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**Author for correspondence:**

Jonathan M. Henshaw

e-mail: [jonathan.henshaw@biologie.uni-freiburg.de](mailto:jonathan.henshaw@biologie.uni-freiburg.de)

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# Hermaphroditic origins of anisogamy

Jonathan M. Henshaw<sup>1</sup>, Markus Bittlingmaier<sup>1,2</sup> and Lukas Schärer<sup>3</sup>

<sup>1</sup>Institute of Biology I, University of Freiburg, Hauptstraße 1, D-79104 Freiburg, Germany

<sup>2</sup>Theoretical and Experimental Ecology Station, CNRS, 2 route du CNRS, 09200 Moulis, France

<sup>3</sup>Zoological Institute, Department of Environmental Sciences, University of Basel, Basel CH-4051, Switzerland

JMH, 0000-0001-7306-170X

Anisogamy—the size dimorphism of gametes—is the defining difference between the male and female sexual strategies. Game-theoretic thinking led to the first convincing explanation for the evolutionary origins of anisogamy in the 1970s. Since then, formal game-theoretic models have continued to refine our understanding of when and why anisogamy should evolve. Such models typically presume that the earliest anisogamous organisms had separate sexes. However, in most taxa, there is no empirical evidence to support this assumption. Here, we present a model of the coevolution of gamete size and sex allocation, which allows for anisogamy to emerge alongside either hermaphroditism or separate sexes. We show that hermaphroditic anisogamy can evolve directly from isogamous ancestors when the average size of spawning groups is small and fertilization is relatively efficient. Sex allocation under hermaphroditism becomes increasingly female-biased as group size decreases and the degree of anisogamy increases. When spawning groups are very small, our model also predicts the existence of complex isogamous organisms in which individuals allocate resources equally to two large gamete types. We discuss common, but potentially unwarranted, assumptions in the literature that could be relaxed in future models.

This article is part of the theme issue ‘Half a century of evolutionary games: a synthesis of theory, application and future directions’.

## 1. Introduction

Multicellular organisms typically produce gametes of two distinct size classes: larger eggs and smaller sperm. This dimorphism—known as ‘anisogamy’—is a remarkable case of convergent evolution. It has arisen independently in multiple distantly related eukaryotic lineages, including in animals [1]; dikaryotic fungi [2]; various groups of green algae, including the ancestors of land plants [3,4]; red algae [5]; brown algae [6,7]; yellow-green algae (Xanthophyceae: *Vaucheria*) [8]; diatoms [9]; oomycetes [10]; dinoflagellates [11]; apicomplexans [12]; and parabasalids (*Trichonympha*) [13]. By contrast, the gametes of most unicellular and some multicellular eukaryotes are isogamous, with a unimodal distribution of gamete sizes. Anisogamy is often taken as the defining difference between ‘male’ and ‘female’ sexual strategies: males produce only sperm; females produce only eggs; and hermaphrodites have the potential to produce both gamete types, either simultaneously or at different life stages. Isogamous species lack sexes by this definition. However, their gametes can often be classified into two, or occasionally more, ‘mating types’, such that fertilization only occurs between gametes of unlike types [2,14–16].

The most convincing explanation for the evolutionary origins of anisogamy invokes disruptive selection on gamete size, which results from two conflicting selection pressures [17–21]. First, large gametes can provision zygotes more effectively. Second, producing many smaller gametes is advantageous in competition for fertilizations, or when fertilization rates are limited by infrequent encounters between gametes [21]. Both selection pressures are inherently frequency-dependent: the benefits of zygote provisioning depend on the resources provided by potential partners, whereas fertilization rates depend on the strategies of both potential partners and competitors. Evolutionary game theory—based on both analytic models and computer simulations—has consequently proved

essential to understanding how anisogamy evolves [17–24]. Under the right conditions, game-theoretic models predict that these opposing pressures can select for specialization into relatively few zygote-provisioning eggs and many fertilization-maximizing sperm. Eggs and sperm may evolve from isogamous mating types [19,21], as has been demonstrated empirically in volvocine green algae [25–28]. Alternatively, they may evolve via evolutionary branching in a population without pre-existing mating types [18].

Most models of the evolution of anisogamy share two important life-history assumptions, neither of which has unequivocal empirical support. First, fertilization is assumed to occur externally in the open water, into which all gametes are released (e.g. ‘broadcast spawning’ in sessile organisms) [17–19,21,22]. By contrast, internal fertilization (e.g. in the form of ‘sperm casting’: [29–31]) is widespread or dominant in many anisogamous groups and might have preceded anisogamy in some cases. Lehtonen & Parker [24] recently extended anisogamy models to internal fertilizers, showing that much of the logic of previous theory carries over to this case.

Second, most models of anisogamy assume that each individual produces only one type of gamete ([17–19,21,24], but see [22]). This assumption leads automatically to separate males and females once anisogamy evolves. By contrast, hermaphroditism is widespread in many anisogamous groups [4,32–35]. Moreover, in isogamous species with binary mating types, a single individual may produce either one or both gamete types [4,36]. Such systems are often described as ‘dioecious’ and ‘monoecious’, respectively, or, in some haplontic taxa, as ‘dioicous’ and ‘monoicous’ [7]. Contemporary diversity in reproductive strategies makes it difficult to infer with any certainty whether the earliest anisogamous organisms were hermaphroditic or had separate sexes. For instance, Sasson & Ryan [37] found that both systems were plausible character states for the earliest animals, regardless of whether sponges or comb jellies are taken as the earliest diverging group. In the volvocine green algae, Hanschen *et al.* [3,36] showed that anisogamy has evolved at least twice independently, and monoecy at least four times. From their ancestral state reconstructions, it appears likely that anisogamy evolved in a dioecious context in the clade containing *Eudorina* and *Volvox carteri*, despite several origins of monoecy within this group. On the other hand, in the clade containing *Platydorina* and *Volvox globator*, their reconstruction places the origins of anisogamy and monoecy close together, so that the evolution of anisogamy against a monoecious background cannot be ruled out here. It is therefore conceivable that monoecy preceded anisogamy in at least some taxa [38].

While Roughgarden & Iyer [22] model a hermaphroditic origin of anisogamy, their model incorporates no ecological or reproductive mechanism that would favour hermaphroditism over separate sexes (e.g. the potential for self-fertilization at low population densities: [39–41]). Moreover, they effectively assume that the fitness returns on gamete investment are linear for both gamete types, conditions that should typically select for separate sexes [42]. Importantly, Roughgarden and Iyer do not model competition between these two allocation strategies, but rather simply assume that individuals produce gametes of both types. Similarly, Lehtonen & colleagues [21,43] consider the evolution of anisogamy in small groups, yet assume that all individuals specialize in one gamete type, even though small mating groups are often expected to favour hermaphroditism [39,40,44,45].

Here, we present a simulation model of the evolution of anisogamy. We allow for individuals to produce either just one or both of two gamete types. Allocation strategies coevolve with gamete sizes in our model, allowing anisogamy to emerge in conjunction with either hermaphroditism or separate sexes. We also consider the effects of group size, self-fertilization and inbreeding depression, all factors known to shape the relative advantages of different sexual systems.

## 2. Methods

We first outline the broad structure of our simulation model and define some terminology, before considering each component in detail. We simulated a population of broadcast spawners of fixed size  $N$  (i.e. our model assumes external fertilization). Generations are non-overlapping and each generation consists of a single continuous breeding season. Each generation, the population is subdivided randomly into local spawning groups, such that the number of individuals in each group is drawn from a Poisson distribution with mean  $\lambda$ . Fertilization takes place exclusively within these local groups. The structure of local spawning groups is ephemeral; groups are redrawn each generation independently of the previous generation’s group structure. Populations consequently lack local relatedness structure. This assumption is consistent with the empirical evidence for sessile marine animals with a pelagic larval stage, as such larvae often disperse widely [46]. However, it may not accurately capture the evolutionary dynamics of systems with limited dispersal, in which competition among close relatives for mating opportunities can play an important role [42,47,48].

