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The interaction between sex-specific selection and local adaptation in species without separate sexes

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Local adaptation in hermaphrodite species can be based on a variety of fitness components, including survival, as well as both female and male sex-functions within individuals. When selection via female and male fitness components varies spatially (e.g. due to environmental heterogeneity), local adaptation will depend, in part, on variation in selection through each fitness component, and the extent to which genetic trade-offs between sex-functions maintain genetic variation necessary for adaptation. Local adaptation will also depend on the hermaphrodite mating system because self-fertilization alters several key factors influencing selection and the maintenance of genetic variance underlying trade-offs between the sex-functions (sexually antagonistic polymorphism). As a first step to guide intuition regarding sex-specific adaptation in hermaphrodites, we develop a simple theoretical model incorporating the essential features of hermaphrodite mating and adaptation in a spatially heterogeneous environment, and explore the interaction between sex-specific selection, self-fertilization and local adaptation. Our results suggest that opportunities for sex-specific local adaptation in hermaphrodites depend strongly on the extent of self-fertilization and inbreeding depression. Using our model as a conceptual framework, we provide a broad overview of the literature on sex-specific selection and local adaptation in hermaphroditic plants and animals, emphasizing promising future directions in light of our theoretical predictions.

This article is part of the theme issue 'Linking local adaptation with the evolution of sex differences'.

1. Introduction

Hermaphrodite species, in which individuals express both male and female sex-functions, have long been important systems for studying local adaptation. For example, Turesson [1] coined the term 'ecotype' based on studies of plant populations (greater than 90% of plant species are hermaphrodites [2]), whereas Cain & Sheppard [3] found evidence of local adaptation in shell colour in the hermaphroditic land snail *Cepaea nemoralis*.

Local adaptation in hermaphrodites depends on selection through several fitness components, including survival and reproductive success through *both* female and male sex-functions within individuals [4–6]. Patterns of local selection may be identical between the sex-functions (favour the same alleles equally), align but differ in magnitude (favour the same alleles, but to different extents) or exhibit trade-offs between them (alleles have opposing fitness effects; [7–9]). The extent of local adaptation therefore depends on both variation in spatial selection, including possible fitness trade-offs, as well as migration/dispersal among subpopulations experiencing different selection regimes. Unfortunately, most empirical studies compare only survival and/or rough estimates of performance or female fecundity among environments (e.g. [5,10–12]), and thus capture only part of the story.

Local selection also depends on the hermaphrodite mating system because the extent of self-fertilization (selfing) potentially mediates several critical factors. Most generally, self-fertilization influences the costs of inbreeding depression [13], the efficacy of selection against deleterious mutations [14,15], the presentation of standing genetic variation to selection and opportunities for balancing selection [9,15–19]. Selfing also influences the effective migration rate between subpopulations by reducing the outcrossing rate between residents and migrants, which also affects conditions for local adaptation [5,20,21]. In this light, it is somewhat surprising that local adaptation appears as widespread among predominantly selfing species as predominant outcrossers, even if the metric of local adaptation is based on incomplete fitness measures [5].

Most theory of local adaptation focuses on viability selection and mating systems with obligately outcrossing sexual reproduction (e.g. [21–26]; but see [27,28]). Consequently, many of the unique population genetic features of hermaphrodites have received little attention in the context of local adaptation. In particular, it remains unclear how self-fertilization and spatially variable selection through both sex-functions jointly impact local adaptation and the maintenance of genetic variation, given that both sex-specific selection and environmental variation are thought to promote the maintenance of variation [7,8,22,25,29,30], while selfing is expected to constrain it [9,14,15,18,19]. This raises several important questions, on which we elaborate below: How does the hermaphrodite mating system influence opportunities for local adaptation through different fitness components? How much scope is there for maintaining the genetic variation necessary for sex-specific local adaptation under different levels of inbreeding and environmental heterogeneity?

In this paper, we develop a simple theoretical model incorporating the essential features of hermaphrodite adaptation across a spatially heterogeneous environment with high gene flow (an extension of Levene's model [22]). The model allows us to address selection on three main fitness components—survival, male function and female function—and incorporates partial selfing and inbreeding depression. We focus our analyses on identifying the conditions necessary for the spread of new mutations that benefit each component of fitness, and the potential for maintaining sexually antagonistic polymorphism, where alleles induce trade-offs between female and male fitness [7,29,31]. We use this theory as a framework for synthesizing empirical research on local adaptation in hermaphrodites, and close by outlining future lines of research on hermaphrodite systems that should be fruitful given our theoretical predictions.

