The joint evolution of separate sexes and sexual dimorphism

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Abstract. Dioecious plants are frequently sexually dimorphic. Such dimorphism, which reflects responses to selection acting in opposite directions for male and female components of fitness, is commonly thought to emerge after separate sexes evolved from hermaphroditism. But associations between allocation to male and female function and traits under sexual conflict could also begin to evolve in hermaphroditic ancestors, and fuel transitions to dioecy. Here, we show that variation in sex allocation and a trait under sexual conflict inevitably generates an advantage to sexual specialisation. In the absence of constraints, this leads to the joint evolution of separate sexes and sexual dimorphism through the build up of an association between sex allocation and the conflict trait, such that eventually the population consists of unisexuals expressing their sex-specific trait optima. We then investigate how such association might materialise genetically, either via recombination suppression or via sex-dependent expression, and show that the genetic architecture of sex allocation and the conflict trait readily evolves to produce the association favoured by selection. Finally, we demonstrate that limited dispersal and self-fertilisation, which are pervasive ecological characteristics of flowering plants, can offset the advantage of sexual specialisation generated by a jointly evolving trait under sexual conflict and maintain hermaphroditism, in agreement with previous theory where sex allocation evolves alone. Taken together, our results indicate that advantages to sexual specialisation are inevitable when there is conflict between sexual functions in hermaphrodites, but can be counterbalanced by ecological benefits of hermaphroditism, underscoring the importance of ecology for sexual system evolution.

1 Introduction

The vast majority of flowering plant species are hermaphroditic, but dioecy (separate sexes) has evolved many times from this ancestral state (Charlesworth, 1985; Renner and Ricklefs, 1995; Barrett, 2002a; Renner, 2014; Käfer et al., 2017). Indeed, dioecious species are rare (about 6% of flowering plants) but widely distributed across the Angiosperm phylogeny, suggesting that hundreds - possibly thousands - of independent transitions to dioecy have taken place in flowering plants (Charlesworth, 1985; Renner and Ricklefs, 1995; Renner, 2014). Evolutionary transitions from hermaphroditism to dioecy are thought to occur along two main pathways (Lloyd, 1980; Charlesworth, 1999; Pannell and Jordan, 2022). First, dioecy may evolve in a stepwise process involving gynodioecy (the coexistence of females and hermaphrodites in a population) as an intermediate state. Theory on this pathway relies on population genetics models that consider the spread of male and female sterility mutations in an initially hermaphroditic population (Charlesworth and Charlesworth, 1978a,b). These models show that partial selfing and inbreeding depression can facilitate the spread of a male-sterility mutation, leading to gynodioecy. In turn, the presence of females in the population can favour the invasion of one or more mutations turning hermaphrodites into males, thereby establishing dioecy.

Second, dioecy may evolve via the gradual divergence of increasingly male- and female-biased morphs that eventually become pure males and females (Lloyd, 1980; Charlesworth, 1999). This pathway, which is sometimes referred to as the 'monoecy-paradioecy' pathway (Lloyd, 1980), has been studied through the evolution of sex allocation, that is of the way individuals divide their limited reproductive resources between their male and female function (Charnov et al., 1976; Charnov, 1982; West, 2009). In sex allocation theory, how resource allocation translates into fitness depends on the shapes of the male and female 'gain curves', which are functions that relate the amount of resources allocated to one sex to fitness gained through that sex. The central prediction of this theory is that saturating gain curves allow the maintenance of hermaphroditism, because such curves lead individuals to accrue diminishing fitness returns as they allocate more resources to a given sex function; whereas accelerating gain curves promote the evolution of dioecy, because individuals then accrue increasing fitness returns from specialising into one sex (Charnov et al., 1976).

Several ecological mechanisms have been proposed to explain when we should see benefits to sexual specialisation (Thomson and Brunet, 1990; Charlesworth and Morgan, 1991; Freeman et al., 1997; Charlesworth,

1999; Pannell and Jordan, 2022). Under the assumption that fruit production is more expensive than the production of pollen-bearing flowers, individuals allocating more to their male function may be able to substantially increase their floral display. This increase could in turn enhance their attractiveness to pollinators, and result in more efficient pollen dispersal. Such coupling between pollen dispersal and production could generate multiplicative benefits to specialising as a male, i.e. an accelerating male gain curve (Bawa, 1980; Ohashi and Yahara, 2001; see also Chap. 3 in De Jong and Klinkhamer, 2005). For female function, there are three main ideas to account for possible accelerating gain curves. First, in plants with animal-dispersed fruits, individuals allocating more heavily into their female function may enjoy more efficient dispersal of their seeds if animals are more attracted to plants bearing larger crops of fruits (Bawa, 1980; Givnish, 1980). This coupling of seed dispersal with sex allocation could cause the female gain curve to accelerate by reducing kin competition among seeds of more female individuals (Vamosi et al., 2007; Biernaskie, 2010). Second, seeds of individuals producing larger crops may sometimes enjoy a lower predation risk due to 'predator satiation' (Janzen, 1971; Lloyd, 1982), which may cause the female gain curve to accelerate through the coupling of seed survival and sex allocation. Third, if the selfing rate in hermaphrodites increases with pollen production, so that selfing is coupled with sex allocation, then high inbreeding depression may lead to multiplicative benefits of specialising into female function, because more female individuals would then produce seeds that are both more numerous and more outcrossed (and thus more fit, Charlesworth and Charlesworth, 1978b; De Jong and Geritz, 2001; Lesaffre et al., 2023).

Previous ecological explanations for accelerating gain curves allow for features of plant ecology, such as the efficiency of pollen and seed dispersal, to vary as a direct consequence of a plant's allocation to male versus female function, but all assume that sex allocation is the only evolving trait. However, transitions to dioecy are typically accompanied by the emergence of trait differences between male and female individuals that go beyond the mere production of pollen or ovules. Indeed, sexual dimorphism is widespread in dioecious plants, with males and females typically differing in several life-history (e.g. lifespan, growth rate or phenology); and reproductive traits (e.g. flowering time or flower size, position, shape and number, Lloyd and Webb, 1977; Geber, 1999; Barrett and Hough, 2013). Sexual dimorphism is commonly thought to be the result of the resolution of conflicts over trait expression between males and females, and therefore to arise after separate sexes have evolved (Barrett and Hough, 2013; Charlesworth, 2018). But these conflicts were likely already at work in the hermaphroditic ancestor, especially over reproductive traits, as what is optimal for reproduction through male function might often not be for reproduction through female function

(Geber, 1999; Delph and Ashman, 2006). In wind-pollinated plants, for instance, efficient pollen dispersal by stamens and pollen capture by stigmas require floral traits with opposite biophysical properties. Pollen dispersal requires that flowers intermittently interrupt the airstream by flopping in the wind to ensure that pollen can escape, whereas pollen capture requires flowers to act as fixed obstacles on which pollen can get stuck (Freeman et al., 1997; Barrett, 2002b). Another example is floral display in animal-pollinated plants (Barrett and Hough, 2013). Pollinators are typically attracted to plants with higher floral displays, and both sexual functions need to attract pollinators. But whereas increased attractiveness is expected to benefit male function through increased pollen dispersal, female function might eventually suffer from increased pollinator attraction as this increases risks of geiotonogamous selfing and of flower damage, which could compromise seed development (Ohashi and Yahara, 2001; De Jong and Klinkhamer, 2005). Conflicts over the expression of traits between sexual functions in hermaphrodites could thus promote the evolution of separate sexes as a means of conflict resolution. In other words, the joint evolution of sex allocation and traits under sexual conflict could generate benefits to sexual specialisation, and lead to the simultaneous, rather than sequential, emergence of separate sexes and sexual dimorphism (Willson, 1979; Geber, 1999).

The joint emergence of separate sexes and sexual dimorphism has so far been studied in the context of the gynodioecy pathway, that is of the spread of unisexuals in a population of hermaphrodites. Several models have investigated the effect of a joint change in sexual phenotype together with another trait such as floral display, allocation to growth vs. reproduction, or to attractive structures vs. gamete production, and shown that it can facilitate invasion by unisexuals (Morgan, 1992; Seger and Eckhart, 1996; Sato, 2002). However, these models assume that invading unisexuals already express the trait value that is optimal for their sex, which is biologically equivalent to assuming either that sterility mutations are pleiotropic in a way that is phenotypically optimal, or that the trait is plastic and expressed conditionally on sexual phenotype. More recently, Olito and Connallon (2019) studied the effect of sexually antagonistic alleles segregating at a partially linked locus on the ability of male and female sterility mutations to invade a hermaphroditic population (see also Blackburn et al. (2010) for the effect of sexually antagonistic variation on the evolution of sex-ratio adjustment in dioecious species). They found that sexually antagonistic variation at a nearby locus could facilitate the spread of sterility mutations through hitchhiking, demonstrating that polymorphism maintained by sexual conflict can aid the establishment of unisexuals. Their approach assumes a constant recombination rate between the two loci and does not consider the emergence of a phenotypic association between sex and a trait, so that sexual dimorphism cannot emerge jointly with separate sexes in their model.

Here, we investigate the joint emergence of separate sexes and sexual dimorphism along the monoecy-paradioecy pathway. We consider the joint evolution of sex allocation and a continuous trait with sex-specific optima (so that it is under sexual conflict). We first use a baseline model to show that selection favours sex allocation and the conflict trait to become associated, thereby generating an advantage to sexual specialisation and promoting the evolution of separate sexes. We then extend our baseline model to explore how this association might come about at a genetic level. Our analyses reveal that the genetic architecture of sex allocation and the conflict trait readily evolves to produce the association favoured by selection, suggesting that genetic constraints are unlikely to constitute a long-term barrier to the joint evolution of separate sexes and sexual dimorphism. Finally, we show that ecological characteristics that are pervasive among flowering plants, limited dispersal and self-fertilisation, can offset the advantage of sexual specialisation driven by variation in sex allocation and a trait under sexual conflict, and maintain hermaphroditism. Taken together, our results indicate that traits under sexual conflict in hermaphrodites can favour the gradual emergence of separate sexes and sexual dimorphism, shedding light on the numerous transitions to dioecy that have taken place in flowering plants.