We assume that populations are initially isogamous with two pre-existing mating types—labelled  $x$  and  $y$ —and that fertilization only occurs between gametes of non-matching types. Each individual in the population carries genes for three coevolving traits (key parameters and variables are summarized in tables 1 and 2):

- the proportion of resources it allocates to producing gametes of each mating type ( $r$  for type  $x$  and  $1 - r$  for type  $y$ ),
- the resources  $m_x$  it invests in each gamete of type  $x$  and
- the resources  $m_y$  it invests in each gamete of type  $y$ .

The size of individual gametes is proportional to the resources invested in them. We assume that larger gametes have lower mortality rates and also contribute greater resources towards the zygote after fusion, which increases zygote survival. On the other hand, there is a direct trade-off between the size and the number of gametes an individual can produce given a fixed resource budget. Furthermore, we allow that individuals specializing in one gamete type (i.e. with  $r = 0$  or  $r = 1$ ) may have a larger resource budget for producing gametes (e.g. because each gamete type requires specialized organs that are costly to produce). The potential for self-fertilization and the strength of inbreeding depression are controlled by fixed parameters.

### (a) Genetics

For simplicity, we assume haploid genetics. Each trait ( $r$ ,  $m_x$ ,  $m_y$ ) is coded for by a single locus that can be occupied by continuum of possible alleles. Meiosis is fair and recombination perfect. This means that offspring inherit an allele at each locus from their mother or father with equal probability, independently of inheritance at any other locus. All traits are determined entirely genetically (i.e. there are no environmental effects). In particular, individuals do not adjust their allocation according to the size or composition of their local spawning group.

The proportion of reproductive resources  $r$  that an individual allocates to gametes of type  $x$  is a real number in the interval  $[0, 1]$ . The sizes  $m_x$  and  $m_y$  of gametes are real numbers in the interval

**Table 1.** Summary of parameters.

parameter	meaning	default value
$A$	specialization advantage: increase in gamete budget for individuals specializing in one gamete type	0.1
$B$	effectiveness of selfing block	varies
$D$	inbreeding depression	varies
$M$	individual gamete budget per unit time for monoecious individuals	100
$N$	population size	1000
$p_r$	per-allele per-generation probability of a mutation in sex allocation	0.001
$p_m$	per-allele per-generation probability of a mutation in gamete size	0.001
$\alpha$	gamete size that maximizes fertilization rate	1
$\beta$	zygote size that maximizes the number of surviving zygotes (e.g. under parthenogenesis)	varies
$\gamma$	fertilization efficiency	varies
$\lambda$	average number of individuals in a spawning group	varies
$\sigma_r$	s.d. of mutational effects for sex allocation	0.5
$\sigma_m$	s.d. of mutational effects for gamete size	1
$\mu(m)$	instantaneous rate at which a gamete of size $m$ is lost from the fertilization arena owing to mortality or dispersion	$\exp(\alpha/m)$
$f(m_x, m_y)$	survival probability of a zygote formed by gametes of sizes $m_x$ and $m_y$	$\exp(-\beta/(m_x + m_y))$

**Table 2.** Summary of variables.

variable	meaning
$m_x, m_y$	size of gametes of type $x, y$
$n_x, n_y$	number of gametes of type $x, y$ that an individual produces per unit time
$r$	proportion of individual gamete budget allocated to gametes of type $x$
$R$	sex allocation: proportion of individual gamete budget allocated to smaller gamete type
$T$	trioecy ratio: population proportion of individuals producing the larger gamete type among all those individuals specializing in one gamete type
$X_i^*, Y_i^*$	equilibrium densities of the $i$ th individual's gametes of types $x$ and $y$ , respectively, in its local spawning group
$Z_{ij}$	rate at which individuals $i$ and $j$ produce surviving zygotes

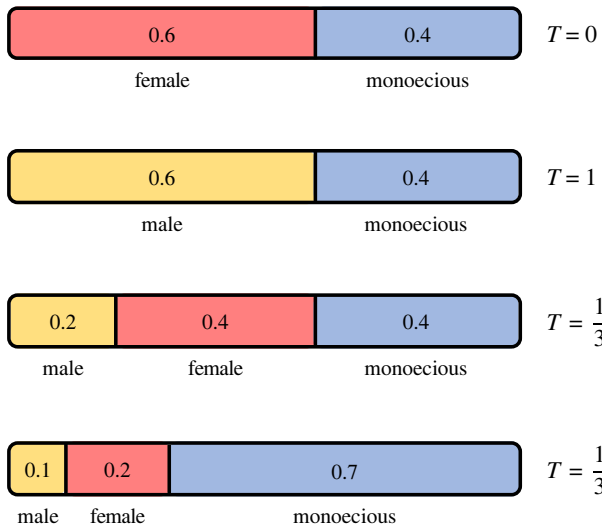
[0.1,  $\infty$ ). The lower bound of 0.1 is of purely practical importance, as it helps to avoid numerical instability when solving simultaneous equations to estimate the fertilization dynamics (see equation (2.4) below). This truncation has little effect on our results, however, as gametes below this size have extremely high mortality rates and consequently have little influence on fertilization dynamics (see equation (2.2) below, noting that we set  $\alpha = 1$  throughout: table 1).

We based our simulations on a haploid continuum-of-alleles model for pragmatic reasons, including reducing run time. However, we believe that our key results would continue to hold under a diploid genetic system or under more realistic genetic architectures that still allow for sufficiently variable sex allocation. Our focus is on the evolution of sex allocation phenotypes, which should face similar selection pressures when gametes are produced by haploid individuals (i.e. in haplontic life cycles) or by diploid individuals (in diplontic or haplodiplontic life cycles). One major exception is the role of inbreeding, which can be a potent agent of selection in diplontic organisms owing to the accumulation of recessive or partially recessive deleterious mutations, but is thought to be low or absent in haplontic species [49]. We consequently allow for both the presence and the absence of inbreeding depression in our model, with the strength of inbreeding depression modelled via a fixed parameter (see *Fitness* below).

### (b) Terminology and population-level trait indices

Anisogamy occurs when mean gamete size differs considerably between the two gamete types, in which case we call the larger type 'eggs' and the smaller one 'sperm'. In practice, we often consider the 'anisogamy ratio'—the average size of the larger gamete divided by the average size of the smaller gamete. The anisogamy ratio provides a continuous measure of the degree of anisogamy. We define 'sex allocation' as the proportion of resources allocated to the smaller gamete type, which is given by  $R = r$  when  $\bar{m}_x < \bar{m}_y$  and  $R = 1 - r$  when  $\bar{m}_x > \bar{m}_y$ . We define an individual's fertilization rate as the proportion of larger-type gametes produced by that individual that are successfully fertilized. The 'average fertilization rate' at the population level is calculated by averaging individual fertilization rates over those individuals that produce gametes of the larger type (i.e. those with  $R < 1$ ). We apply these latter definitions both to anisogamous populations, where their meaning is natural, and to isogamous populations, in which the two gamete types invariably differ slightly in their average size owing to random noise.

To standardize terminology, we refer to a population as 'monoecious' if individuals produce both gamete types (i.e.  $0 < r < 1$ ) and 'dioecious' if each individual specializes in one gamete type (i.e.  $r = 0$  or  $r = 1$ ), regardless of the underlying genetic system or the presence of anisogamy. Thus, for anisogamous populations, 'monoecy'



**Figure 1.** Illustration of the trioecy index  $T$  in four different anisogamous populations. Numbers indicate the proportions of each population that are female, male and monoecious. The trioecy index equals the proportion of males divided by the total proportion of males and females. For example, in the bottommost population, we have  $T = 0.1/(0.1 + 0.2) = 1/3$ . Note that populations with different proportions of monoecious individuals can nonetheless have the same trioecy index (the bottom two populations).

corresponds to hermaphroditism and ‘dioecy’ to separate sexes. Note that our usage differs from that in the botanical literature, where ‘monoecy’ is typically reserved for angiosperms in which pistils and stamens occur on separate flowers of the same plant. In addition to these population descriptors, we refer to individuals with  $0 < r < 1$  as ‘monoecious’ and those with  $r = 0$  or  $r = 1$  as ‘specialists’ (or, in anisogamous populations, simply as ‘males’ and ‘females’). For mixed populations consisting of both monoecious and specialist individuals, we define a ‘trioecy index’  $T$  as the proportion of individuals with sex allocation  $R = 1$  among all specialists (figure 1). In anisogamous populations,  $T = 0$  corresponds to gynodioecy (females and monoecious individuals),  $T = 1$  to androdioecy (males and monoecious individuals), and  $0 < T < 1$  to trioecy (males, females and monoecious individuals).