2. A simple model of spatially variable sex-specific selection in hermaphrodites

(a) The model

We consider the evolution of a single diploid locus, with alleles *A* and *a*, in a large population (i.e. with minimal drift) of simultaneous hermaphrodites with discrete generations. The life cycle proceeds as follows: (i) birth; (ii) viability selection due to inbreeding depression in self-fertilized offspring; (iii) local selection on female investment in gamete (ovule/egg) production arising from self-fertilization, and local selection on both female investment in gamete production and male traits involved in siring (i.e. pollination or mating) success during random outcrossing/fertilization and (iv) random dispersal of offspring. Our model captures viability selection due to inbreeding depression and through aligned selection on female and male function (e.g. see scenario 1, below). We develop results using (i) general fitness expressions for selection through each sex-function in each patch and (ii) standard fitness expressions for sexually antagonistic selection in each patch, where *A* is arbitrarily defined as the allele that benefits female fitness (table 1). For simplicity, we assume that an individual's rate of self-fertilization, *C*, is constant and independent of their genotype at the selected locus ($C = C_{\mathrm{AA}} = C_{\mathrm{Aa}} = C_{\mathrm{aa}}$). As in Levene's model [22], the population is subdivided among n local habitats, and individuals from the kth patch contribute an equal proportion, $c_{\mathrm{k}} = 1/n$, to the total pool of gametes of the next generation (i.e. there is maximal migration among patches), with random outcrossing among individuals from all patches.

Table 1. Patch-specific fitness expressions for each sex-function and genotype used in the models of spatially variable selection. We parameterize the fitness expressions for sexually antagonistic selection after Kidwell *et al.* [7], where selection coefficients can take values between 0 and 1 ($0 \leq s_{\mathrm{f}}, s_{\mathrm{m}} \leq 1$).

	genotype		
	AA	Aa	aa
general fitness expressions			
female sex-function	$w^{f\,(k)}_{\mathrm{AA}}$	$w^{f\,(k)}_{\mathrm{Aa}}$	$w^{f\,(k)}_{\mathrm{aa}}$
male sex-function	$w^{m\,(k)}_{\mathrm{AA}}$	$w^{m\,(k)}_{\mathrm{Aa}}$	$w^{m\,(k)}_{\mathrm{aa}}$
sexually antagonistic selection			
female sex-function	1	$1 - h^{(k)}_{\mathrm{f}}\, s^{(k)}_{\mathrm{f}}$	$1 - s^{(k)}_{\mathrm{f}}$
male sex-function	$1 - s^{(k)}_{\mathrm{m}}$	$1 - h^{(k)}_{\mathrm{m}}\, s^{(k)}_{\mathrm{m}}$	1

In partially selfing populations under weak selection, change in allele frequencies due to selection will be slow relative to that due to non-random mating [32]. Assuming weak selection, we may therefore assume a separation of timescales and substitute quasi-equilibrium (QE) genotypic frequencies for each patch (i.e. in the absence of selection) into the genotypic recursions for allele frequency change due to selection [33]. This approach allows us to approximate the evolutionary trajectory of allele frequencies and simplifies our analytic results (see electronic supplementary material, appendix A for further details; comparisons between analytical approximations and deterministic simulation of exact genotypic recursions are presented in figure 1 and electronic supplementary material, figures A2–A5). Using this method, we track the overall frequency of the *a* allele among adults (i.e. after viability selection among self-fertilized offspring due to inbreeding depression). The frequency, q, of the a allele in the next generation is $q' = \sum_{k=1}^{n} c^{(k)} q'^{(k)}$ [22], where $q'(k)$ is the frequency of a in the kth patch after inbreeding depression and selection. Under a model of constant selfing,