2 Sexual conflict in hermaphrodites always favours sexual specialisation

We first propose a simple model as a basis to investigate the joint evolution of separate sexes and sexual dimorphism.

2.1 Baseline model

Our baseline model considers a large population of haploid hermaphrodites with the following life cycle. *(i) Sexual development:* First, individuals undergo sexual development and produce a large number of female and male gametes. *(ii) Mating:* Female and male gametes then fuse randomly, leading to the production of a large number of diploid zygotes that immediately divide to give rise to two haploid seeds each. *(iii) Recruitment:* Finally, adults die and are replaced by juveniles sampled uniformly from the produced seeds.

Each individual is characterised by two continuous traits, $x \in [0, 1]$ and $z \in \mathbb{R}$, that determine their fecundity through female and male functions. The first trait x is sex allocation, i.e. x is the proportion of its reproductive

resources that an individual allocates to its female function during sexual development (so that the remaining $1-x$ is allocated to its male function). Meanwhile the second trait (z), which we will refer to as 'trait z' for short, is a continuous trait that affects reproduction differently through female and male function. This could be a trait that enhances reproductive success through one sexual function at the expense of the other, such as floral stem length in wind-pollinated plants, or traits related to pollinator attraction in animal-pollinated plants (Delph, 1996; Friedman and Barrett, 2009); but could also represent a physiological trade-off underlying the expression of distinct male- and female-beneficial phenotypes.

Overall, the effective fecundity of individual i with traits $\mathbf{y}_i = (x_i, z_i)$ through its female and male function are given by

$$F(\mathbf{y}_i) = \; x_i \, V_{♀}(z_i), \quad \text{and,} \quad M(\mathbf{y}_i) = (1-x_i) V_{♂}(z_i), \tag{1}$$

respectively, where $V_{♀}(z_i)$ and $V_{♂}(z_i)$ are functions capturing the effect of trait z on reproduction through female and male functions. We assume that $V_{♀}(z_i)$ and $V_{♂}(z_i)$ are positive, smooth and continuous functions, with a unique maximum each. Without loss of generality, we assume that this maximum is larger for female than for male function, so that the optimal trait value is greater for female than for male function. We derive most of our results with these general functions, but where necessary we assume that $V_{♀}(z_i)$ and $V_{♂}(z_i)$ are Gaussian, i.e.

$$V_u(z_i) = \exp\left(-\omega_u (z_i - \theta_u)^2\right), \tag{2}$$

with $u \in \{♀, ♂\}$, and where $\theta_u \in \mathbb{R}$ and $\omega_u > 0$ denote the optimal trait value and the strength of selection in sex u, respectively.

We assume that sex allocation x and trait z are each determined by a quantitative trait locus that evolves via the input of rare mutations with weak phenotypic effects ('continuum-of-alleles' model; Kimura, 1965, p. 883 in Walsh and Lynch, 2018). We assume for now that the loci encoding x and z are fully-linked (i.e. no recombination, we later relax this). We analyse this model in detail in Appendix A and summarise our main results below.

2.2 Joint evolutionary dynamics of sex allocation and a trait under sexual conflict

When mutations are rare and with weak phenotypic effects, trait evolution can be decomposed into two phases (Geritz et al., 1998). First, the population evolves under directional selection, whereby positively selected mutations sweep to fixation so that the population transits from being largely monomorphic for one trait value to being monomorphic for another. Through the sequential fixation of mutations altering sex allocation x and trait z in the direction favoured by selection, we show in Appendix A.1.1 that the population eventually attains the equilibrium $\mathbf{y}^* = (x^*, z^*)$ where

$$x^* = \frac{1}{2}, \tag{3a}$$

and z^* is such that,

$$\frac{V'_{♀}(z^*)}{V_{♀}(z^*)} = -\frac{V'_{♂}(z^*)}{V_{♂}(z^*)}. \tag{3b}$$

Therefore, at this equilibrium, individuals divide their reproductive resources equally between their female and male functions (eq. 3a), and express a trait value z^* that is such that the marginal fitness gained through male and female function compensate each other (eq. 3b).

Once the population expresses $\mathbf{y}^*$, it either remains monomorphic or becomes polymorphic in a process referred to as 'evolutionary branching', whereby two discrete morphs gradually diverge from one another (Geritz et al., 1998; Pásztor et al., 2016). Whether or not this occurs depends on the so-called Hessian matrix,

$$\mathbf{H}(\mathbf{y}^*) = \begin{pmatrix} h_{xx}(\mathbf{y}^*) & h_{xz}(\mathbf{y}^*) \\ \\ h_{xz}(\mathbf{y}^*) & h_{zz}(\mathbf{y}^*) \end{pmatrix} = \begin{pmatrix} 0 & \dfrac{V'_{♀}(z^*)}{V_{♀}(z^*)} - \dfrac{V'_{♂}(z^*)}{V_{♂}(z^*)} \\ \\ \dfrac{V'_{♀}(z^*)}{V_{♀}(z^*)} - \dfrac{V'_{♂}(z^*)}{V_{♂}(z^*)} & \dfrac{1}{2}\left(\dfrac{V''_{♀}(z^*)}{V_{♀}(z^*)} + \dfrac{V''_{♂}(z^*)}{V_{♂}(z^*)}\right) \end{pmatrix}, \tag{4}$$

with polymorphism requiring that the leading eigenvalue of $\mathbf{H}(\mathbf{y}^*)$ is positive (Leimar, 2009; Débarre et al., 2014; Geritz et al., 2016, see eq. A12 in Appendix A.1.2 for the mathematical definition of $\mathbf{H}(\mathbf{y}^*)$). Before determining the conditions for polymorphism from this matrix, let us remark that each entry of $\mathbf{H}(\mathbf{y}^*)$ captures a different aspect of selection (Lande and Arnold, 1983). Diagonal entries $h_{xx}(\mathbf{y}^*)$ and $h_{zz}(\mathbf{y}^*)$, which are the quadratic selection coefficients on sex allocation x and trait z, respectively, tell us whether selection on each trait is disruptive (if positive) or stabilising (if non-positive) when traits evolve independently from

one another. Meanwhile, the off-diagonal entry $h_{xz}(\mathbf{y}^*)$ is the coefficient of correlational selection acting on x and z. A positive (resp. negative) $h_{xz}(\mathbf{y}^*)$ indicates that selection favours a positive (negative) association between the two traits when they evolve jointly. Using the fact the $\mathbf{H}(\mathbf{y}^*)$ is symmetric, we can identify two ways for its leading eigenvalue to be positive and thus for selection to favour polymorphism: *(i)* either one of the diagonal entry is positive and thus one trait is independently experiencing disruptive selection, i.e.

$$h_{xx}(\mathbf{y}^*) > 0 \quad \text{or} \quad h_{zz}(\mathbf{y}^*) > 0; \tag{5a}$$

or, *(ii)* if condition (5a) does not hold, then polymorphism is favoured when

$$h_{xz}(\mathbf{y}^*)^2 > h_{xx}(\mathbf{y}^*)h_{zz}(\mathbf{y}^*), \tag{5b}$$

i.e. when correlational selection is sufficiently strong to overcome stabilising selection acting on each trait independently.

Because $h_{xx}(\mathbf{y}^*) = 0$ for our baseline model (top-left element in eq. 4), selection is stabilising on sex allocation here when x evolves independently (and z is fixed). This is because we assumed a linear trade-off between male and female allocation so that there is no inherent advantage to sexual specialisation here (Charnov et al., 1976). When trait z evolves independently (so when sex allocation is fixed at $x^* = 1/2$), inspection of $h_{zz}(\mathbf{y}^*)$ reveals that z experiences disruptive selection when $V''_{♀}(z^*)/V_{♀}(z^*) + V''_{♂}(z^*)/V_{♂}(z^*) > 0$, i.e. when $V_{♀}(z)$ and $V_{♂}(z)$ are on average accelerating when $z = z^*$. In this case, conflict between female and male trait expression is so strong that it favours the emergence of two hermaphroditic morphs that allocate equally into their female and male functions ($x^* = 1/2$), with one morph expressing the optimal-female trait value (such that $V'_{♀}(z) = 0$) and the other morph the male-optimum (such that $V'_{♂}(z) = 0$).

Plugging the entries of $\mathbf{H}(\mathbf{y}^*)$ (eq. 4) into condition (5b), we see that this condition always holds in our baseline model. This indicates that selection always favours polymorphism when both sex allocation x and trait z evolve jointly, even when each trait experiences stabilising selection in isolation. In other words, hermaphroditism is never evolutionarily stable here. Using numerical analyses and individual-based simulations to investigate the polymorphism that results from correlational selection (Appendices A.2 and A.3 for details), we find that eventually, the population consists of two types: *(i)* pure females that express the optimal trait value for their reproduction (i.e. $x = 1$ and z such that $V'_{♀}(z) = 0$); and *(ii)* pure males that express the

optimal trait value for their reproduction (i.e. $x = 0$ and z such that $V'_{♂}(z) = 0$), as shown in Figure 1. Selection thus always leads to the joint emergence of separate sexes and sexual dimorphism in our baseline model.

For the rest of our manuscript, we extend our baseline model to explore potential factors that may maintain hermaphroditism against this selective advantage of sexual specialisation. These factors are broadly classified as to whether they are genetic (Section 3) or ecological (Section 4).