We initially present the exact proportions of monoecious individuals in simulated populations (see Results: figure 2). However, when focussing on other aspects of the results, it is convenient to roughly classify all populations as either ‘monoecious’ or ‘dioecious’. We arbitrarily designated all populations in which more than a quarter of individuals produced both gamete types as ‘monoecious’ (marked with a circle ● in all figures) and those in which three quarters or more produced only one gamete type as ‘dioecious’ (marked with a triangle ▲). This threshold was chosen because, in empirical contexts, a minority of monoecious individuals is typically sufficient for researchers to classify a population as monoecious. In practice, most populations were close to fully monoecious (greater than 95% monoecious individuals) or fully dioecious (less than 5% monoecious individuals) (see Results: figure 2), so the choice of this arbitrary threshold had no substantial impact on our conclusions. We now consider each component of the model in more detail.

### (c) Gamete production

Each individual produces gametes continuously at a uniform rate over the breeding season. We assume that monoecious individuals (with  $0 < r < 1$ ) have a fixed resource budget of  $M$  per unit time for gamete production. Individuals that specialize in one gamete type (with  $r = 0$  or  $r = 1$ ) have a potentially larger resource budget of  $(1 + A)M$ , where  $A \geq 0$  [31,40,50]. The parameter  $A$  represents an efficiency advantage of specializing in one gamete

type. In both cases, the number of gametes produced per unit time is simply the resource budget divided by the size of the gametes. For individuals with  $0 < r < 1$ , the numbers of gametes of each type produced per unit time are consequently:

$$n_x = r \frac{M}{m_x}, \quad \text{and} \quad n_y = (1 - r) \frac{M}{m_y}. \quad (2.1a)$$

Similarly, individuals specializing in type- $x$  gametes produce these at a rate of

$$n_x = \frac{(1 + A)M}{m_x}. \quad (2.1b)$$

Lastly, for individuals specializing in type- $y$  gametes, we have:

$$n_y = \frac{(1 + A)M}{m_y}. \quad (2.1c)$$

### (d) Gamete loss and zygote survival

We assume that gametes cease to be available for fertilization when they either die or disperse too far from other spawning individuals (e.g. owing to water currents, turbulence or their own locomotion). Since mortality rates, in particular, tend to be higher for smaller gametes, we assume that each gamete is lost at a constant instantaneous rate  $\mu(m)$  that decreases with its size  $m$ , according to [21]:

$$\mu(m) = \exp\left(\frac{\alpha}{m}\right). \quad (2.2)$$

The parameter  $\alpha$  determines the optimal gamete size from the perspective of maximizing the number of gametes available for fertilization. To see this, note that the expected fertilizable lifespan of an individual gamete is given by  $1/\mu(m)$  and that the number of such gametes produced per unit time equals  $E/m$ , where  $E$  is the individual’s resource budget for that particular gamete type. In our model, the resource budget for specialists is  $E = (1 + A)M$ , and the resource budgets for monoecious individuals are  $E = rM$  and  $E = (1 - r)M$  for type- $x$  and type- $y$  gametes, respectively (see equations (2.1a–c)). Before accounting for successful fertilizations, the expected number of an individual’s gametes of that type that are available for fertilization at any given point in time is thus  $E/(m\mu(m))$ , which has a global maximum at  $m = \alpha$ .

When two gametes fuse during fertilization, we assume that the survival probability of the resulting zygote increases as a sigmoidal function of the sum  $m_x + m_y$  of the sizes of the fusing gametes, according to [19,21]:

$$f(m_x, m_y) = \exp\left(-\frac{\beta}{m_x + m_y}\right). \quad (2.3)$$

The parameter  $\beta$  determines the optimal zygote size when fertilization is guaranteed and sexual conflict is absent. To see this, consider a hypothetical parthenogenetic individual that reproduces via unfertilized eggs of size  $m$ . The total number of eggs produced per unit time is given by  $E/m$ , where  $E$  is the individual’s resource budget for egg production, and the proportion of surviving zygotes is given by  $\exp(-\beta/m)$ . The expected number of surviving zygotes per unit time is thus  $E/(m\exp(-\beta/m))$ , which has a global maximum at  $m = \beta$ .

In practice, there is a trade-off between producing many small gametes, which maximizes fertilization success, and fewer large gametes, which maximizes the survival of zygotes. This trade-off is more severe when  $\beta$  is much larger than  $\alpha$ . Larger values of  $\beta/\alpha$  consequently tend to result in disruptive selection on gamete size, which leads to anisogamy. We follow previous authors in referring to  $\beta/\alpha$  as ‘organismal complexity’ [21]. The assumption underlying this term is that optimal zygote size tends to grow with complexity in multicellular organisms [3], whereas the optimal gamete size for fertilization purposes shows no such pattern.



### (e) Fertilization dynamics

At the beginning of each generation, the total population of  $N$  individuals is divided into local spawning groups. The size of each group is drawn from a Poisson distribution with mean  $\lambda$ . Groups are filled successively by sampling individuals at random without replacement from the population until no individuals remain. Note that the size of the last group is less than  $\lambda$  on average and does not follow a Poisson distribution.

Within each spawning group, we assume for simplicity that gametes diffuse evenly over a fixed volume of water that we call the ‘fertilization arena’. We define units such that the fertilization arena has a volume of one; this ensures that we can write equivalently about the number or density of gametes within a fertilization arena. Gamete densities are affected by three processes: production, loss and fertilization. We assume that the breeding season is long enough that the rate of gamete loss and fertilization reach an equilibrium with the influx of newly produced gametes. As a consequence, the densities of each gamete type produced by each individual are approximately constant within the fertilization arena over the course of the breeding season. If gametes of types  $x$  and  $y$  have densities of  $X$  and  $Y$ , respectively, then gamete encounters occur at a rate of  $\gamma XY$ , where the parameter  $\gamma$  controls the efficiency of fertilization. Encounters between opposite-type gametes from different individuals always lead to fertilization. We allow, however, that self-fertilizations may sometimes be ‘blocked’, meaning that an encounter between opposite-type gametes of the same individual does not lead to fertilization, and both gametes subsequently remain alive in the fertilization arena. The proportion of self-fertilizations that are blocked is given by the parameter  $B \in [0, 1]$ , such that there is no selfing block when  $B = 0$  and a complete block when  $B = 1$ . The possibility of polyspermy—egg mortality owing to fertilization by multiple sperm—is not considered in this model, even though it can generate selection on egg size (i.e. we effectively assume an efficient polyspermy block) [51–55].