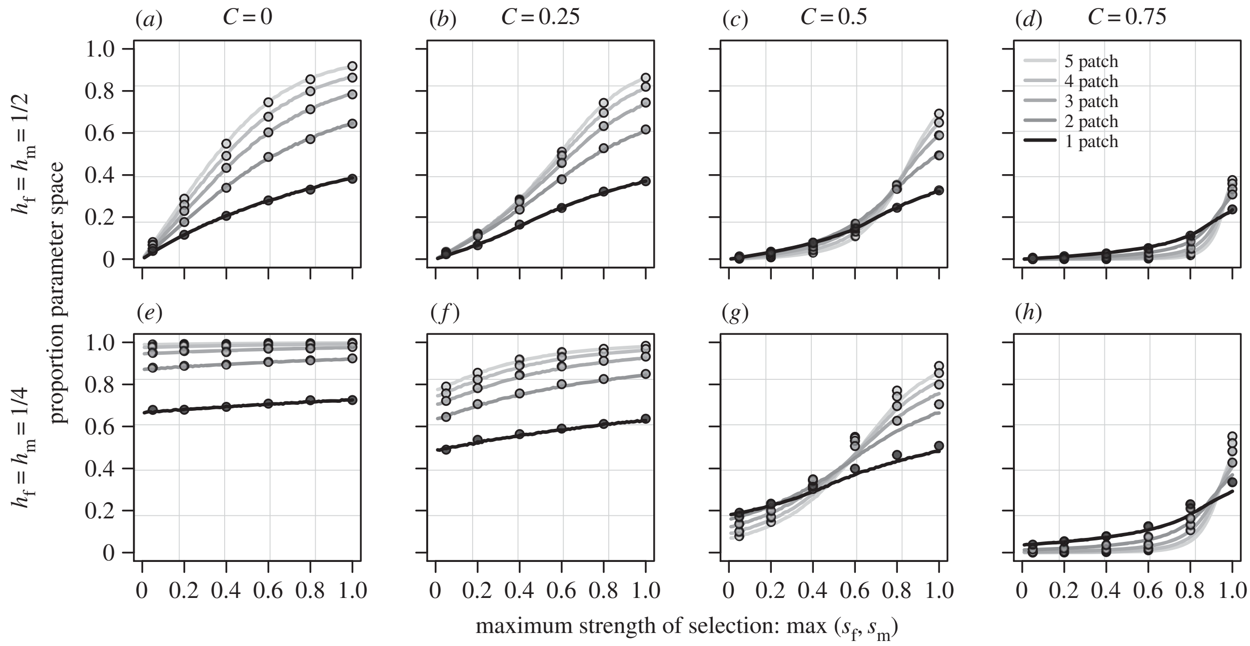

Figure 1. Spatially heterogeneous selection expands the total parameter space where sexually antagonistic polymorphism is maintained for predominantly outcrossing populations ($C < \frac{1}{2}$) under both additive (*a*,*b*) and partially recessive ($h_f = h_m = \frac{1}{4}$; *e*,*f*) sexually antagonistic fitness effects, but has the reverse effect on predominantly selfing populations unless selection is very strong ($C \geq \frac{1}{2}$; *c*,*d* for additive effects; *g*,*h*, for dominance reversal). Analytical results (solid lines) are based on numerical evaluation of $\lambda^{(k)}_{q=\hat{q}} = (\mathrm{d}q'^{(k)}/\mathrm{d}q)|_{q=\hat{q}}$ at the boundary equilibria ($\hat{q} = 0$, $\hat{q} = 1$; see electronic supplementary material, equations A4.1a,b) for 10^5 simulated pairs of selection coefficients (one value for s_f, one for s_m, for each patch) drawn independently from uniform distributions with minimum = 0, and maximum defined by max(s_f, s_m). Hence, max(s_f, s_m) defines the size of the square portion of $s_f \times s_m$ parameter space being sampled uniformly and ranges from weak selection only (max(s_f, s_m) = 0.025) to all of plausible selection parameter space (max(s_f, s_m) = 1). Plots show the proportion of randomly drawn pairs of selection coefficients for which both alleles can invade when rare as a function of max(*s*) for a single population with constant selection (black line), and populations with 2–5 patches in which selection may differ (greyscale lines) with no inbreeding depression ($\delta = 0$). Results for deterministic simulations of the exact genotypic recursions based on 10^4 simulated pairs of selection coefficients for each patch are plotted over the lines (greyscale points) and show the proportion of parameter sets for which simulations converged on a polymorphic equilibrium. Tight correspondence between the simulation and analytic results indicates that the model predictions are robust to the assumption of weak selection. Effects of inbreeding depression ($\delta > 0$) are presented in electronic supplementary material, appendix A, figure A2.

$q'(k)$ follows the general form

$$q'^{(k)} = \frac{(1-C)((q_f'^{(k)} + q_m'^{(k)})/2) + C q_f'^{(k)}(1-\delta)}{1 - C\delta}, \tag{2.1}$$

where $q_f'^{(k)}$ and $q_m'^{(k)}$ denote the frequency of *a* among female and male gametes from the *k*th patch after selection, respectively, and δ represents inbreeding depression, the density-independent mortality rate among self-fertilized offspring (e.g. due to deleterious recessives [13]). Following prior theory for hermaphrodites, we assume that self-fertilization reduces the opportunity for selection to act via the male sex-function ($q_m'^{(k)}$ does not appear in the right-hand side of the numerator in equation (2.1)) because, for example, self-fertilization does not require the export of male gametes, but may still involve selection on ovule production [9,34,35] (see [31] for an alternative modelling approach without selection during self-fertilization; a full development of the recursions is presented in electronic supplementary material, appendix A). Equation (2.1) reduces to several familiar models under certain parameter conditions: with equal selection through both sex-functions ($w_{ij}^{f\,(k)} = w_{ij}^{m\,(k)} = w_{ij}^{\;(k)}$), it reduces to a Levene model with partial selfing [27,28]; under obligate outcrossing ($C = 0$), it is equivalent to a multi-patch model of sex-specific selection for separate-sexed species [30]; and with both, it reduces to a standard Levene model [22]. We performed linear stability analyses of the boundary equilibria (i.e. $\hat{q} = 0$ and $\hat{q} = 1$) to determine the necessary conditions for invasion of either allele (*A* or *a*) when rare and the maintenance of polymorphism (*sensu* [36]; see electronic supplementary material, appendix A).