3 Genetic constraints and their resolution

The transition to dioecy due to correlational selection that we described in the preceding section relies on the build up of an association between sex allocation x and trait z. In our baseline model (Section 2.1), this is achieved by linkage disequilibrium between alleles improving reproductive success through the same sexual function. These genetic associations between co-adapted alleles are free to build up here, because loci influencing x and z do not recombine.

We ran simulations allowing for recombination to occur at a fixed rate $r \in [0, 1/2]$ between the loci during the diploid zygotic stage. We found that while low recombination may still allow the emergence of polymorphism, although it leads to the production of unfit recombinant females and males that express a trait z value that is optimal for the sex opposite to theirs (Fig. 2A); higher recombination rates prevent polymorphism from emerging entirely (Figure 2B-C). This is because recombination breaks the positive genetic association that is necessary for correlational selection to act upon. Nevertheless, correlational selection should favour the evolution of genetic architectures that improve the heritability of beneficial associations between x and z. We investigate two potential routes for this to occur. First, we model the evolution of recombination between the two loci influencing x and z (Section 3.1). Second, we study the evolution of sex allocation-dependent expression of trait z (Section 3.2).

3.1 Evolution of recombination

We extend our baseline model (Section 2.1) to include recombination evolution. We assume that the recombination rate in a zygote is controlled by an unlinked modifier locus at which alleles are additive and subject

to rare, small-effect mutations, so that r evolves gradually (Appendix B.1.1 for details).

We first investigate recombination evolution by considering the fate of a rare mutant allele coding for recombination rate r_{m} at the modifier, in a population otherwise fixed for rate r. We assume that two alleles segregate at the sex allocation locus. We label these alleles by their phenotypic effect $x_{♀}$ and $x_{♂}$, where $x_{♂} < x_{♀}$. Similarly, two alleles $z_{♀}$ and $z_{♂}$ ($z_{♂} < z_{♀}$) segregate at the locus encoding trait z. Therefore, there is four possible haplotypes in the population: two 'adapted' haplotypes carrying matching alleles, with one haplotype adapted to female reproduction $\mathbf{y}_1 = (x_{♀}, z_{♀})$ and the other to male reproduction $\mathbf{y}_2 = (x_{♂}, z_{♂})$; and two 'maladapted' haplotypes that carry mismatched alleles $\mathbf{y}_3 = (x_{♀}, z_{♂})$ and $\mathbf{y}_4 = (x_{♂}, z_{♀})$.

We show in Appendix B.1.2 that the selection gradient on r, which gives the direction and intensity of selection on recombination in a population expressing r can be written as

$$s(r) = -\frac{1}{2}\Big(v_{\mathrm{A}}^{\circ}(r) - v_{\mathrm{M}}^{\circ}(r)\Big)\Big(Q_{\mathrm{A}}^{\circ}(r) - Q_{\mathrm{M}}^{\circ}(r)\Big), \tag{6}$$

where $v_{\mathrm{A}}^{\circ}(r)$ and $v_{\mathrm{M}}^{\circ}(r)$ are the mean reproductive values of adapted and maladapted haplotypes, respectively (eq. B9b), which measure the asymptotic demographic contribution of individuals carrying a given haplotype to the future population (for a mathematical definition, see e.g. p. 153 in Rousset, 2004); and $Q_{\mathrm{A}}^{\circ}(r)$ and $Q_{\mathrm{M}}^{\circ}(r)$ are the frequencies of double-heterozygous zygotes carrying adapted and maladapted haplotypes, respectively (only double-heterozygous zygotes appear in eq. 6, as these zygotes are those in which recombination has an effect on the frequency of haplotypes in the produced seeds; see eqs. B9c-B9d in Appendix B.1.2.2). The first term in brackets in eq. (6) measures the difference in reproductive values between adapted and maladapted haplotypes. Given that adapted haplotypes have higher fitness, this term is always positive. The second term in brackets in eq. (6) measures the difference in frequency between double-heterozygous zygotes carrying adapted vs. maladapted haplotypes. This is also positive as adapted haplotypes are maintained at higher frequencies and so form more zygotes. Therefore, eq. (6) is always negative. In other words, selection always favours a decrease in the recombination rate between the loci encoding x and z. This should eventually lead to complete recombination suppression ($r \to 0$).

We checked this analytical prediction with individual-based simulations in which sex allocation x, trait z and recombination rate r all evolve. Loci for x and z are initially freely recombining (i.e. $r = \frac{1}{2}$ at the beginning of each simulation run; the program is described in detail in Appendix B.1.3). We find that recombination

suppression always evolves, in agreement with our analytical prediction (Fig. 3A). This allows for positive genetic linkage to build up between the loci encoding x and z, and thus for the simultaneous evolution of separate sexes and sexual dimorphism (Fig. 3B-C). However, recombination suppression can take a long time to occur. This is because selection on the recombination rate is proportional to the divergence between alleles at the loci encoding x and z, and so is initially weak. Recombination can thus delay transitions to dioecy in the short-term, but is unlikely to prevent them from taking place in the long-term as mutations and chromosomal rearrangements leading to recombination suppression are always favoured by selection.

3.2 Evolution of conditional trait expression

Another potential route for sex allocation x and trait z to become associated is through the evolution of conditional expression of z on x. This would allow individuals that allocate more to a given sexual function to express traits that are better suited to this function, but does not require physical linkage between the loci encoding x and z.

To investigate this possibility, we now let trait z of an individual with sex allocation x be given by

$$z = a \cdot x + b, \tag{7}$$

where $b \in \mathbb{R}$ is the component of z that is independent of sex allocation, and $a \in \mathbb{R}$ is the sex allocation-dependent component of z. When $a = 0$, z is determined by b and is therefore independent of sex allocation. In contrast, z increases in more female individuals when $a > 0$ (and decreases when $a < 0$). We assume that there is a cost to plasticity, which could for instance be due to the cost of maintaining the additional physiological and regulatory machinery required for conditional trait expression (DeWitt et al., 1998). This cost decreases fecundity for individuals with larger sex allocation-dependent trait components (i.e. larger $|a|$). Specifically, we assume that female and male fecundities of an individual expressing $\mathbf{y}_i = (x_i, a_i, b_i)$ are now given by

$$F(\mathbf{y}_i) = \; x_i \, V_{♀}(a_i x_i + b_i) \; \exp(-c \, {a_i}^2) \quad \text{and,} \quad M(\mathbf{y}) = (1 - x_i) V_{♂}(a_i x_i + b_i) \; \exp(-c \, {a_i}^2). \tag{8}$$

Sex allocation x and trait z components a and b are assumed to be encoded by unlinked loci that each evolve according to a ‘continuum-of-alleles’ model.

We show in Appendix B.2.1 that first, directional selection leads the population to express the equilibrium $\mathbf{y}^* = (x^*, a^*, b^*)$, where

$$x^* = \frac{1}{2}, \tag{9a}$$

so that individuals divide their reproductive resources equally between their male and female function; meanwhile

$$a^* = 0, \tag{9b}$$

and b^* is such that

$$\frac{V'_{♀}(b^*)}{V_{♀}(b^*)} = -\frac{V'_{♂}(b^*)}{V_{♂}(b^*)}, \tag{9c}$$

i.e. such that individuals express a trait value $z^* = b^*$ that is independent of sex allocation ($a^* = 0$) and sits between the female and male optima, as in our baseline model (eq. 3).

Once the population expresses $\mathbf{y}^*$, we find that two distinct cases need to be considered. The first is when functions $V_{♀}(z)$ and $V_{♂}(z)$ are saturating on average, i.e. when

$$\frac{V''_{♀}(b^*)}{V_{♀}(b^*)} + \frac{V''_{♂}(b^*)}{V_{♂}(b^*)} \leqslant 0. \tag{10}$$

In this case, quadratic selection is stabilising on all three traits, and so the population should remain unimodally distributed around $\mathbf{y}^*$ (recall that because loci are unlinked here, genetic associations are constantly being removed by recombination so that correlational selection cannot act). Nevertheless, standing variation for sex allocation around x^* maintained at mutation-selection-drift balance may generate selection on trait components a and b. To investigate this, we assume that two sex allocation alleles weakly diverging from x^*, denoted $x_{♀} = x^* + \Delta x$ and $x_{♂} = x^* - \Delta x$, where $\Delta x > 0$ is small, segregate. We study selection on a and b assuming Gaussian fecundity functions for simplicity (eq. 2; see Appendix B.2.2 for details on the analysis).

We find that selection leads the polymorphic population to evolve sex allocation-dependent trait expression, with the sex-allocation dependent and independent components of z evolving to

$$a^*_{\text{poly}} = 4\Delta x^2 \frac{\theta_{♀} - \theta_{♂}}{c(\omega_{♀} + \omega_{♂})} \omega_{♀}\omega_{♂} + \mathcal{O}(\Delta x^3), \tag{11a}$$

and,

$$b^*_{\text{poly}} = \theta_{♀}\frac{\omega_{♀}}{\omega_{♀}+\omega_{♂}} + \theta_{♂}\frac{\omega_{♂}}{\omega_{♀}+\omega_{♂}} - 2\Delta x^2\frac{\theta_{♀}-\theta_{♂}}{c(\omega_{♀}+\omega_{♂})}\omega_{♀}\omega_{♂} + \mathcal{O}(\Delta x^3), \tag{11b}$$

so that individuals that are more female ($x > x^*$) express larger female-beneficial z values, and individuals that are more male ($x < x^*$) express smaller male-beneficial z values. As indicated by eq. (11), the dependence of z on sex allocation that evolves is especially strong when selection is strong ($\omega_{♀}$ and $\omega_{♂}$ large) and the male and female optima are far apart ($\theta_{♀} - \theta_{♂}$ large).