Let us now consider the processes affecting the density  $X_i$  of type- $x$  gametes produced by the  $i$ th individual. This individual produces new type- $x$  gametes at a rate of  $n_{xi}$  per unit time (equation (2.1)). These gametes are lost owing to mortality or dispersion at a total rate of  $\mu(m_{xi})X_i$  per unit time (equation (2.2)). When calculating fertilization rates, it is helpful to consider selfing and outcrossing separately. We write  $G_i$  for the set of all individuals in the same spawning group as the  $i$ th individual; the set  $G_i \setminus \{i\}$  then represents all individuals in this group except for the  $i$ th individual itself. The total concentration of type- $y$  gametes produced by other individuals is given by the sum  $\sum_{j \in G_i \setminus \{i\}} Y_j$ . Consequently, fertilizations between type- $x$  gametes of the  $i$ th individual and type- $y$  gametes of other individuals occur at a rate of  $\gamma X_i \sum_{j \in G_i \setminus \{i\}} Y_j$ . Self-fertilizations similarly occur at a rate of  $\gamma(1 - B)X_i Y_i$ , where  $B$  represents the proportion of self-fertilizations that are blocked (see above). The total rate of change in  $X_i$  with respect to time is thus [56,57]:

$$\frac{\partial X_i}{\partial t} = n_{xi} - \mu(m_{xi})X_i - \gamma X_i \left( (1 - B)Y_i + \sum_{j \in G_i \setminus \{i\}} Y_j \right). \quad (2.4a)$$

Analogously, the total rate of change in the density  $Y_i$  of type- $y$  gametes produced by the  $i$ th individual is given by:

$$\frac{\partial Y_i}{\partial t} = n_{yi} - \mu(m_{yi})Y_i - \gamma Y_i \left( (1 - B)X_i + \sum_{j \in G_i \setminus \{i\}} X_j \right). \quad (2.4b)$$

At equilibrium, we have  $\partial X_i / \partial t = \partial Y_i / \partial t = 0$  for all  $i$ . This leads to a system of  $2N_{G_i}$  nonlinear simultaneous equations, where  $N_{G_i}$  is the number of individuals in the spawning group. We solved such systems numerically using Wolfram Mathematica (version 12.1.0.0) to obtain equilibrium gamete

densities  $X_i^*$  and  $Y_i^*$  for each individual (see Mathematica code in the electronic supplementary material).

### (f) Fitness

Using the equilibrium gamete densities, we calculated a parental table containing the rates at which surviving zygotes are produced by each pair of individuals in the population. Consider individuals  $i$  and  $j$  from the same spawning group and suppose first that  $i \neq j$ . The rate at which the  $i$ th individual’s type- $x$  gametes fertilize the  $j$ th individual’s type- $y$  gametes is  $\gamma X_i^* Y_j^*$  and the survival probability of the resulting zygotes is  $f(m_{xi}, m_{yj})$ . Similarly, the  $i$ th individual’s type- $y$  gametes fertilize the  $j$ th individual’s type- $x$  gametes at a rate of  $\gamma X_j^* Y_i^*$ , and the resulting zygotes survive with probability  $f(m_{xj}, m_{yi})$ . The total rate with which this pair produces surviving zygotes is consequently:

$$Z_{ij} = \gamma X_i^* Y_j^* f(m_{xi}, m_{yj}) + \gamma X_j^* Y_i^* f(m_{xj}, m_{yi}). \quad (2.5a)$$

For zygotes arising via self-fertilization, we allow that their fitness may be reduced by a fixed factor of  $D \in [0, 1]$  owing to inbreeding depression. Inbreeding depression is absent if  $D = 0$ , corresponding to theoretical expectations for haplontic species, whereas diplontic species might experience  $D > 0$ . The total rate at which the  $i$ th individual produces surviving zygotes via selfing is then:

$$Z_{ii} = \gamma(1 - B)X_i^* Y_i^* (1 - D) f(m_{xi}, m_{yi}). \quad (2.5b)$$

For individuals  $i$  and  $j$  that are not in the same spawning group, we have  $Z_{ij} = 0$ .

At the end of each breeding season, we chose  $N$  pairs from the population at random with replacement to be the parents of the next generation. Each pair was chosen with probability proportional to their entry  $Z_{ij}$  in the parental table. For each chosen pair, we generated a single offspring. All other surviving zygotes were assumed to suffer mortality prior to reaching maturity (e.g. owing to predation or resource competition during dispersal, settlement and recruitment).

### (g) Mutation

Mutations were assumed to affect allocation  $r$  and gamete sizes  $m_x$  and  $m_y$  with probabilities of  $p_r$  and  $p_m$  per locus per generation. Mutational effects were drawn from normal distributions with mean zero and s.d. of  $\sigma_r$  and  $\sigma_m$ , respectively. After mutation, allelic values for allocation  $r$  were truncated below at zero and above at 1. Allelic values for gamete size were truncated below at 0.1 (see *Genetics* above).

### (h) Initialization

We assumed that populations were initially isogamous and dioecious (qualitatively similar results were obtained assuming that populations were initially monoecious: data not shown). Anisogamy and monoecy could emerge over evolutionary time, however. To ensure faster convergence, initial values of the individual gamete sizes  $m_x$  and  $m_y$  were chosen to be near the equilibrium for isogamous populations. Preliminary results indicated that this equilibrium occurs at approximately  $m_x = m_y = \max(\alpha, \beta/3)$  [19], so we initially chose both  $m_x$  and  $m_y$  from normal distributions with a mean of  $\max(\alpha, \beta/3)$  and a s.d. of 1, then truncated both distributions below at 0.1. Individual allocation values  $r$  were drawn initially from  $\{0, 1\}$  with equal probability.

### (i) Simulation runs

We simulated the coevolution of gamete size and sex allocation under the following three conditions:

- full selfing block ( $B = 1$ ),
- no selfing block ( $B = 0$ ) with no inbreeding depression ( $D = 0$ ), and
- no selfing block ( $B = 0$ ) with strong inbreeding depression ( $D = 0.5$ ).

For each condition, we considered four levels of fertilization efficiency ( $\gamma = 0.01, 0.1, 1, 10$ ). We ran 200 simulations over 10 000 generations for each combination of condition and fertilization efficiency level (2400 simulation runs in total). To test whether dioecy could persist in the absence of a specialization advantage, we also ran 100 simulations for the same parameter choices, but with the specialization advantage  $A$  set to zero (1200 simulation runs in total). In each run, the average group size  $\lambda$  was chosen randomly from a uniform distribution on  $[0, 20]$ . With  $\alpha = 1$  held fixed,  $\beta$  was chosen randomly from a uniform distribution on  $[1, 20]$  to generate varying levels of organismal complexity  $\beta/\alpha$ . All other parameter values were as in table 1. All results presented are based on trait values in the final generation of the relevant simulation runs. To confirm that 10 000 generations were sufficient for convergence, we inspected the evolutionary dynamics in 10 randomly chosen runs for each parameter combination. We present only the results for  $\gamma = 0.01$  and  $\gamma = 10$ , since intermediate values of  $\gamma$  led to results that were intermediate between these two extremes.

### 3. Results

All four combinations of isogamy or anisogamy with monoecy or dioecy evolved in our simulations, whereby the occurrence of each combination was highly predictable from the parameter choices. We will first outline the conditions for the evolution of monoecy and anisogamy, before considering patterns of sex allocation in anisogamous monoecious populations.

#### (a) Small group sizes favour monoecy, except when fertilization is inefficient and selfing is impossible

Monoecy emerged only in simulations in which the average size of spawning groups was relatively small (figure 2). In addition, either efficient fertilization (figure 2*a,c,e*) or the possibility of selfing (figure 2*c-f*) were necessary for monoecy to evolve. By contrast, inefficient fertilization and the absence of selfing selected for dioecy, even in small groups (figure 2*b*). These results are explained by the two possible advantages of monoecy in our model. First, in the absence of partners producing the appropriate gamete type(s) for outcrossing to occur, monoecious individuals could self-fertilize. The benefits of selfing were highest when groups were small and inbreeding depression was low. When selfing was possible, strong inbreeding depression reduced the range of mean group sizes over which monoecy was favoured (compare figure 2*c,d* with figure 2*e,f*, respectively).

Second, when marginal fitness returns diminished with increasing production of one or both gamete types, monoecious individuals could adjust allocation to each gamete type so as to avoid strongly diminishing returns (see below). Strongly diminishing fitness curves only occurred when both of the following conditions were met:

- small average group size*: when spawning groups are small, individuals that increase their production of one gamete type may reduce the proportion (although not the number) of such gametes that are fertilized, because their own gametes compete with one another for fertilization. This leads to diminishing marginal

fitness returns on gamete production. Such 'local gamete competition' is often acute for sperm in anisogamous populations [44], but in principle can affect both gamete types [31], even under isogamy. By contrast, large group sizes lead to strong fertilization competition among multiple individuals, at least when fertilization is efficient. This ensures that, for both gamete types, fitness returns increase nearly linearly with the number of gametes produced; and

- efficient fertilization*: local gamete competition only occurs when fertilization is relatively efficient. This is because inefficient fertilization leads to low fertilization rates, resulting in a small probability that two gametes from the same individual will compete for the same opposite-sex gamete. Inefficient fertilization can thus lead to nearly linear fitness returns for both gamete types, even when groups are small.