The above model makes several key simplifying assumptions worth highlighting. As in other Levene-type models, ours assumes both high and equal migration rates among patches and ‘soft’ selection [24]. The former assumption is unlikely to be met in natural populations, while the later represents a scenario that is more permissive of polymorphism compared to alternative models of ‘hard’ selection (e.g. [37]). We also assume that the population rate of self-fertilization is constant, across both patches and genotypes, even though intraspecific variation in the self-fertilization rate is common among self-compatible hermaphrodites [38]. We elaborate on each of these important assumptions in the discussion (see §4a), with emphasis on new directions for theory that emerge from relaxing them.

Below, we develop analytical and simulation results in three scenarios: (1) equal selection through both sex-functions (equivalent to survival selection only); (2) sex-specific (but not necessarily sexually antagonistic) selection through female and male sex-functions and (3) sexually antagonistic selection through female and male sex-functions (setting pleiotropy and correlation issues aside, sexual antagonism cannot act via survival to maturity in hermaphrodites because both sex-functions will be equally impacted by a reduction in survival; see §3a below for more details). We focus on two main results: the relation of mean selection coefficients among patches to the invasion of rare alleles (for scenarios 1 and 2), and the proportion of parameter space in which sexually antagonistic polymorphism is maintained by balancing selection in subdivided populations (scenario 3) relative to a single population with homogeneous selection (i.e. a single-patch model).

To complement our analytical results and validate the assumption of weak selection made throughout our analytical derivations, we performed deterministic simulations of the exact genotypic recursions (i.e. without using QE frequencies). Exact recursions follow the same life cycle described above. For each simulation run, we iterated the deterministic recursions until one allele became fixed in the population (frequency of AA or aa homozygotes greater than 0.9999), or genotypic frequencies converged on a polymorphic equilibrium (frequency of either homozygote less than 0.9999 *and* single generation frequency change $<10^{-9}$ for all genotypes). We explored the behaviour of the genotypic simulations using sexually antagonistic fitness effects (table 1; scenario 3) for the same parameter combinations presented in our analytical results. The recursions as well as computer code necessary to reproduce the analyses are available at https://github.com/colin-olito/SA-SexSystem-LocalAdapt.

(b) Results

(i) Conditions for the spread of new mutations

When fitness effects are equal through both sexes (scenario 1), our model is mathematically equivalent to a model of viability selection (see [27,28] for detailed analyses of this type of model), and our results can be interpreted in either context (see Discussion). Under additive fitness effects, we may re-parametrize the model to express the invasion criteria in terms of the mean selection coefficient favouring rare heterozygotes only (electronic supplementary material, appendix A). For simplicity, we temporarily ignore inbreeding depression ($\delta = 0$). Assuming that selection favouring rare heterozygotes in each patch is a random variable, the invasion conditions for rare alleles at both boundary equilibria ($\hat{q} = 0$ and $\hat{q} = 1$) can be expressed as follows:

$$0 < \frac{2}{2 - C}\bar{s}, \tag{2.2}$$

where $\bar{s}$ is the mean selection coefficient favouring rare heterozygotes across all n patches, with $s^{(k)} = (w^{(k)}_{\mathrm{Aa}} - w^{(k)}_{\mathrm{AA}})/w^{(k)}_{\mathrm{AA}}$ at $q = 0$ and $s^{(k)} = (w^{(k)}_{\mathrm{Aa}} - w^{(k)}_{\mathrm{aa}})/w^{(k)}_{\mathrm{aa}}$ at $q = 1$. Equation (2.2) reveals two important outcomes. First, the contribution of the average selective advantage of heterozygotes (and therefore homozygotes because fitness is additive) across patches increases with higher selfing. Hence, the effective selection for (when $0 < \bar{s}$) or against (when $\bar{s} < 0$) rare alleles increases with selfing, consistent with a large body of prior theory on partially selfing populations (e.g. [16,19,39]). Second, equation (2.2) highlights a somewhat counterintuitive feature of classic Levene-type models of spatially heterogeneous selection: the variance in selection across habitats does not influence the invasion of rare alleles.

Under sex-specific selection (scenario 2), we again assume that fitness effects are additive, and that selection favouring rare heterozygotes through each sex-function is a random variable that varies across patches. Under this scenario, the invasion condition for rare alleles with respect to mean selection through male and female fitness is

$$0 < \frac{(1 + C)}{(2 - C)}\bar{s}_{\mathrm{f}} + \frac{(1 - C)}{(2 - C)}\bar{s}_{\mathrm{m}}, \tag{2.3}$$

where ${s_j}^{(k)}$ is the selection coefficient favouring rare heterozygotes through each sex-function in the kth patch (i.e. $s_j^{(k)} = (w^j(k)_{\mathrm{Aa}} - w^j(k)_{\mathrm{AA}})/w^j(k)_{\mathrm{AA}}$ at $q = 0$, $s_j^{(k)} = (w^j(k)_{\mathrm{Aa}} - w^j(k)_{\mathrm{aa}})/w^j(k)_{\mathrm{aa}}$ at $q = 1$ and j indexes sex-function ($j \in \{f, m\}$); see electronic supplementary material, appendix A). Equation (2.3) reveals several additional implications: the invasion conditions now depend on the combined effects of selection through each sex-function, and higher selfing rates increase the importance of mean fitness through female relative to male function [9,35] (but again, see [31] for an alternative approach without selection during self-fertilization). Equation (2.3) also highlights that neither the variance nor the covariance in selection through male and female fitness components influences the invasion of rare alleles in these models—a point that we return to briefly in our discussion. Inbreeding depression ($\delta > 0$) reduces the effect of selfing on the allele frequencies and hence tends to equalize the relative importance of selection through female versus male function (see electronic supplementary material, figure A1).