We show that in turn, sex allocation-dependent expression of z generates selection on alleles $x_{♀}$ and $x_{♂}$ to diverge further (eq. B67 in Appendix B.2.2). Specifically, we show that the selection gradients $s_{♀}(\mathbf{y}_{♀}, \mathbf{y}_{♂})$ and $s_{♂}(\mathbf{y}_{♀}, \mathbf{y}_{♂})$ on each sex allocation allele are given by

$$s_{♀}(\mathbf{y}_{♀}, \mathbf{y}_{♂}) = \frac{\Delta x^3}{c}\left(4\omega_{♀}\omega_{♂}\frac{\theta_{♀}-\theta_{♂}}{\omega_{♀}+\omega_{♂}}\right)^2 + \mathcal{O}(\Delta x^4), \tag{12a}$$

and,

$$s_{♂}(\mathbf{y}_{♀}, \mathbf{y}_{♂}) = -\frac{\Delta x^3}{c}\left(4\omega_{♀}\omega_{♂}\frac{\theta_{♀}-\theta_{♂}}{\omega_{♀}+\omega_{♂}}\right)^2 + \mathcal{O}(\Delta x^4). \tag{12b}$$

These gradients are positive and negative, respectively, indicating that selection favours the female-biased allele $x_{♀}$ to become more female-biased (i.e. to code for larger values of x) and the male-biased allele $x_{♂}$ to become more male-biased (i.e. to code for smaller values of x).

Selection on conditional trait expression and sex allocation should therefore reinforce each other, leading to the joint emergence of separate sexes and sexual dimorphism. To check this, we used individual-based simulations (Appendix B.2.3 for details on the simulation program). These simulations always show the emergence of separate sexes and sexual dimorphism (Figure 4), with trait components a and b evolving to

$$a = \theta_{♀} - \theta_{♂} \quad \text{and} \quad b = \theta_{♂}, \tag{13}$$

such that females ($x = 1$) express the female optimum $z = \theta_{♀}$, and males ($x = 0$) express the male optimum $z = \theta_{♂}$ (recall eq. 7).

The second case to consider is when

$$\frac{V''_{♀}(b^*)}{V_{♀}(b^*)} + \frac{V''_{♂}(b^*)}{V_{♂}(b^*)} > 0. \tag{14}$$

so that selection on trait components a and b is disruptive when population expresses $\mathbf{y}^*$ (eq. 9). Under these conditions, individual-based simulations show the joint evolution of separate sexes and sexual dimorphism occurring most of the time, with conditional trait expression given by eq. (13). However, in some simulations where $V''_{♀}(b^*)$ and $V''_{♂}(b^*)$ are particularly large, conditional expression fails to evolve and evolutionary branching instead occurs for b, the component of trait z that is independent of sex allocation. This leads to a hermaphroditic population where female-adapted individuals expressing $b = \theta_{♀}$ coexist with male-adapted individuals expression $b = \theta_{♂}$ (while the population remains fixed for $x^* = 1/2$ and $a^* = 0$). Such a population is evolutionarily stable, as there is no more selection for trait z to evolve conditional expression. Nevertheless, polymorphism for b generates selection for recombination suppression between the loci encoding sex allocation x and trait b, as seen in Section 3.1. We therefore expect that if recombination between loci influencing x and b could evolve, separate sexes would readily emerge here.

4 The role of ecology in maintaining hermaphroditism

We now explore the effects of two prevalent ecological factors in flowering plants, limited dispersal (Section 4.1) and self-fertilisation (Section 4.2), on the joint evolution of separate sexes and sexual dimorphism.

4.1 Limited dispersal and kin competition

A distinctive ecological feature of plants is that they are immobile and have limited dispersal abilities. This leads to pervasive kin competition effects. Indeed, most pollen is dispersed over short distances so that related pollen grains often compete with one another to fertilise neighbouring ovules ("Local Mate/Sperm Competition"; Hamilton, 1967; Schärer, 2009). Similarly, seeds are often dispersed in the close vicinity of maternal plants, so that related offspring compete with one another for recruitment ("Local Resource Competition", see Clark (1978) for the first use of the term; Charnov, 1982). Competition among related pollen grains and related seeds increases as a focal parent allocates more heavily into its male and female functions, respectively, which in turn generates diminishing fitness returns to sexual specialisation and is thus expected to favour hermaphroditism (Chap. 8 in Maynard Smith, 1978; Lloyd and Bawa, 1984; Fromhage and Kokko, 2010; Biernaskie, 2010). Here, we extend our baseline model (Section 2) to consider the effect of limited dispersal on the joint evolution of sex allocation and a trait under sexual conflict.

In this extended model, the population is subdivided in an effectively infinite number of patches that each carry N individuals, and are uniformly connected by seed dispersal (the 'Island Model', Wright, 1931). At the beginning of each generation, individuals undergo sexual development, expressing sex allocation x and trait z, and then mate randomly within each patch, leading to the production of a large number of haploid seeds. A fraction $d_{\mathrm{s}} \in [0, 1]$ of the produced seeds is dispersed to other patches in the population, while the remaining fraction $1 - d_{\mathrm{s}}$ stays in their natal patch. Following seed dispersal, all adults die and seeds present on each patch compete for recruitment. Due to limited seed dispersal, individuals thus compete with relatives through male function for siring ovules in their patch, and through female function for recruitment of non-dispersed seeds. To focus on the effects of kin competition, we assume that sex allocation x and trait z are encoded by fully-linked quantitative trait loci evolving according to a continuum-of-alleles model (as in our baseline model).

We show in Appendix C that the population first converges to the equilibrium $\mathbf{y}^* = (x^*, z^*)$ where

$$x^* = \frac{1}{2} + \frac{1}{2N}, \tag{15a}$$

and z^* is such that,

$$\frac{V'_{♀}(z^*)}{V_{♀}(z^*)} = -\frac{N-1}{N+1}\frac{V'_{♂}(z^*)}{V_{♂}(z^*)}. \tag{15b}$$

The equilibrium for sex allocation x^* corresponds exactly to Hamilton (1967)'s result for the effect of local mate competition on sex-ratio evolution in dioecious species (see also eq. 12 in Roux et al., 2024 for the diploid case with selfing). This allocation becomes increasingly female-biased as patch size N decreases, owing to an intensification of kin competition in the pollen pool (Fig. 5A). The equilibrium z^* is affected by limited dispersal in a similar way to sex allocation, with decreasing patch size selecting for more female-biased trait values (Fig. 5B). Neither x^* nor z^* depend on the seed dispersal rate d_{s}. This is because decreasing d_{s} causes an increase in kin competition through male and female function that cancel out exactly here (Frank, 1986; Biernaskie, 2010).

Once the population expresses $\mathbf{y}^*$, we find that the effect of limited dispersal on the Hessian matrix (eq. 4) depends on patch size N and seed dispersal d_{s} in a complicated way (Appendix C.1.2 for derivation and Mathematica Notebook for full expression). Key insights can however be gained from considering the case of large patches connected by low seed dispersal, i.e. $N \to \infty$ and $d_{\mathrm{s}} \to 0$ such that the number of immigrants

Nd_{s} remains constant. In this case, the entries of the Hessian matrix (eq. 4) read as

$$\begin{aligned}
h_{xx}(x^*) &= -8F_{\mathrm{ST}}\frac{1-F_{\mathrm{ST}}}{1+F_{\mathrm{ST}}},\\
h_{xz}(x^*) &= \frac{(1-F_{\mathrm{ST}})^2}{1+F_{\mathrm{ST}}}\left(\frac{V'_{♀}(z^*)}{V_{♀}(z^*)}-\frac{V'_{♂}(z^*)}{V_{♂}(z^*)}\right),\\
h_{zz}(x^*) &= 4F_{\mathrm{ST}}\frac{1-F_{\mathrm{ST}}}{1+F_{\mathrm{ST}}}\frac{V'_{♀}(z^*)}{V_{♀}(z^*)}\frac{V'_{♂}(z^*)}{V_{♂}(z^*)}+\frac{1-F_{\mathrm{ST}}}{2}\left(\frac{V''_{♀}(z^*)}{V_{♀}(z^*)}+\frac{V''_{♂}(z^*)}{V_{♂}(z^*)}\right),
\end{aligned} \tag{16}$$

where $F_{\mathrm{ST}} = 1/(1+2Nd_{\mathrm{s}})$ is Wright's measure of population structure (e.g., p. 28 in Rousset, 2004), and the equilibrium $\mathbf{y}^* = (x^*, z^*)$ is identical to the well-mixed case (as eq. 15 reduces to eq. 3 when $N \to \infty$). The first thing to notice from eq. (16) is that each selection coefficient is factored by $1 - F_{\mathrm{ST}}$, reflecting the well-known effect that the intensity of selection is weaker under limited dispersal as an individual's reproductive success comes at the expense of genetic relatives (Frank, 1998; Rousset, 2004). Once this first effect is factored out, the second thing to notice is that quadratic selection on x and z is more negative in populations that are more structured (since $V'_{♀}(z^*)V'_{♂}(z^*) < 0$). This is because kin competition among related pollen grains and among seeds leads to diminishing returns to specialising into one sexual function (also a well-known result for sex allocation x; Lloyd and Bawa, 1984; Biernaskie, 2010). Overall, this entails that condition (5b) is harder to fulfill, indicating that limited dispersal tends to stabilise hermaphroditism against correlational selection on x and z. To see this more clearly, we can substitute eq. (16) into condition (5b) assuming Gaussian fecundity functions (eq. 2). Re-arrangements then yield the following necessary condition for correlational selection to lead to evolutionary branching

$$F_{\mathrm{ST}} < \frac{2(\omega_{♀}\omega_{♂})^2(\theta_{♀}-\theta_{♂})^2}{2(\omega_{♀}\omega_{♂})^2(\theta_{♀}-\theta_{♂})^2+(\omega_{♀}+\omega_{♂})^3}. \tag{17}$$

In other words, F_{ST} must be sufficiently low compared to the strength of sexual conflict, which here is measured by $(\omega_{♀}\omega_{♂})^2(\theta_{♀}-\theta_{♂})^2$ (i.e. the distance between the male and female optima weighted by the product between selection strength on male and female traits).