As a consequence, monoecy only evolved when small group sizes were combined with either efficient fertilization or the possibility of selfing (figure 2). By contrast, the only advantage to dioecy in our model was the specialization advantage. Setting  $A = 0$  consequently led reliably to monoecious populations, regardless of other parameter values (electronic supplementary material, figure S1). This remained true even if selfing was unrestricted ( $B = 0$ ) and inbreeding depression was as high as  $D = 0.8$  (data not shown).

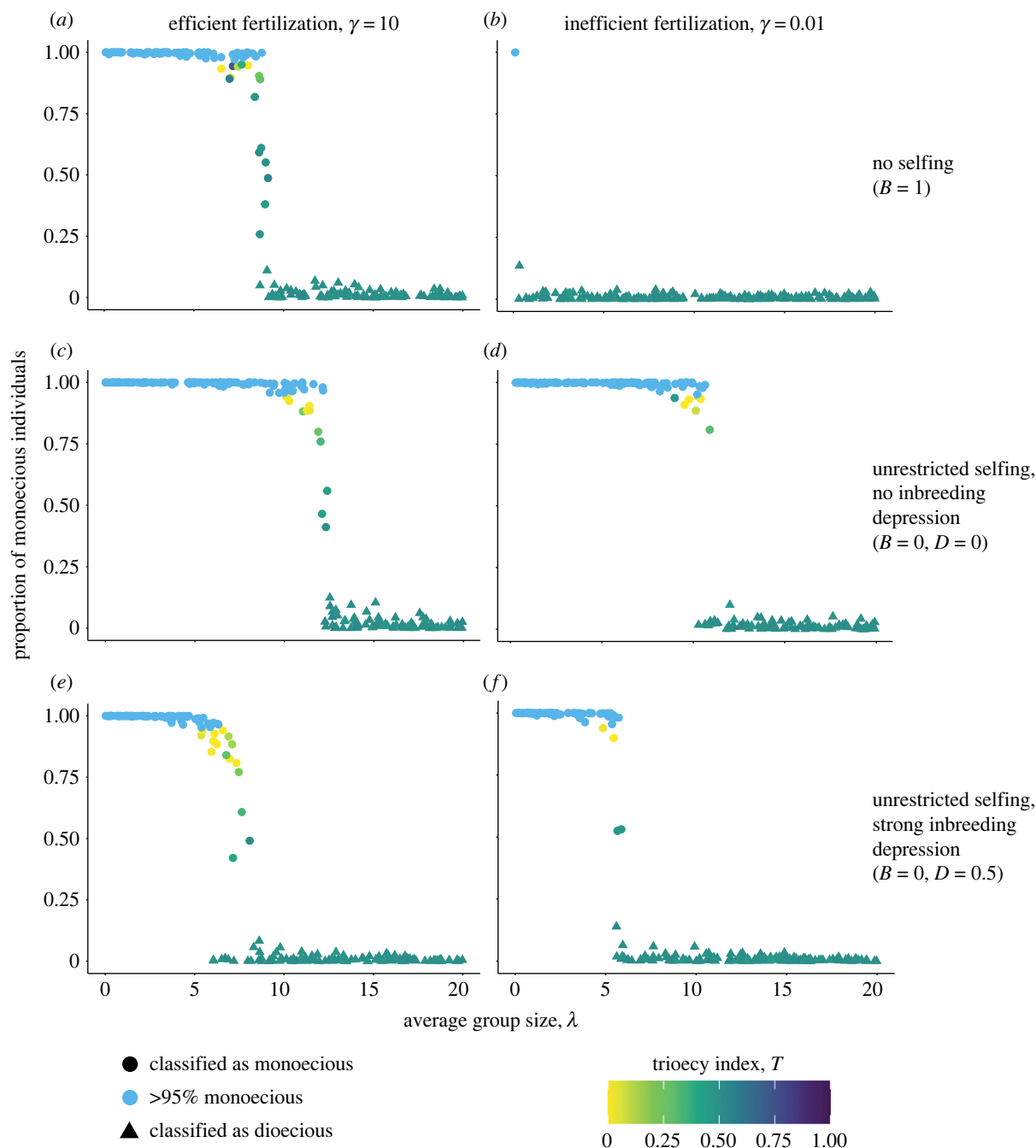
#### (b) Gynodioecy and trioecy occurred at the boundary between monoecy and dioecy

Most populations were close to either pure monoecy or pure dioecy (figure 2). However, at intermediate average group sizes, where monoecy and specialization were approximately equally fit, mixtures of these two systems arose. In populations close to pure monoecy, females often appeared alongside monoecious individuals (gynodioecy: yellow circles in figure 2). This is consistent with relatively weak local sperm competition in these populations, which causes fitness to initially increase gradually with sperm production and then level off slowly. The weakly diminishing returns are sufficient to select against pure males. However, pure females perform about as well as monoecious individuals, since small investments in sperm achieve only slightly greater fitness returns than equivalent investments in eggs. Such small differences are offset by the specialization advantage to pure females. In mixed populations with a greater proportion of pure males and females, the ratio of pure males to pure females was approximately equal (trioecy: dark green circles in figure 2).

#### (c) Organismal complexity selects for anisogamy, except when groups are small and fertilization is efficient

The degree of organismal complexity  $\beta/\alpha$  was the primary determinant of anisogamy in our simulations (figures 3 and 4), in line with previous theory [19,21]. Isogamy persisted in all simulations with low organismal complexity, corresponding to  $\beta/\alpha$  of less than approximately five. Above this threshold, populations were typically anisogamous, in which case the anisogamy ratio increased linearly with  $\beta/\alpha$ .

Complex isogamous organisms still emerged under particular circumstances, however. The combination of