(ii) Conditions for the maintenance of sexually antagonistic genetic variation

Equation (2.3) also suggests that the conditions for maintaining sexually antagonistic polymorphism are probably more restrictive in partially selfing species relative to outcrossing ones under spatially heterogeneous selection. This is because selfing introduces a bias that favours the invasion of female-beneficial alleles, so that the maintenance of polymorphism in partially selfing populations will require that, on average, selection is suitably balanced with stronger selection on male than female fitness. Unless the distributions of selection coefficients influencing male and female fitness components among patches are assumed to follow this pattern (a strong assumption given the lack of data; see Discussion), the maintenance of sexually antagonistic polymorphism in partially selfing species should become more difficult in heterogeneous relative to constant environments.

To examine the interaction between self-fertilization and spatially variable selection on the maintenance of polymorphism in a more specific context, we now parametrize fitness following standard sexually antagonistic fitness expressions (scenario 3; table 1) and numerically evaluate the invasion conditions for populations across a gradient of spatial subdivision (see electronic supplementary material, appendix A). For simplicity, we assume that sex-specific selection coefficients in each patch are drawn from a uniform distribution (i.e. we do not explicitly model sex-specific variances or covariance in selection), a point that we return to in the discussion. We focus our analysis on the case of additive sexually antagonistic fitness effects ($h_{\mathrm{f}} = h_{\mathrm{m}} = \frac{1}{2}$), as might be expected for alleles with small-to-intermediate fitness effects (e.g. [40]). We only briefly discuss results for partially recessive fitness effects yielding 'dominance reversals' (h_{f}, $h_{\mathrm{m}} < \frac{1}{2}$), which are commonly predicted by fitness landscape models of sexually antagonistic selection (e.g.

[29,41]). Stable polymorphism occurs when each allele can invade a population fixed for the alternate allele [36].

For predominantly outcrossing populations without inbreeding depression ($C < \frac{1}{2}$, $\delta = 0$), spatially variable selection increases the proportion of parameter space where polymorphism is maintained relative to spatially homogeneous selection (i.e. a single patch), although greater population subdivision yields smaller increases in polymorphic parameter space (figure 1*a*,*b*). However, for predominantly selfing populations ($C \geq \frac{1}{2}$), polymorphic parameter space is reduced in multi-patch models relative to a single patch unless selection is quite strong (figure 1*c*,*d* for additive fitness; figure 1*g*,*h* for dominance reversal). Consistent with our predictions for scenario 2, polymorphism due to sexually antagonistic selection in predominantly selfing populations requires either (i) that the scenario of weak (strong) selection through female (male) function occurs within enough patches [9,35] or (ii) on average, selection through male function is sufficiently strong relative to female function among patches. The likelihood of either scenario becomes very small for more subdivided populations in our simulations, where we draw selection coefficients for each sex-function from identical uniform distributions. As in previous sexually antagonistic selection models, dominance reversals are more permissive of polymorphism than additive sexually antagonistic fitness effects, but the effects of selfing and population subdivision remain the same (figure 1*e*–*h*; [9,35]).

As noted earlier, inbreeding depression in our model ($\delta > 0$) reduces the female bias in selection introduced by selfing [9,35] (electronic supplementary material, appendix A), causing predominantly selfing populations to behave more like outcrossing ones. With non-zero inbreeding depression, sexually antagonistic polymorphism is maintained when selection coefficients through each sex-function are more evenly balanced (relative to $\delta = 0$), over a larger proportion of parameter space (see electronic supplementary material, figures A1 and A2).

(c) Key predictions

Three key theoretical predictions emerge from our model of spatially heterogeneous selection in hermaphrodites: (i) regardless of whether selection acts equally (scenario 1; equivalent to selection on survival), or differently on male and female fitness components (scenarios 2 and 3), the population selfing rate plays a critical role in determining the fate of rare alleles; (ii) with unequal selection on male and female fitness (scenarios 2 and 3), higher self-fertilization rates cause fitness though the female sex-function to become increasingly important relative to the male sex-function. This female bias probably creates more stringent conditions for the maintenance of sexually antagonistic polymorphism in partial selfers because selection must, on average, be appropriately balanced, with a female-benefit allele that confers weaker benefits for female fitness than a male-benefit allele does for male fitness, across a heterogeneous environment; (iii) spatially variable selection promotes the maintenance of sexually antagonistic polymorphism (scenario 3) in predominantly outcrossing populations, but inhibits it for predominant selfers. In fact, the maintenance of sexually antagonistic polymorphism in the face of spatially heterogeneous selection becomes extremely difficult in populations with high selfing rates unless selection can be very strong. Overall, our models suggest that the genetic variation necessary for sex-specific local adaptation in hermaphrodites will be most easily maintained in subdivided populations with low effective selfing rates (e.g. when inbreeding depression is high), or with sufficiently strong selection on male function under non-trivial selfing.