We also computed numerically the eigenvalue of the Hessian matrix for arbitrary values of patch size N and seed dispersal d_{s} assuming Gaussian functions (eq. 2). We first set the intensity of selection to be equal through female and male function ($\omega = \omega_{♀} = \omega_{♂}$). In line with condition (17), we see in Figure 5C that polymorphism occurs more readily when patches are large, seed dispersal is high, and selection is strong

(i.e. larger ω). Figure 5D also shows that increasing selection on male function is more conducive to polymorphism than increasing selection on female function (i.e. increasing $\omega_{♂}$ compared to increasing $\omega_{♀}$). To understand this, it is useful to first note that sexual conflict over trait z, which drives sexual specialisation here, is strongest when the population expresses an intermediate value of z that is far from both the male and female optima. All else being equal, local mate competition entails that the equilibrium z^* is female-biased (i.e. closer to the female optimum) when N is finite (recall eq. 15b and Fig. 5B). When selection is stronger over male traits ($\omega_{♀} < \omega_{♂}$), this can offset the effects of local mate competition and thus bring the equilibrium z^* closer to an intermediate where sexual conflict is stronger, and so make selection for sexual specialisation more intense.

4.2 Self-fertilisation and inbreeding depression

Hermaphroditic plants produce both pollen and ovules, which grants them the ability to self-fertilise. Although self-fertilisation (selfing for short) can incur a fitness cost due to inbreeding depression (Charlesworth and Charlesworth, 1987; Charlesworth and Willis, 2009), it allows hermaphrodites to produce offspring even when mating opportunities are scarce or absent (i.e. it brings "reproductive assurance"), a situation that may be particularly frequent in plants as they cannot move in search of mates (Lloyd, 1992; Kalisz et al., 2004; Busch and Delph, 2012). Moreover, selfing has a transmission advantage because a parent transmits twice as many gene copies to its selfed relative to its outcrossed progeny (Fisher, 1941). As a result, selfing yields higher fitness returns than outcrossing when inbreeding depression is weak, which further favours hermaphroditism (Charlesworth and Charlesworth, 1978b; De Jong and Geritz, 2001). In this section, we extend our baseline model (Section 2) to investigate the effect of the interplay between the transmission advantage of selfing and inbreeding depression on transitions to dioecy via correlational selection. We do not consider the benefits of reproductive assurance for simplicity.

As in our baseline model, we consider a large population of hermaphrodites in which at each generation, individuals first undergo sexual development, dividing their reproductive resources between their female and male functions in proportions x and $1 - x$, respectively, and expressing a trait value z. In contrast to our baseline model, individuals now retain a fraction $\alpha \in [0, 1]$ of their pollen for self-fertilisation and disperse the remainder for outcrossing, distributing it equally among other individuals in the population. The selfing rate of an individual is determined by the amount of pollen it retained relative to the total pollen it received,

following a mass-action model (Holsinger, 1991). We assume throughout that enough pollen is produced for all ovules to be fertilised. This 'competing' mode of selfing (Lloyd, 1979) leads the selfing rate of an individual to depend on its sex allocation, with more male individuals achieving higher selfing rates. Mating results in the formation of a large number of outcrossed and selfed diploid zygotes. Outcrossed zygotes become viable with probability 1. Selfed zygotes suffer from inbreeding depression, so that they become viable and give rise to haploid seeds with probability $1-\delta$, where $\delta \in [0,1]$ measures inbreeding depression (Charlesworth and Charlesworth, 1987). Finally, all adults die and the next generation is sampled from the produced seeds. We assume that the genetic basis of sex allocation x and trait z is the same as in our baseline model (Section 2).

We show in Appendix D that the population first converges to the equilibrium $\mathbf{y}^* = (x^*, z^*)$ where

$$x^* = \frac{1}{2-\alpha}, \tag{18a}$$

and z^* is such that

$$\frac{V'_{♀}(z^*)}{V_{♀}(z^*)} = -(1-\alpha)\frac{V'_{♂}(z^*)}{V_{♂}(z^*)}. \tag{18b}$$

Eq. (18a) reduces to eq. (3) in the absence of selfing $\alpha = 0$ and increases with α, indicating that populations where selfing is more common should evolve more female-biased sex allocations (Fig. 6A). This is because selfing reduces the number of ovules available for siring as an outcrossing male, which reduces opportunities to gain fitness through male function and selects for female-biased strategies (Charlesworth and Charlesworth, 1981; Lesaffre et al., 2023). For the same reason, populations where selfing is more common should also express more female-beneficial trait values as seen from eq. (18b) and Figure 6B.

Once the population expresses $\mathbf{y}^*$, we show in Appendix D.2 that the entries of the Hessian matrix (eq. 4) are given by

$$\begin{aligned}
h_{xx}(x^*) &= -\alpha\frac{(2-\alpha)^2(1-2\delta)}{(1-\alpha)(1-\alpha\delta)} \\
h_{xz}(x^*) &= -\alpha^2\frac{(2-\alpha)(1-2\delta)}{2(1-\alpha)(1-\alpha\delta)}\frac{V'_{♀}(z^*)}{V_{♀}(z^*)} + \frac{2-\alpha}{2(1-\alpha\delta)}\left(\frac{V'_{♀}(z^*)}{V_{♀}(z^*)} - \frac{V'_{♂}(z^*)}{V_{♂}(z^*)}\right) \\
h_{zz}(x^*) &= \alpha\frac{1-2\delta}{1-\alpha\delta}\frac{V'_{♀}(z^*)}{V_{♀}(z^*)}\frac{V'_{♂}(z^*)}{V_{♂}(z^*)} + \frac{1+\alpha(1-2\delta)}{2(1-\alpha\delta)}\left(\frac{V''_{♀}(z^*)}{V_{♀}(z^*)} + (1-\alpha)\frac{V''_{♂}(z^*)}{V_{♂}(z^*)}\right).
\end{aligned} \tag{19}$$

The term $h_{xx}(x^*)$ in eq. (19) shows that quadratic selection on sex allocation can either promote or oppose polymorphism under partial selfing, depending on the magnitude of inbreeding depression (e.g., Charlesworth and Charlesworth, 1978b; De Jong and Geritz, 2001; Lesaffre et al., 2023). When inbreeding depression is too weak to offset the twofold transmission advantage of selfing (i.e. when outbred zygotes have less than twice the chance to survive than selfed zygotes, $\delta < 1/2$), selfing leads $h_{xx}(\mathbf{y}^*)$ to become more negative and thus opposes the emergence of polymorphism. In contrast, when inbreeding depression is strong enough to offset the twofold transmission advantage of selfing (i.e. when $\delta > 1/2$), selfing generates increasing fitness returns to becoming more female and thus leads quadratic selection to favour polymorphism in sex allocation (see Lesaffre et al., 2023 for further explanations).

The effects of selfing on quadratic selection on z and correlational selection on x and z ($h_{zz}(x^*)$ and $h_{xz}(x^*)$) are not immediately clear from eq. (19), and so neither is the overall effect of selfing on sexual specialisation through correlational selection. To gain insights into this, we substitute eq. (19) into condition (5b) assuming Gaussian fecundity functions, with equal strength of selection on female and male traits (eq. 2 with $\omega = \omega_{♀} = \omega_{♂}$). After some re-arrangements, we obtain that for polymorphism to occur due to correlational selection, the strength of selection must be over some threshold; specifically that

$$\omega > \frac{\alpha(1-2\delta)(2-\alpha)^2}{4(1-\alpha)\Big\{2-\alpha\big[1+\alpha(1-2\delta)\big]\Big\}}, \tag{20}$$

holds. This threshold increases with the selfing rate when $\delta < 1/2$. This shows that where inbreeding depression is weak enough, selfing opposes the emergence of polymorphism, which requires greater strong sexual conflict over z as α increases and δ decreases (i.e. higher ω values, Fig. 6C). We analyse the effect of asymmetrical selection through male and female function numerically in Figure 6D (i.e. $\omega_{♀} > \omega_{♂}$ or $\omega_{♀} < \omega_{♂}$). Similarly to what we observed under limited dispersal, an increase of selection on male traits favours polymorphism to a greater extent than an increase of selection on female traits. Again, this is because selfing favours an equilibrium z^* that is closer to the female optimum (eq. 18b, Fig. 5B), so that an increase of selection in males intensifies sexual conflict over z more significantly than an increase in females, thus promoting sexual specialisation.

5 Discussion

Sex allocation theory predicts that transitions to dioecy should occur when male and female fitness gain curves are accelerating, whereas hermaphroditism should be maintained when gain curves are saturating (Charnov et al., 1976; Charnov, 1982). Because hermaphroditism is so prevalent among flowering plants (more than 90% of species; Renner, 2014), it is generally thought that gain curves should be saturating in the absence of other ecological mechanisms that might cause them to become accelerating (Charlesworth and Morgan, 1991; Charlesworth, 1999; Pannell and Jordan, 2022). However, previous theory has largely assumed that sex allocation evolves in isolation.

Here, we have shown that the joint evolution of sex allocation with a trait that affects fitness gained through female and male function differently generates an inevitable advantage to sexual specialisation. When ecological or genetic constraints are absent, as in our baseline model, this advantage readily leads to the simultaneous emergence of separate sexes and sexual dimorphism. Given that many life-history and reproductive traits may have conflicting effects on fitness gained through female and male function (Freeman et al., 1997; Barrett, 2002b; Barrett and Hough, 2013), our results suggest that as a baseline, fitness gain curves may well be accelerating rather than saturating. Dioecy should therefore evolve whenever mechanisms stabilising hermaphroditism are insufficient to offset the advantage of sexual specialisation brought about by variation in traits under sexual conflict.