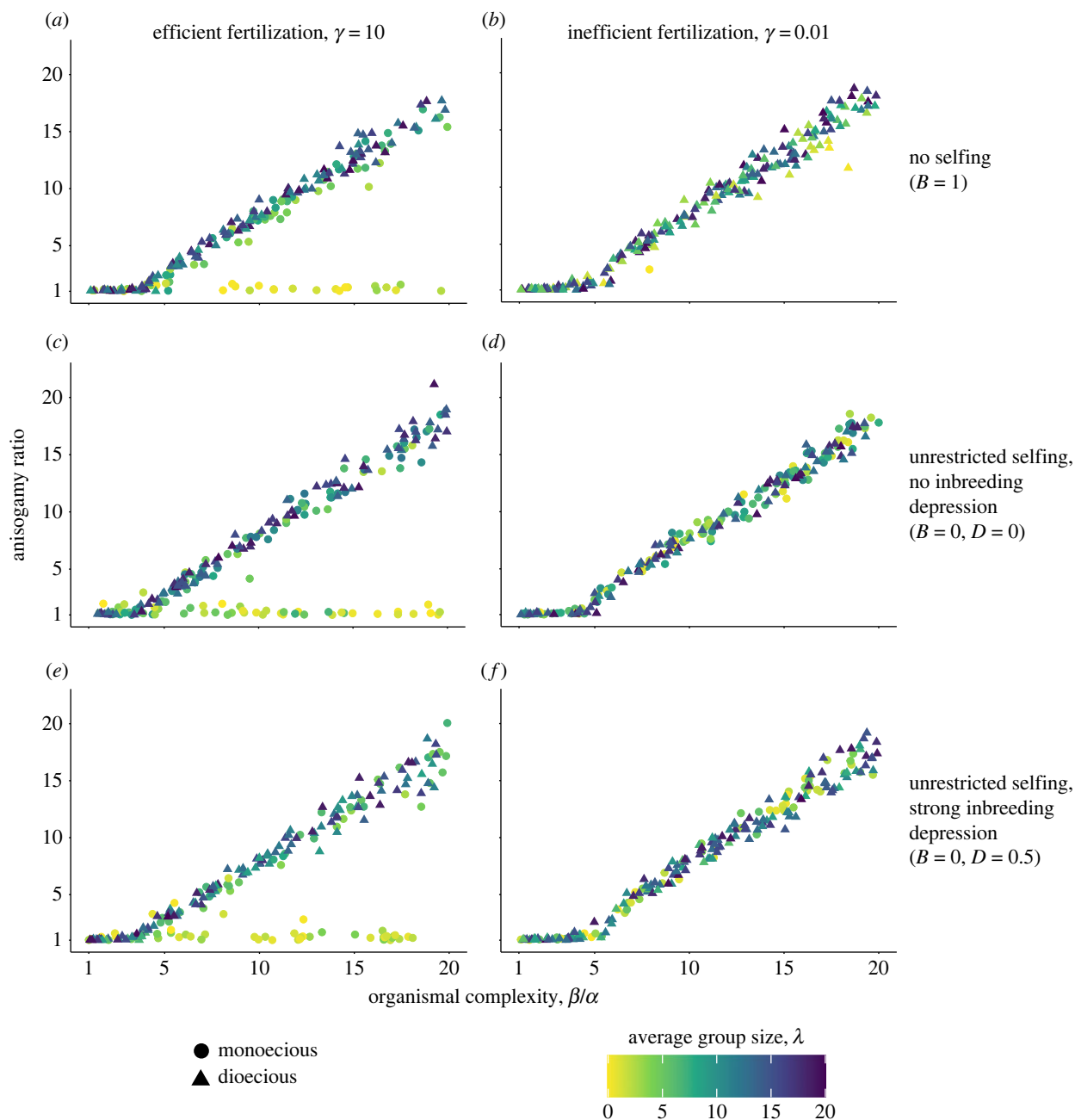
**Figure 2.** The proportion of monoecious individuals shown against variation in the average group size,  $\lambda$ . Populations were classified roughly as ‘monoecious’ (circles) if more than a quarter of individuals were monoecious and otherwise as ‘dioecious’ (triangles). Blue circles represent monoecious population in which greater than 95% of individuals were monoecious. For populations with less than 95% monoecious individuals, colouring represents the trioecy index (i.e. the proportion of individuals producing the smaller gamete type among all those specializing in one gamete type; see inset legend and figure 1). Under anisogamy,  $T = 0$  and  $T = 1$  represent gyno- and androdioecy, respectively. Fertilization was either efficient ( $\gamma = 10$ ; (a,c,e)) or inefficient ( $\gamma = 0.01$ ; (b,d,f)). Selfing was either absent ( $B = 1$ ; (a,b)); unrestricted with no inbreeding depression ( $B = 0, D = 0$ ; (c,d)); or unrestricted with strong inbreeding depression ( $B = 0, D = 0.5$ ; (e,f)). Median fertilization rates (i.e. the proportion of the larger gamete type that was successfully fertilized) across simulation runs were approximately 0.995 when fertilization was efficient (a,c,e) and approximately 0.5 when fertilization was inefficient (b,d,f). All other parameter values are as in table 1.

small average group size and highly efficient fertilization (large  $\gamma$ ) resulted in both weak gamete competition and little gamete limitation. In the absence of the two main forces promoting anisogamy, isogamy was maintained even when organismal complexity  $\beta/\alpha$  was high (figure 3a,c,e). Isogamy could persist in these circumstances even when selfing was impossible ( $B = 1$ ) (figure 3a). The isogametes of such populations were large—often closer in size to anisogamous eggs than to sperm—owing to strong selection for large zygotes (figure 4). In all other cases, the gametes of isogamous species were closer in size to the sperm of

anisogamous species. Complex isogamous organisms were consistently monoecious (figure 4).

#### (d) Sex allocation is female-biased under monoecious anisogamy

Isogamous populations allocated resources roughly equally to both gamete types, with mean allocations near  $\bar{r} = 1/2$  (yellow circles and yellow triangles in figure 5). Equal allocation occurred either at the individual level (i.e. modal allocation at  $r = 1/2$ ) or via even ratios of individuals specializing in each



**Figure 3.** The anisogamy ratio (i.e. the ratio of larger gamete size to smaller gamete size) shown against variation in the degree of organismal complexity  $\beta/\alpha$ . Colouring represents the average group size,  $\lambda$  (see inset legend). Fertilization was either efficient ( $\gamma = 10$ ; (a,c,e)) or inefficient ( $\gamma = 0.01$ ; (b,d,f)). Selfing was either absent ( $B = 1$ ; (a,b)); unrestricted with no inbreeding depression ( $B = 0, D = 0$ ; (c,d)); or unrestricted with strong inbreeding depression ( $B = 0, D = 0.5$ ; (e, f)). Populations were classified roughly as ‘monoecious’ (circles) if more than a quarter of individuals were monoecious and otherwise as ‘dioecious’ (triangles). All other parameter values are as in table 1.

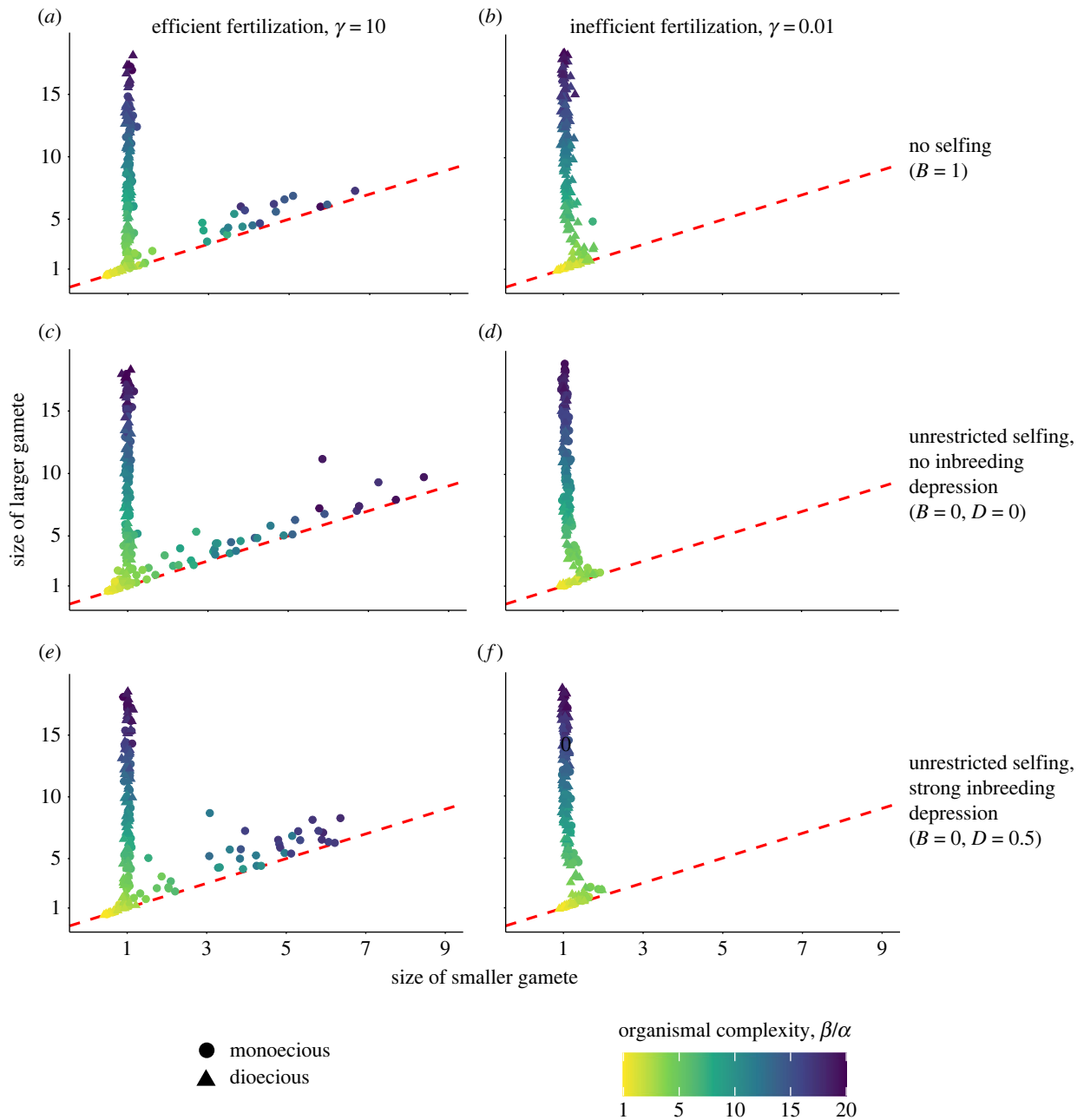
gamete type (i.e. with  $r=0$  and  $r=1$  in equal proportions). Similarly, anisogamous populations with separate sexes had even sex ratios (darker coloured triangles in figure 5). By contrast, sex allocation was female biased in monoecious anisogamous populations (darker coloured circles in figure 5). The degree of female bias was determined by the intensity of local sperm competition, which leads to diminishing fitness returns on sperm production (see above). Female-biased allocation was consequently most pronounced when average group size was small and fertilization was efficient (figure 5), consistent with classical predictions [42,44,45]. Unlike classical models, however, we never predict maximal allocation to female function, even when fertilization is efficient and average group size is very small. There are two reasons for this. First, stochastic variation in group size means that fertilization competition still occurs occasionally, even when average group