3. Empirical data

Very few studies directly examine spatial variation in sex-specific selection in hermaphrodites, in large part because estimating siring success is labour intensive (see [42]). Even fewer studies have directly tested for local adaptation through both sex-functions using a reciprocal transplant experiment. In a rare exception, Kalske *et al*. [6] found significant sex-specific variation in the extent of local adaptation of *Vincetoxicum hirundinaria* for both fruit production (female fitness) and pollinia removal (surrogate for male fitness), despite the challenges that its partial self-fertilization habit [43] presents for local adaptation (see Results). However, a wealth of studies provides indirect evidence for the plausibility of spatially variable sex-specific (including sexually antagonistic) selection in hermaphrodite species, and for scenarios addressed by the model. Here, we provide a broad overview of such indirect evidence. In this conceptual review, we highlight the types of data that can inform studies of spatially variable sex-specific selection in hermaphrodites (and how they relate to traits for separate-sexed species), rather than provide a comprehensive review, to stimulate and guide future research.

(a) Connecting sexually antagonistic traits in dioecious versus hermaphrodite species

Sexually antagonistic selection may ultimately arise from the same mechanism in separate-sexed species as hermaphrodites (i.e. sexually antagonistic polymorphism), but the characteristics of sexually antagonistic traits differ between these cases in two important ways. First, in separate-sexed species, sexually antagonistic selection is often inferred from a positive between-sex genetic correlation for a trait with contrasting fitness optima in each sex [44]. In hermaphrodites, however, genetic variance for the trait is paramount because *individuals* express both sex-functions. Any polymorphic locus causing variation in a trait (e.g. flower size) that induces a trade-off between female and male fitness will be sexually antagonistic in a hermaphrodite. Second, a locus that strictly affects survival to reproduction cannot harbour sexually antagonistic polymorphism in hermaphrodites, because death prior to reproductive maturity affects female and male fitness equally. Hence, unlike separate-sexed species, sexually antagonistic loci in hermaphrodites must affect fitness through reproduction, possibly in addition to survival [9]. However, we note that correlation between survival and reproductive traits can be very important [45] and viability selection could therefore contribute to sexually antagonistic selection on reproductive traits before they are expressed.

Despite these differences, sexual dimorphism in dioecious (separate-sexed plants) or gonochoristic (separate-sexed animals) species can help identify candidate sexually antagonistic traits in hermaphrodites. In plants, dioecious species typically evolve from a hermaphrodite ancestor [46]. Theory emphasizes that this transition involves a change in sex expression (e.g. invasion of unisexual sterility mutations [34,47], which we consider a primary sexual character [48]). Therefore, secondary sexual characters (which, by definition, are sexually dimorphic) of dioecious species may reflect a history of sexually antagonistic selection for those traits. By extension, we expect that homologous traits will often experience sexually antagonistic selection in a hermaphrodite ancestor.

Lloyd & Webb [48] provide an early, comprehensive review of plant secondary sexual characters. They found that female and male plants can differ in many respects, including, for example, growth rate, total size or vegetative reproduction (e.g. *Aciphylla scott-thomsonii*; *Asparagus officinalis*; hemp; *Spinacia oleracea*; *Silene latifolia* and *S. dioica*), niche preferences (e.g. *Mercurialis perenis*), morphology (e.g. *Ginko biloba*; *Cannabis sativa* and *Mercurialis annua*), phenology (e.g. *Rumex acetosella* and *Gingidia decipiens*) and reproductive effort (e.g. *R. acetosella*). Delph *et al*. [49] examined unisexual flowers produced by 436 dioecious or monoecious (i.e. hermaphrodites that produce separate female and male flowers) species; female and male flowers differed in size in 85% of cases, suggesting widespread opposing selection on flower size for female versus male fitness (assuming size differences are not a pleiotropic effect of a sterility mutation; see [50] for discussion). Collectively, these observations from dioecious species suggest many candidate sexually antagonistic traits in hermaphrodite plant species.