The advantage of sexual specialisation in our model relies on the build up of an association between sex allocation and a trait under sexual conflict. This association is free to arise under haploidy and complete linkage between the loci encoding the two phenotypes, as in our baseline model. In that case, correlational selection generates linkage disequilibrium between female-beneficial alleles on the one hand, and male-beneficial alleles on the other hand, so that the population eventually consists of sexually dimorphic females and males that are each encoded by a different haplotype.

Several genetic mechanisms may interfere with the build up of an association among traits. Recombination between the loci encoding sex allocation and the trait under sexual conflict can prevent polymorphism from emerging, as it breaks up the genetic associations favoured by selection (Fig. 2). However, selection readily leads to the suppression of recombination here (Fig. 3), as individuals with lower recombination rates are

more likely to produce offspring that express the fittest haplotypes associating one sexual function with its optimal trait value (Fisher, 1930; Crow, 1970; Barton and Charlesworth, 1998). Furthermore physical linkage is not the only way sex allocation and sexual trait can become associated. In fact, the associations between sex and other traits that lead to sexual dimorphism are commonly achieved through sex-biased and sex-specific gene expression, which does not rely on any physical linkage (Ellegren and Parsch, 2007; Barrett and Hough, 2013; Mank, 2017). In the context of our model, we have shown how correlational selection favours traits under sexual conflict to evolve conditional expression on sex allocation, which in turn promotes the emergence of separate sexes (Fig. 4). This suggests that sexual dimorphism resulting from differences in gene regulation can easily begin to evolve in hermaphrodites and in turn fuel the transition to dioecy.

Our model ignores the complexities of diploidy and polygenicity, which could also hamper the joint evolution of separate sexes and sexual dimorphism. Diploidy would lead to the production of intermediate heterozygous offspring due to matings between well-differentiated homozygotes, and the expression of alleles segregating at many loci would prevent the production of discrete, well-differentiated sexual morphs. However, the production of unfit heterozygotes due to diploidy generates a 'segregation load', and thus favours the evolution of dominance (Van Dooren, 1999; Billiard et al., 2021). Furthermore, selection for discrete, highly-differentiated morphs on a trait with an initially polygenic basis favours the concentration of its genetic basis such that it ends up being encoded by one or few loci, as this allows greater heritability of the discrete phenotypes favoured by selection (van Doorn and Dieckmann, 2006; Kopp and Hermisson, 2006; Yeaman and Whitlock, 2011). This process is explored for sexual systems in Lesaffre et al. (2023), where it is shown that when sex allocation evolves alone, disruptive selection for dioecy favours the concentration of an initially polygenic basis of sex to a single locus at which complete dominance evolves. This results in the gradual emergence of dioecy underlain by a heterogametic sex-determining locus, and so to nascent sex chromosomes.

When sex allocation evolves jointly with a trait under sexual conflict, as we have explored here, we might expect the genetic architecture of sex determination resulting from this joint evolution to differ depending on the way sex allocation and the other trait become genetically associated. If the association comes about from sex-dependent expression (e.g. via gene regulation), then the concentration of the genetic basis of sex should unfold in a similar way to when sex allocation evolves alone (Lesaffre et al., 2023), with the genetic basis of the trait under sexual conflict remaining polygenic. The resulting sex-determining region could therefore

contain as little as a single gene, and so initially show no sign of recombination suppression around the sex-determining locus. In contrast, if sex allocation and the trait under sexual conflict become associated through recombination suppression, then the resulting sex-determining region might consist of a non-recombining chromosomal segment capturing the loci encoding sex and (at least) one conflict trait, which could constitute a first step towards the extension of recombination suppression along sex chromosomes (Rice, 1984).

Our results indicate that although genetic constraints can hinder the joint emergence of separate sexes and sexual dimorphism in the short-term, they are unlikely to prevent it in the long-term. The maintenance of hermaphroditism may thus be better explained by ecological benefits of hermaphroditism that offset the selective advantage of sexual specialisation brought about by jointly evolving traits. Here we have explored the effects of limited dispersal, which characterises many flowering plant species (Vekemans and Hardy, 2004). Our analyses show that kin competition induced by limited dispersal stabilises hermaphroditism against correlational selection for dioecy and sexual dimorphism, because local mate and resource competition generate diminishing returns to sexual specialisation (Fig. 5). We have additionally studied the effect of partial selfing, which is another common feature of hermaphroditic plants (Goodwillie et al., 2005), and showed that selfing can also stabilise hermaphroditism when inbreeding depression is weak relative to its inherent transmission advantage (Fig. 6). These results are in line with much previous theoretical work that assumed sex allocation evolves alone (e.g. Charlesworth and Charlesworth, 1978b; Lloyd and Bawa, 1984; De Jong and Geritz, 2001; Biernaskie, 2010), and demonstrate that ecology can readily explain the maintenance of hermaphroditism in spite of ever-present correlational selection for sexual specialisation.

With the above considerations in mind, it is interesting to note that dioecy appears to be more common in species in which the ecological benefits associated with hermaphroditism are expected to be weakest. Dioecy is for instance more common among long-lived plant species (Friedman, 2020), in which inbreeding depression is typically high and selfing rates low (Duminil et al., 2009; Angeloni et al., 2011; Munoz et al., 2016), and is also correlated with mechanisms thought to enhance dispersal and so reduce kin competition, such as wind-pollination and seed dispersal by animals (Bawa, 1980; Renner and Ricklefs, 1995). Altogether, our work contributes further to the idea that ecology plays an important role in the evolution of sexual systems.

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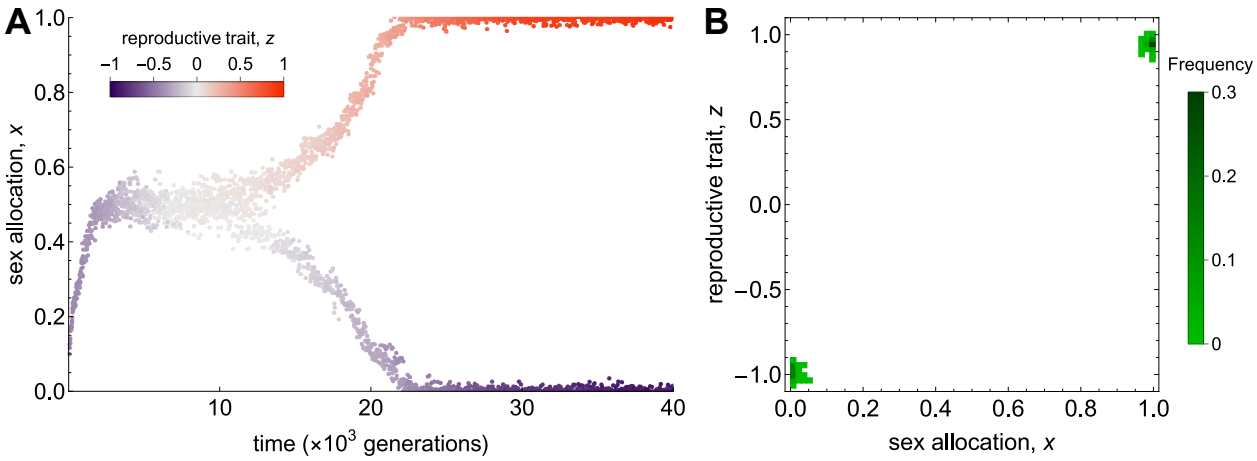

Figure 1: Joint evolutionary dynamics of sex allocation x and trait z in the baseline model leading to the simultaneous emergence of separate sexes and sexual dimorphism. Simulations assume Gaussian fecundity functions (eq. 2, Appendix A.3 for details on the simulation process). **A** Sex allocation x (y-axis) and trait z (colour scale) of three randomly sampled individuals every 10 generations as a function of time. Orange indicates more female-beneficial trait values, whereas purple indicates more male-beneficial values. The population first converges to the equilibrium $\mathbf{y}^* = (x^*, z^*)$, where $x^* = 1/2$ and $z^* = 0$, and then sees the gradual emergence of two morphs, a female morph ($x = 1$) expressing the female-optimal trait value $\theta_{♀} = 1$, and a male morph expressing the male-optimal trait value $\theta_{♂} = -1$. **B** Distribution of phenotypes averaged over the last $1,000$ generations of the simulation. Darker colours indicate higher frequencies. Parameters used in simulations: $\theta_{♀} = 1$, $\theta_{♂} = -1$, $\omega_{♀} = \omega_{♂} = 1/6$, $N = 5 \times 10^3$, $\mu = 5 \times 10^{-3}$, and standard deviation $\sigma = 10^{-2}$.