size is small. Second, at very small group sizes, the anisogamy ratio is typically low. This selects for greater male allocation in order to ensure full fertilization of female gametes, even if fertilization is efficient.

## 4. Discussion

Our results show that hermaphroditism (referred to here as ‘monoecy’) can emerge alongside anisogamy under biologically plausible conditions. Three requirements must be met for these two strategies to coexist in our model. First, organismal complexity—the ratio of optimal zygote size to the optimal gamete size for fertilization purposes—must be relatively high for anisogamy to evolve. Second, monoecy arises only when local spawning groups are relatively small on





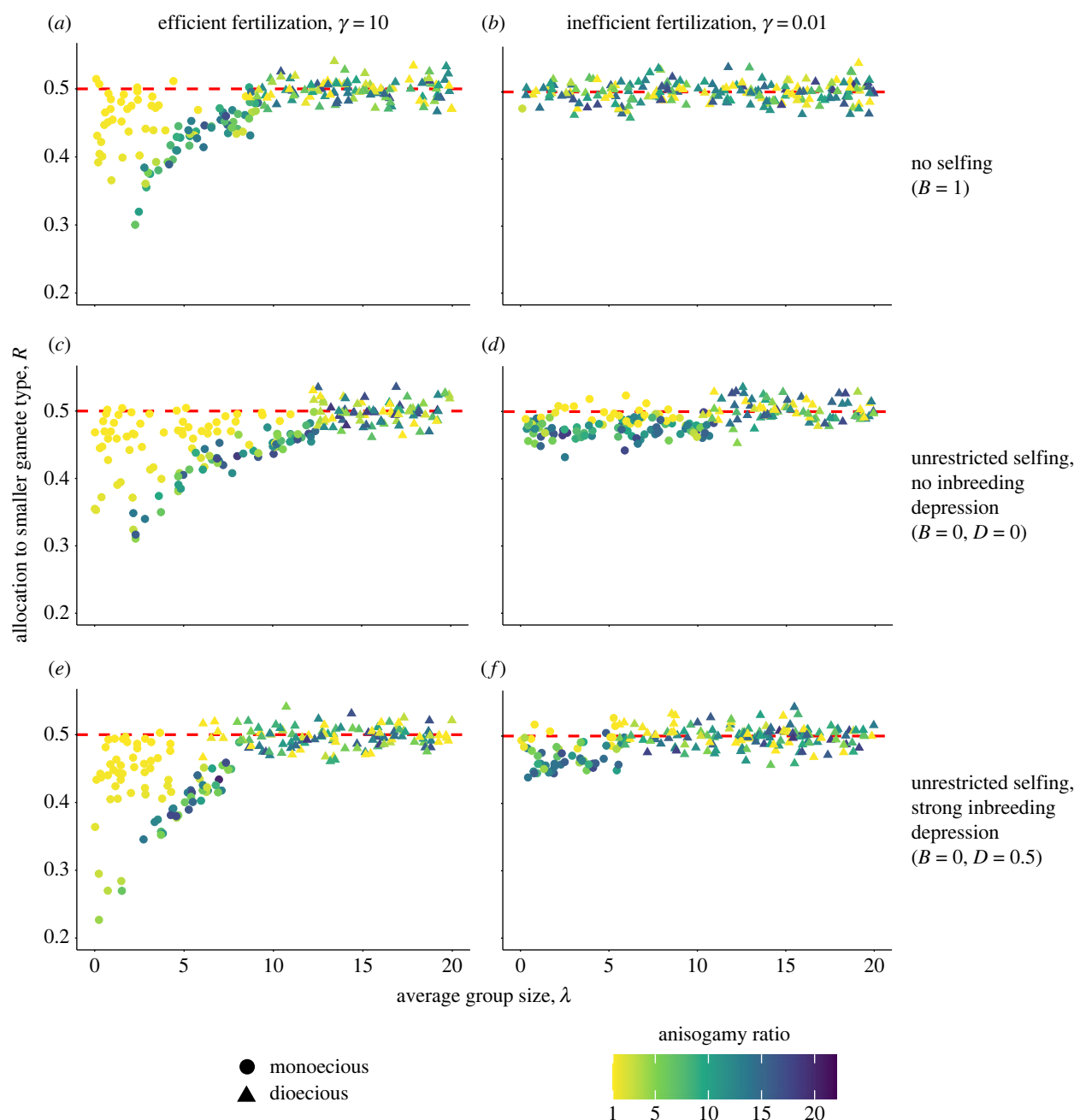
**Figure 4.** Sizes of the smaller and larger gamete types. The dashed red line indicates isogamy. Colouring represents the degree of organismal complexity,  $\beta/\alpha$  (see inset legend). Fertilization was either efficient ( $\gamma = 10$ ; (a,c,e)) or inefficient ( $\gamma = 0.01$ ; (b,d,f)). Selfing was either absent ( $B = 1$ ; (a,b)); unrestricted with no inbreeding depression ( $B = 0, D = 0$ ; (c,d)); or unrestricted with strong inbreeding depression ( $B = 0, D = 0.5$ ; (e,f)). Populations were roughly classified as ‘monoecious’ (circles) if more than a quarter of individuals were monoecious and otherwise as ‘dioecious’ (triangles). All other parameter values are as in table 1.

average. Third, monoecy will evolve only if either fertilization is efficient or self-fertilization is possible (and inbreeding depression is not too severe). Given that these conditions are likely to hold in a wide range of natural systems, there is no reason to believe that monoecy invariably emerged secondarily in taxa where it co-occurs with anisogamy [37]. Rather, anisogamy can plausibly arise in combination with either monoecy or dioecy.

An interesting exception to the above conditions occurs when spawning groups are very small and fertilization is efficient: in this case, isogamous monoecy evolves, even when organismal complexity is high. Lehtonen & Kokko [21] similarly found in dioecious populations that isogamy could persist despite high organismal complexity if fertilization is efficient and spawning groups are very small. As in their study, our model predicts isogamy with large gametes in such cases, with the size of isogametes increasing with the

degree of organismal complexity [21,58]. Under all other conditions in our model, isogametes are comparable in size to the sperm of anisogamous species.

Four aspects of our model are likely to unduly favour dioecy over monoecy and thus to predict a more restricted distribution of monoecy than might be found in nature. First, we assume that individual sex allocation is genetically fixed, regardless of the size or composition of the group an individual finds itself in. Sex allocation under monoecy is often highly plastic, however, responding in particular to variation in the social environment [44,59–62]. Theory predicts that the sex allocation of monoecious anisogamous populations should become more female biased as the local group size decreases [42]. Any potential for adaptive plasticity in sex allocation should allow monoecious individuals to more closely track local variation in fitness optima and therefore should tend to favour monoecy over dioecy.