We note that the perspective used above may not apply when hermaphroditism evolves from a separate-sexed species (e.g. clam shrimp, reviewed in [51]; see also [46]). Here, the hermaphrodite will have evolved from either a female or male ancestor, and its phenotype may reflect a legacy of selection on that ancestral sex. Hence, analyses of secondary sexual traits in the separate-sexed ancestor will less probably reflect differential selection on female versus male function in the hermaphrodite. This scenario may be more common in animal than plant taxa. In addition, although investigation of separate-sexed animals may inform studies of sexual *conflict* in hermaphroditic animals (i.e. conflicts between individuals over mode and frequency of mating [52]), doing the same for sexually *antagonistic* traits (i.e. selected in opposite directions in each sex-function) may be more problematic. This is because many plants are pollinated by animal vectors, and pollen export will therefore be influenced by how attractive flowers are to the vectors, leading to similar selection pressures on males and hermaphrodites with respect to pollinator attraction. By contrast, investment in ornaments or other pre-copulatory attractiveness traits seems to be disfavoured in hermaphroditic animals compared to post-copulatory traits (sperm competition or cryptic female choice; [53]). Some candidate traits that are expected to be more important contributors to fitness in one sex role in hermaphroditic animals include mating rate (male-selected) and body size (female-selected [53]).

(b) Studies of sex allocation

Loci that control sex allocation may experience sexually antagonistic selection when allocation of limited resources induces a trade-off between female and male fitness [54]; hence, spatially variable selection on sex allocation may reflect variable sex-specific (or sexually antagonistic) selection. Classic models of sex allocation [55–57] require that one fitness gain function be saturating in order for hermaphroditism to be stable, and it is usually expected that this occurs in the male function if there are constraints on how many partners can be fertilized (but see [58] for an example of a saturating female gain function). Optimal sex allocation depends on the marginal fitness returns for both sex-functions, which may vary among environments or according to an individual's phenotype. For example, in animals, allocation to male function should increase with increasing mating group size [57]. Although it is often difficult to disentangle social group size and mating group size, there is good empirical evidence that larger social group sizes result in increased allocation to male function in animals (e.g. [59–61]). Mating group size is probably correlated with density in many species and is therefore highly relevant to local adaptation as densities often vary across populations. For example, expected levels of sperm competition differ among populations of trematode parasites [62]. In plants, resource allocation to female versus male function can vary both within and among populations or conditions (e.g. [63–65]; reviewed in [66]). Here, resource availability may relate to plant size, which commonly affects allocation to female versus male sex-function (e.g. [63]; reviewed in [67]). Sexual conflict that involves partner manipulation could also affect individual sex allocation (e.g. allohormones or seminal fluid proteins that increase or skew the partner's sex allocation towards increased female investment; [68]). To maintain their preferred allocation under partner manipulation, individuals may then be expected to evolve reduced female allocation in high-density populations. Hence, for both animals and plants, we expect that spatial variation in population density and/or intensity of sexual conflict will affect selection on sex allocation.

Finally, plasticity in sex allocation itself may experience locally variable sex-specific selection. For example, Friedman & Barrett [69] showed that families of *Ambrosia artemisiifolia* differed in allocation to female flowers between sun and shade environments: families that allocated relatively more to female flowers in the shade allocated relatively less in the sun, whereas other families had the opposite tendency. These results suggest that genes underlying phenotypic plasticity in sex allocation may experience locally variable selection, and highlight the importance of studying local selection on reaction norms of sex allocation to identify a role for such genes.

(c) Evidence from floral evolutionary ecology

Floral evolutionary ecology has long emphasized selection on floral traits arising from interactions with animal pollinators and the consequences for both female and male components of reproductive success (e.g. [70,71]). However, the vast majority of floral selection studies have estimated female fitness only [72], and the few that estimate siring success often use indirect measures such as pollen removal or insect visitation [72–74]. Yet studies that measure selection on floral traits through both female and male fitness within single populations often report contrasting patterns of selection, suggesting that phenotypic optima differ between the sex-functions (e.g. [74–79]; reviewed in [73]). However, an important caveat is that very few studies adequately address the consequences of pleiotropy and multivariate genetic constraints on selected floral traits [73,80–82].

Manipulative experiments also offer compelling indirect evidence for spatially heterogeneous selection by demonstrating that selection through male and female fitness depends on the pollinator context. For example, Ellis & Johnson [83] tested for sex differences in selection on floral spur length in the orchid *Satyrium longicauda* Lindl using spur length manipulations in two populations with different pollinator faunas. They found opposing selection on spur length at one location, and sexually congruent selection at the other. Other studies have used experimental treatments as proxies for environmental heterogeneity, and found unequal, but not necessarily conflicting, selection through male and female function (e.g. [84,85]).

Spatially heterogeneous sex-specific and sexually antagonistic selection may also arise from non-pollinating agents. Herbivory, florivory and seed predation can exert biased selection through both direct and indirect effects on male and female fitness [86–88], and certainly exhibit spatially and temporally variable density-dependent effects (e.g. [6]). Pollen larceny is another understudied potential source of asymmetric selection between the sex-functions. Pollen theft reduces siring opportunities, directly influencing selection on traits promoting male fitness, but can also influence female fitness when it reduces pollen receipt by stigmas enough to cause pollen limitation (reviewed in [89]). Overall, the study of floral evolution has generated perhaps the largest body of evidence of spatially heterogeneous sex-specific (and, to some extent, sexually antagonistic) selection in hermaphrodites.