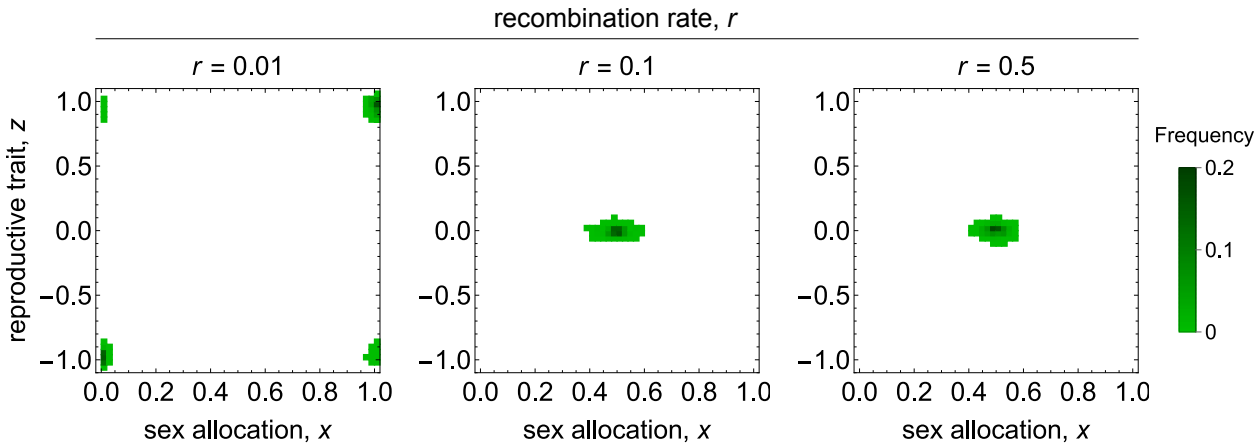

Figure 2: Recombination breaks the necessary genetic associations for the joint evolution of separate sexes and sexual dimorphism. Panels show the distribution of phenotypes expressed in simulations populations averaged over $25,000$ generations after a $50,000$ generations burn-in period, with higher densities indicated by darker colours. Results are shown for three recombination rates ranging from $r = 0.01$ on the left-hand side to $r = 0.5$ (free recombination) on the right-hand side. Parameters used in simulations: $\theta_{♀} = 1$, $\theta_{♂} = -1$, $\omega_{♀} = \omega_{♂} = 0.4$, $N = 5 \times 10^3$, $\mu = 10^{-3}$, $\sigma = 10^{-2}$.

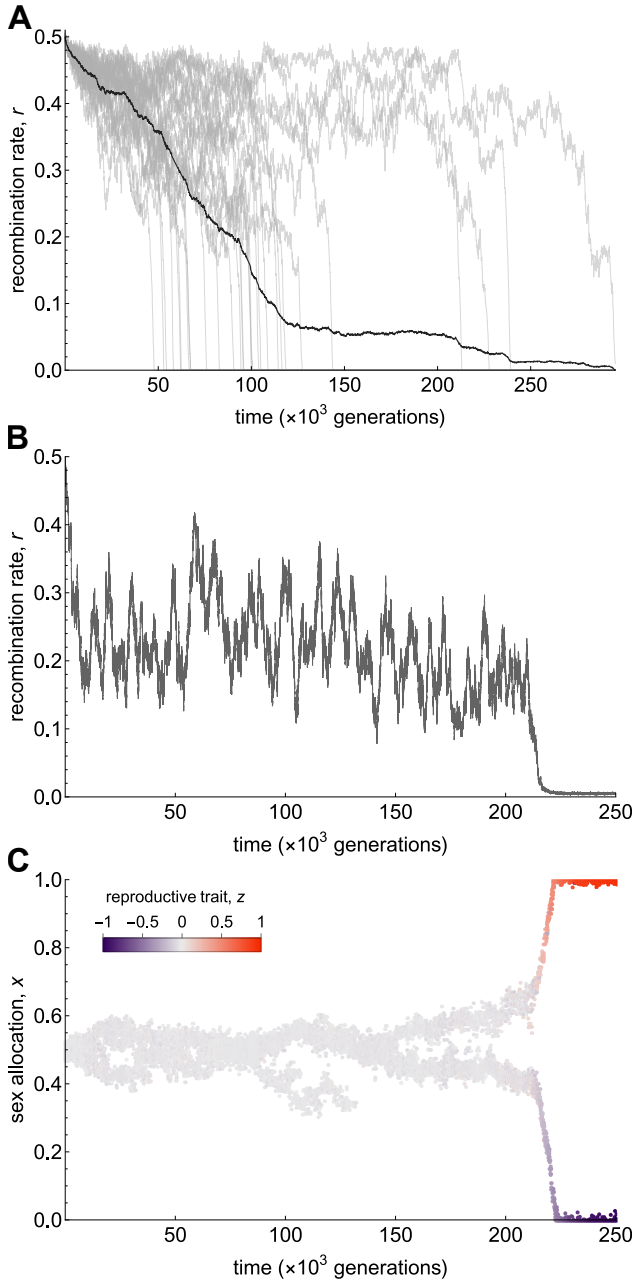

Figure 3: Evolution of recombination suppression. **A** Recombination rate as a function of time in 30 replicate populations where the recombination rate r evolves jointly with sex allocation x and trait z (Appendix B.1.3 for details on the simulation process). Each grey line corresponds to one replicate. The black line indicates the average trajectory. Parameters used in simulations: $\theta_{♀} = 1$, $\theta_{♂} = -1$, $\omega_{♀} = \omega_{♂} = 0.4$, $N = 10^4$, $\mu = 5 \times 10^{-3}$, $\sigma = 10^{-2}$ for all three evolving traits (x, z and r). **B-C** Recombination rate (panel B) and phenotypes expressed (panel C) in a single replicate as a function of time. In panel C, sex allocation is given on the y-axis, and trait z by the colour scale (as in Fig. 1). This shows that recombination suppression allows the simultaneous emergence of separate sexes and sexual dimorphism. Parameters used in simulations: $\theta_{♀} = 1$, $\theta_{♂} = -1$, $\omega_{♀} = \omega_{♂} = 0.4$, $N = 10^4$, $\mu = 10^{-3}$, $\sigma = 10^{-2}$ for x and z, and $\mu = 5 \times 10^{-3}$, $\sigma = 5 \times 10^{-2}$ for r).

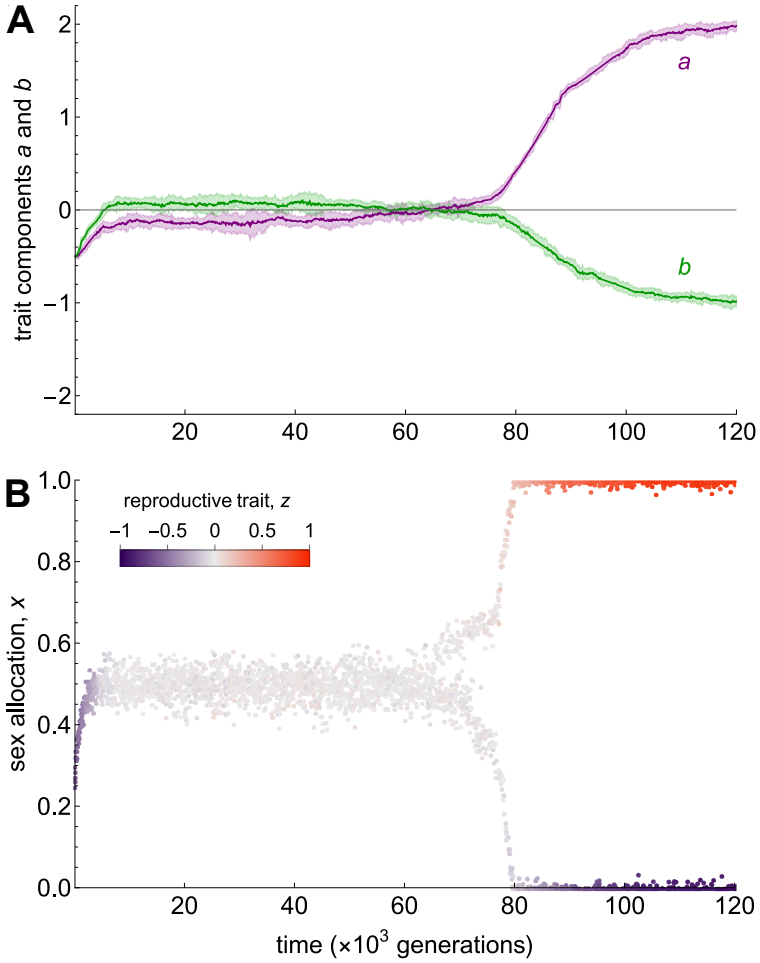

Figure 4: Evolution of conditional trait expression. **A** Sex allocation-dependent a (in purple) and -independent b (in green) components of trait z as a function of time. Solid lines indicate mean values in the population, and shaded areas indicate two standard deviations around these means. **B** Sex allocation x (y-axis) and trait $z = a \cdot x + b$ (colour scale) during the same simulation. The population first evolves to an intermediate equilibrium $\mathbf{y}^* = (x^*, a^*, b^*)$ such that $x^* = 1/2$ and $a^* = b^* = 0$ (so that $z^* = 0$), and then undergoes the simultaneous emergence of conditional expression of z and polymorphism in sex allocation, ultimately leading to the stable coexistence of females and males expressing their sex-specific optima. Parameters used in the simulation: $\theta_{♀} = 1$, $\theta_{♂} = -1$, $\omega_{♀} = \omega_{♂} = 1/3$, $N = 5 \times 10^3$, $\mu = 10^{-3}$, $\sigma = 10^{-2}$ for all traits (x, a and b).