**Figure 5.** Sex allocation (i.e. the average proportion of resources allocated to the smaller gamete type) shown against variation in the average group size,  $\lambda$ . The red dashed line indicates equal allocation to each gamete type. Colouring represents the anisogamy ratio (ratio of larger gamete size to smaller gamete size; see inset legend). Fertilization was either efficient ( $\gamma = 10$ ;  $(a,c,e)$ ) or inefficient ( $\gamma = 0.01$ ;  $(b,d,f)$ ). Selfing was either absent ( $B = 1$ ;  $(a,b)$ ); unrestricted with no inbreeding depression ( $B = 0, D = 0$ ;  $(c,d)$ ); or unrestricted with strong inbreeding depression ( $B = 0, D = 0.5$ ;  $(e,f)$ ). Populations were classified roughly as ‘monoecious’ (circles) if more than a quarter of individuals were monoecious and otherwise as ‘dioecious’ (triangles). All other parameter values are as in table 1.

Second, we assume that gamete encounter dynamics work similarly for selfing and outcrossing. In practice, however, selfing is often a more reliable path to fertilization, because gametes of both sexes are produced in physical proximity [63–65]. Environmental or ecological conditions that render outcrossing inefficient (e.g. turbulence, diffuse spawning groups and predation of gametes) may consequently have little or no effect on selfing efficiency.

Third, individuals have no control over the rate of self-fertilization in our model. Facultative selfing is common in nature, however [66]. For instance, individuals may self only if an appropriate partner is not available, if eggs remain unfertilized for too long, or if environmental conditions remain stable [66–70]. In the presence of inbreeding depression, delayed selfing is often adaptive, as it

favours outcrossing while still ensuring that all eggs are fertilized [66–68].

Fourth, we allow that there is a specialization advantage to producing only one type of gamete (although we do also consider the case of no specialization advantage: see the electronic supplementary material). If the requirements for producing both gamete types are relatively similar, however, as they presumably are in many primitively anisogamous organisms, then the advantage of specialization may be relatively small. We might consequently expect the specialization advantage—and thus the advantage of separate sexes—to grow with organismal complexity and the degree of anisogamy. This would lead to hermaphroditism being more common in primitively anisogamous species and less so in more complex organisms. The evolution of copulatory

organs and secondary sexual traits, which are common in motile animals, would also presumably increase the benefits of specialization. In some other cases, there may even be an efficiency advantage to producing both gamete types, for example if there are differences in the resources needed to produce each gamete type, leading to a weaker allocation trade-off [40,71,72]. Given that the above four modelling assumptions all tend to favour separate sexes, hermaphroditism might potentially emerge under even broader conditions than predicted by our model.

The assumption of binary mating types might appear to sit uneasily with the evolution of monoecy in our model, given that an often-cited evolutionary function of mating types is to ensure self-incompatibility and thereby avoid inbreeding depression [2,73]. By producing both mating types, monoecious individuals potentially undermine this mechanism of self-incompatibility. This is certainly a subtle issue, but several points are worth noting. First, inbreeding depression is only likely to be a problem for diplontic and, perhaps to a lesser extent, haplodiplontic organisms. In haplontic organisms, on the other hand, inbreeding depression is predicted to be low or absent in general [49]. Second, although self-incompatibility is probably important for the evolution of mating types in many systems, there are also other possible explanations [2]. For instance, binary 'lock-and-key' mechanisms may help ensure efficient gamete fusion during syngamy [74], although it is unclear whether such efficiency gains would outweigh the loss of potential mating partners. The fact that mating types exist even in many haplontic organisms suggests that self-incompatibility to avoid inbreeding depression cannot be the only explanation. Third, even when inbreeding depression is strong, there are many other ways to avoid self-fertilization, including the temporal separation of male and female gamete production or release (e.g. 'dichogamy' and 'heterostyly' in plants) [66,75]. Nonetheless, it would be interesting to remove the assumption of binary mating types in future models and investigate whether this impedes the evolution of monoecious anisogamy from isogamous ancestors.

It should also not be forgotten that selfing is often adaptive, even in the presence of strong inbreeding depression. Each selfed offspring carries two sets of the parents' genes, which generates a strong transmission advantage [76–78]. Thus, if inbreeding depression is less than one half, a selfed offspring is worth more than an outcrossed one in fitness terms [79]. Whether selfing is favoured consequently depends on both the strength of inbreeding depression and the nature of trade-offs between selfing and outcrossing [66,79,80]. Here, we model inbreeding depression via a fixed parameter that does not depend on the extent of selfing in the population. However, in diplontic and haplodiplontic organisms, frequent selfing is expected to expose recessive deleterious alleles to selection and thereby purge them from the population, leading to weaker inbreeding depression (although factors such as epistasis can complicate this picture [81]). This potentially results in a positive feedback mechanism that maintains either low selfing rates in conjunction with high inbreeding depression or high selfing rates with low inbreeding depression [32,78]. Future studies could incorporate more realistic models of the dynamic evolution of inbreeding depression [80–82].

Although our simulations are based on haploid genetics for simplicity, we expect that our predictions would also hold if all loci were diploid. Crucially, however, we assume that each individual carries the genetic machinery to produce both gamete types and to allocate resources strategically to each. In some

taxa this is not the case (e.g. if mating type or sex is determined by alternative alleles at a single locus in haploid individuals, then each individual can only produce one gamete type) [4]. Empirically, the ploidy of gamete-producing individuals varies taxonomically. Gametes are produced by diploid individuals in taxa with a diplontic life cycle (e.g. animals, most diatoms), or by haploid individuals when the life cycle is haplontic (e.g. many fungi and green algae) or haplodiplontic (e.g. red algae, land plants and most brown algae) [83]. This variation in life cycles potentially adds interesting complications that are not covered by our model. In particular, in haplodiplontic life cycles, monoecy—in a more general sense—can occur on two distinct levels. First, gametophytes can produce either one or both gamete types. Second, if gametophytes specialize in one gamete type, then sporophytes can produce spores of either or both sexes. Moreover, size dimorphism may evolve in both gametes and spores. Heterospory is well known from land plants, in which micro- and macrospores become male and female gametophytes, respectively. The relationship between such variation and anisogamy is only just beginning to be unravelled theoretically [84]. Future studies could accommodate a broader swathe of these diverse life histories in which anisogamy has evolved (for recent examples, see [24,58]).

Our model was inspired by existing analytic models [19,21], but it identifies evolutionarily stable states using individual-based simulations. Computer simulations have a long history in evolutionary game theory, extending back to the first formal treatment of evolutionarily stable strategies by Maynard Smith & Price [85]. The first non-group-selectionist models of the evolution of anisogamy also relied on simulations [17] and were game-theoretic in spirit, despite slightly predating the formal mathematical framework. Simulations are most valuable when the processes shaping selection and evolution are complex and not easily captured in an analytically tractable model. For example, when the average size of spawning groups is small in our model, the size and composition of individual groups is highly variable. Given an average group size of five or fewer, there is an appreciable probability that an individual will spawn alone or, in dioecious population, in a single-sex group. This stochastic absence of appropriate mating partners is an important factor selecting for hermaphroditism, but accounting for such variation in an analytic model is combinatorically prohibitive. A tedious mix of exact enumeration for small groups and mean-field approximation for larger groups might suffice to bring variation in group composition into the reach of analytic methods. On the other hand, individual-based simulations allow us to consider the full diversity of group composition with a minimum of mathematical complexity. In addition, this approach accommodates the full range of sex allocation strategies—including, e.g. andro- and gynodioecy—so that the evolution of 'pure' monoecy or dioecy is a result, not a baked-in assumption. Such flexibility makes computer simulations an essential tool for studying evolution under frequency-dependent selection [86], often viewed as the defining task of evolutionary game theory [87,88].

**Data accessibility.** All data on which figures are based are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.glx3ffbsk> [89].

Extra information is also provided in the electronic supplementary material [90].

**Authors' contributions.** J.M.H.: conceptualization, formal analysis, methodology, software, writing—original draft, writing—review and editing; M.B.: conceptualization, formal analysis, methodology,

writing—review and editing; L.S.: conceptualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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