortality for dispersed seeds, as indicated by curve labels.

panel II). (4) It shifts the invasion limits (Eq. (7)) towards higher dispersal rates (Fig. 5 panel I).

Points (1) and (2) are due to the non-linearity of Eq. (5) (therefore to dispersal stochasticity) and the fact that the effect of a dispersal cost increases when dispersal rate increases. Point (3) means that decreasing adult mortality permits to make up for an extra mortality for seeds. Point (4) is due to the fact that dioecious species can make up for the seed shadow handicap by having high dispersal rates, which increases mortality at the seed stage, which can be further compensated by higher dispersal rates. Taken together, adding a dispersal cost as both a positive—increase in the frequency of cases where all persistent hermaphrodite species are invaded (case (A), and (B) for high dispersal rates)—and a negative effect—higher dispersal rates are needed for the dioecious invasion—on the competitivity of dioecious species relatively to their equivalent hermaphrodite species.

8. Discussion

Mathematical criterions for the persistence of a population in isolation (Eq. (5)), and for the reciprocal invasions of equivalent hermaphrodite and dioecious species (Eq. (7)) show that recolonizing local patches freed by the death of adults is a key point of plant demography. This leads to a demographic disadvantage for dioecious species, for which recolonizing patches freed by males relies on seed dispersal. For dioecy to be favorable, females must produce enough seeds (ϕ) to make up for the absence of seed production by males as found by previous models aiming directly at studying the evolution of dioecy in plants (Charnov and Maynard Smith, 1976; Charlesworth and Charlesworth, 1978). Besides, it is obvious that the longer the seed dispersal distance, the more likely the recolonization of local patches freed by the death of males. Our analytical model only permits to distinguish between locally and globally dispersed seeds and the spatial pattern of individuals is not considered. Yet, when dispersal rate increases, the number of seeds reaching each cell becomes more homogeneous (if $d=1$ then $\gamma_i = \lambda_i$ Eq. (1)). For this reason, efficient seed dispersal diminishes the impact of the seed-shadow handicap. Dioecy also tends to be more favorable than hermaphroditism for species with high survival rates. This is due to dispersal stochasticity which leads to the existence at equilibrium of a non-null proportion of empty local patches depending on all life-history parameters (Eq. (4)). This results in invasion criterions depending on this proportion of empty patches, and thus depending on all life-history parameters (Eq. (7)). In this way, empty patches are responsible for the possibility to make up for the seed-shadow handicap by a long life span.

These results do not only mean that if a dioecious species increases its dispersal or survival rate it is more likely to persist or to invade a hermaphrodite species having fixed parameters values. We compare the persistence and the competitive ability of dioecious and hermaphrodite species taking the same life-history parameters, as if dioecious individuals were mutants of a resident hermaphrodite population. Consequently, our results suggest that the seed-shadow handicap disappears when the survival or the dispersal rate is high enough.

Decreasing fecundity and switching to more aggregated seed distributions increase the number of empty patches and dispersal stochasticity. In these cases the persistence criterion becomes more restrictive, i.e. persistence becomes only possible for lower mortality rates. It becomes easier for the dioecious species than for the hermaphrodite species to persist. Mortality becomes more important than dispersal for the relative competitivity of equivalent dioecious and hermaphrodite species. Although a dispersal cost does not increase dispersal stochasticity as expressed in the persistence criterion, increasing this cost also increases the frequency of cases where low mortality rates are required for persistence and where all persistent hermaphrodite species are invaded by their equivalent dioecious species. Taken together, the link between dioecious invasion and mortality is intuitively due to two causes. First, the shorter a life-cycle, the more often a species depends on dispersal, dispersal stochasticity and dispersal cost for the recolonization of patches freed by adult death. Second, due to the difficulty to recolonize male patches, dioecious species depend more than hermaphrodite species on dispersal and dispersal stochasticity.

At first sight, our conclusions contradict Heilbuth et al. (2001) who found that the maintenance of dioecy is possible only if the dioecious species increases the fitness of the seeds or the dispersal distance relative to the hermaphrodite species, and that increasing the survival rate of a dioecious species competing with an hermaphrodite species only increases its time to extinction. The reason for this discrepancy maybe in their choice of $\phi = 2$, while we have demonstrated that $\phi > 2$ is a necessary condition for dioecy to be favorable. Wilson and Harder (2003) do not find any effect of mortality on the relative competitivity of equivalent dioecious and hermaphrodite populations. This is due to their assumption that every site is reached by a few seeds, while we have shown that the effect of mortality is due to imperfect dispersal, i.e. some sites are not reached by any seed. The discrepancy between the two models is also due to Wilson and Harder not assessing competitivity using invasion criterions.

We have shown that the seed-shadow handicap should lead for dioecious species to lower capability to invade a hermaphrodite population and to avoid an invasion especially when they have low dispersal and survival rates. This is likely to lead to higher extinction rates for dioecious species than for hermaphrodite species (Heilbuth et al., 2001). This could also lead to the observed correlations between dioecy and ecological traits (Bawa, 1980; Thomson and Brunet, 1990). This interpretation is supported by empirical data showing that dioecious lineages do experience higher extinction rates (Heilbuth, 2000).

As Pannel and Barrett's and Heilbuth et al.'s models (Pannell and Barrett, 1998; Heilbuth et al., 2001), our model considers neither the genetic determinism of sexual expression, nor gene exchanges between hermaphrodite and dioecious individuals. However, contrary to earlier studies (Heilbuth et al., 2001; Wilson and Harder, 2003), we have used the criterion for the invasion of a resident hermaphrodite species by dioecious individuals initially at a very small density. Since these individuals have the same life history parameters as the resident hermaphrodite individuals they can be considered as dioecious mutants. This invasion criterion, the so-called invasion fitness, should lead to better estimations of fitness (Metz et al., 1992) than precedent results involving the competition of a dioecious species and a hermaphrodite species initially at equal densities. This invasion fitness is the base of the adaptive dynamics approach which has been shown to model correctly the evolution of traits and speciations, initially in haploid population (Dieckmann, 1997), and more recently in diploid sexually reproducing species (Kisdi and Geritz, 1999; Kisdi and Geritz, 2000).

Thus, however we interpret our model, our results help to explain the correlation observed between dioecy and perennial life history (Bawa, 1980; Thomson and Barrett, 1981). Dioecy would be more frequent in perennial species and especially in trees, than in annual species, because, due to the seed-shadow handicap, dioecious species compete more efficiently with hermaphrodite species when they are long-lived. We found that equivalent dioecious and hermaphrodite species are never able to invade each other reciprocally. According to the adaptive dynamics interpretation (Dieckmann, 1997), this suggests that the evolution of dioecy under the seed-shadow handicap constraint should not lead to speciation because stable coexistence is not possible. However, tackling thoroughly this issue would require studying jointly the adaptive dynamics of dioecy/hermaphroditism, dispersal and mortality rate.

The seed-shadow handicap could also explain partly why the general frequency of dioecious species is low, probably between 4% and 6% (Bawa, 1980; Renner and Ricklefs, 1995). The specialization of individuals into male and female reproductions is likely to result in an increase in female fecundity at the population scale (either due to higher resource use efficiency or to inbreeding avoidance). Yet, if this increase is small, dioecy is only favorable for a low proportion of species having a high dispersal rate and a long life-span. In this context, understanding the evolution of dioecy and testing for the validity of our results would require new empirical studies comparing the seed dispersal efficiency and the longevity of dioecious and hermaphrodite species and assessing the increase in realized fecundity resulting from the segregation of male and female reproductions on different individuals.

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