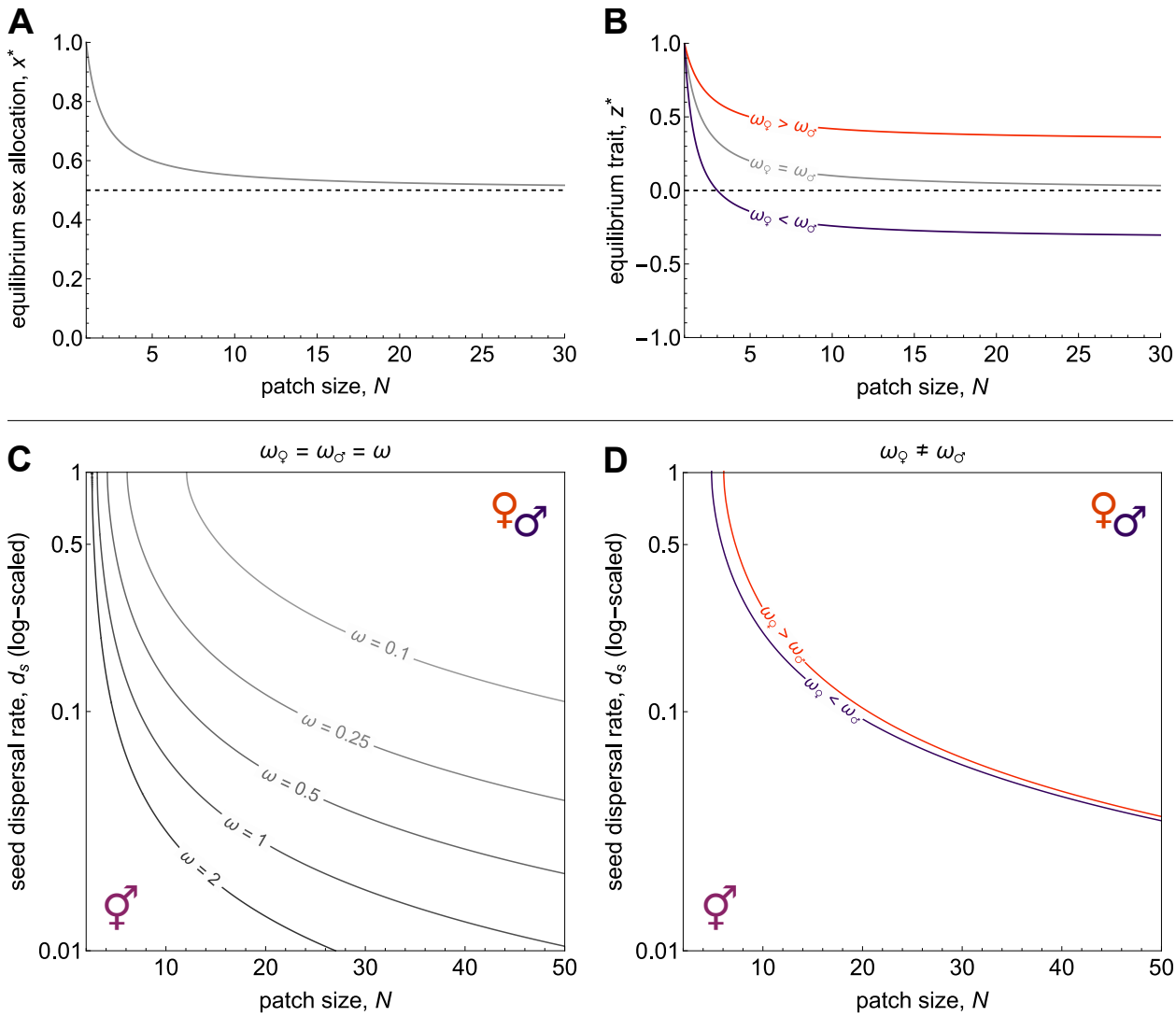

Figure 5: Effect of limited dispersal on the joint evolution of sex allocation x and trait z. Gaussian fecundity functions with sex-specific optima set to $\theta_{♀} = 1$ and $\theta_{♂} = -1$ are assumed throughout (eq. 2). **A** Equilibrium sex allocation x^* favoured by directional selection under limited dispersal (eq. 15a). The population becomes increasingly female-biased as patch size N decreases due to local mate competition. **B** Equilibrium trait z^* as a function of patch size N (eq. 15b with Gaussian functions). The grey line shows a case where selection is equally strong between sexual functions ($\omega_{♀} = \omega_{♂} = 1/4$). The orange line shows a case where selection is stronger through female function ($\omega_{♀} = 1/2$ and $\omega_{♂} = 1/4$), and the purple line shows the symmetrical case where selection is stronger through female function ($\omega_{♀} = 1/4$ and $\omega_{♂} = 1/2$). **C-D** Patch size N and seed dispersal d_{s} (log-scaled) leading to polymorphism when selection is equally strong through female and male function ($\omega_{♀} = \omega_{♂} = \omega$, panel C), and when the strength of selection differs between the two sexual functions ($\omega_{♀} \neq \omega_{♂}$, panel D). For a given strength of selection ω polymorphism is favoured above the line (as indicated by the female and male symbols shown in the top-right corner), whereas hermaphroditism is maintained below. In panel D, the orange line shows a case where selection is twice as strong through female function ($\omega_{♀} = 1/2$ and $\omega_{♂} = 1/4$), and the purple line shows the opposite case where $\omega_{♀} = 1/4$ and $\omega_{♂} = 1/2$.

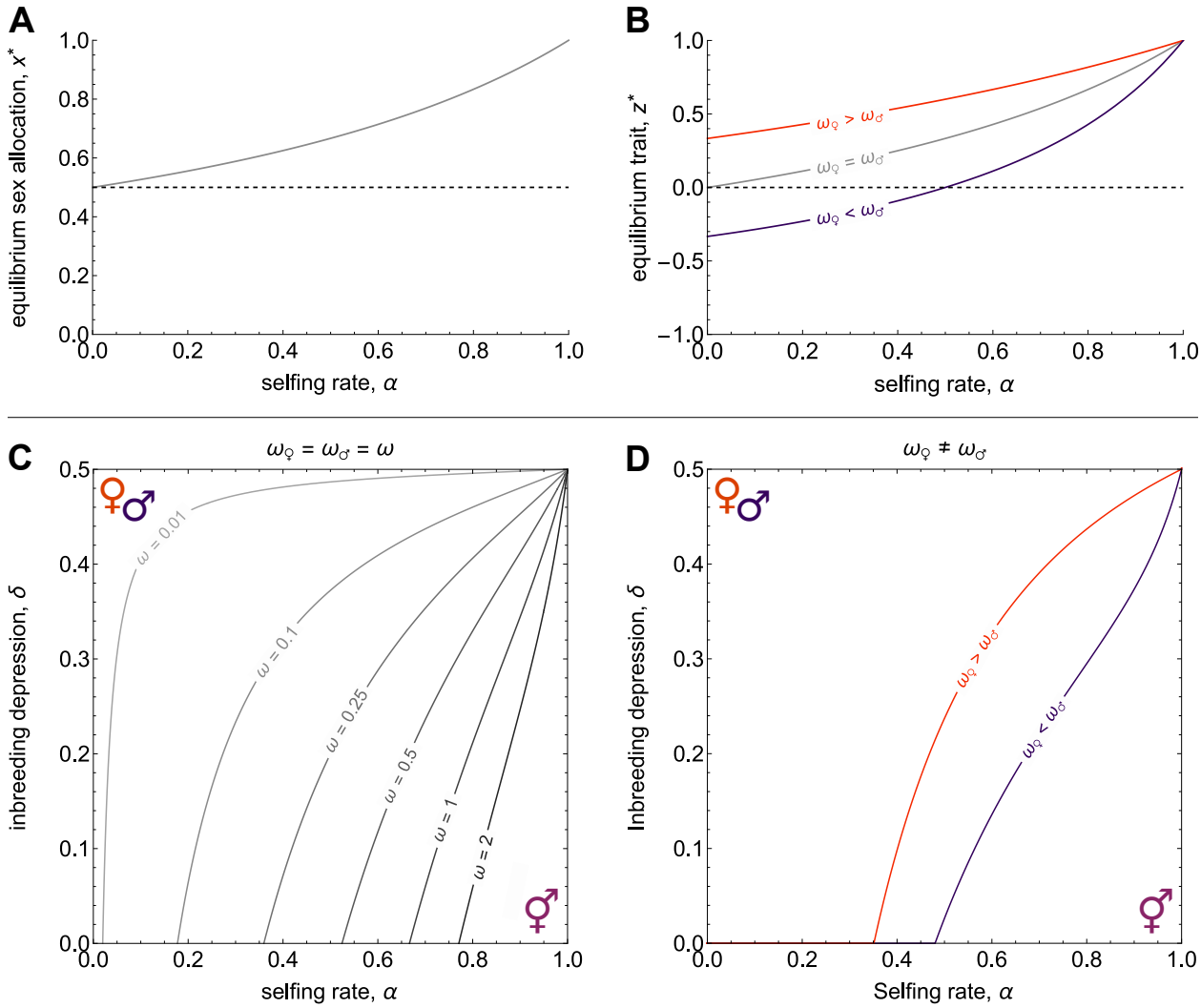

Figure 6: Effect of selfing on the joint evolution of sex allocation x and trait z. We assume Gaussian fecundity functions throughout, with sex-specific optima set to $\theta_{♀} = 1$ and $\theta_{♂} = -1$ (eq. 2). **A** Equilibrium sex allocation x^* favoured by selection under partial selfing (eq. 18a). The population becomes increasingly female-biased as the selfing rate (α) increases because selfing reduces the relative contribution of male function to fitness . **B** Equilibrium trait z^* as a function of the selfing rate (eq. 18b with Gaussian functions, eq. 2). The grey line shows a case where selection is equally strong between sexual functions ($\omega_{♀} = \omega_{♂} = 1/4$). The orange line shows a case where selection is stronger through female function ($\omega_{♀} = 1/2$ and $\omega_{♂} = 1/4$), and the purple line shows the symmetrical case where selection is stronger through female function ($\omega_{♀} = 1/4$ and $\omega_{♂} = 1/2$).**C-D** Selfing rate α and inbreeding depression δ leading to polymorphism when selection is equally strong through female and male function ($\omega_{♀} = \omega_{♂} = \omega$, panel C), and when the strength of selection differs between the two sexual functions ($\omega_{♀} \neq \omega_{♂}$, panel D). For a given strength of selection ω polymorphism is favoured above the line (as indicated by the female and male symbols shown in the top-right corner), whereas hermaphroditism is maintained below. In panel D, the orange line shows a case where selection is twice as strong through female function ($\omega_{♀} = 1/2$ and $\omega_{♂} = 1/4$), and the purple line shows the opposite case where $\omega_{♀} = 1/4$ and $\omega_{♂} = 1/2$.