4. Model assumptions and future directions

(a) Future directions for theory

Sex-specific selection and environmental variability each have well-developed bodies of population genetic theory [7,17,22,25,90], but their interaction has only recently been examined in detail [30,91–93]. Our model builds upon previous theory for dioecious species to demonstrate that, for hermaphrodites, the dynamics of sex-specific adaptation and the maintenance of sexually antagonistic genetic variation in heterogeneous environments also depends critically on the mating system and extent of inbreeding depression. Below, we briefly discuss several important model assumptions and future directions for theoretical study.

Our assumption that population density regulation occurs before random mating among patches follows the concept of 'soft selection' [24,37]. Models of spatially heterogeneous selection form a continuum from 'soft' to 'hard' selection [37], and the conditions for polymorphism are less stringent at the 'soft' end of this spectrum [22–24,37]. Our model therefore represents a permissive limiting case. Interestingly, recent theory for separate-sexed species suggests that under 'hard' selection, the dynamics of sex-specific local adaptation are highly sensitive to species-specific demographic and life-history characteristics and are more permissive of polymorphism than models without sex-specific selection [30]. Exploring the evolutionary dynamics of sex-specific adaptation for hermaphrodites in the context of 'hard' selection represents fertile ground for future theoretical study, where the mating system may introduce further asymmetry in sex-specific selection.

We also assumed high migration with all n patches contributing an equal proportion to the total pool of gametes of the next generation ($c_k = 1/n$). These assumptions introduce a major limiting constraint because it prevents our model from addressing the interaction between migration, environmental heterogeneity and sex-specific local adaptation. Exploring the theoretical consequences of varying migration among subpopulations for sex-specific adaptation in hermaphrodites would be particularly interesting, as the extent of selfing will influence opportunities for both sex-specific adaptation (as our model has shown) and the magnitude of gene flow [20,94–96]. Examining the consequences of finite population size in these types of models would also be interesting, as this could address the joint effects of selfing and drift to limit opportunities for local adaptation [26].

Our model also assumed a constant rate of self-fertilization, even though this assumption may be violated in at least three ways in natural populations, and each may affect model predictions differently. First, empirical studies show that selfing rates are not constant, but vary among populations (e.g. [38,97–99], among individuals (e.g. [100]) and in time (e.g. [97,100,101]), meaning that it is important to calculate an appropriately averaged selfing rate. Second, the predominant mode of self-fertilization might vary in space, even if average selfing rates are constant. In flowering plants, diverse mechanisms can cause self-fertilization (e.g. [97,102,103]), which should influence sex-specific local adaptation because sexually antagonistic polymorphism is predicted under broader conditions when self- and outcross pollen compete for ovules (e.g. geitonogamy) than when they do not (e.g. when self-fertilization occurs before outcross pollen arrives) [9]. Finally, self-fertilization rates may vary due to standing genetic variation that affects the selfing rate (e.g. [104–106]). The consequences of pleiotropy between sexually antagonistic alleles and selfing rate for the maintenance of genetic variance await exploration, but Jordan & Connallon [9] provide a suitable framework. Variation in the self-fertilization rate may have important consequences for the maintenance of genetic variance and could depend on both spatially variable selection and on sexually antagonistic variance itself. These observations deserve future theoretical and experimental analyses.

Finally, our analyses of sexually antagonistic selection (scenario 3) manipulated the extent of spatially heterogenous selection indirectly by varying population subdivision. While this approach makes possible direct comparisons with prior theory of sexually antagonistic selection (e.g. [7,9,31,35]), it limits the conclusions we may draw about the effects of spatial heterogeneity in selection on polymorphism. Exploring the interaction between population subdivision and spatial heterogeneity in selection by manipulating the joint distribution of selection coefficients for female and male fitness components among patches can yield different predictions for the maintenance of sexually antagonistic polymorphism by influencing the region of selection parameter space being sampled (see appendix A, figures A6 and A7), even if the invasion of rare alleles in a given population ultimately depend on the weighted mean of the selection coefficients in each patch. However, we caution that empirical estimates of selection through both sex-functions at multiple sites (which will be challenging to obtain) should ideally inform these theoretical analyses to avoid exploration of arbitrarily biased subsets of selection parameter space.

(b) Testing the key predictions

Our first key prediction is that, regardless of the fitness component selection acts on, self-fertilization plays a critical role in determining the fate of rare alleles. This suggests that unless selection through each sex-function is appropriately balanced to account for the female bias introduced by selfing, either within demes or at the landscape level, appreciable levels of sexually antagonistic polymorphism are unlikely in predominantly selfing species. However, the details may depend on how sexually antagonistic selection acts. Both this model and previous ones [9,35] assume that antagonistic selection acts on traits that affect fertilization success for gametes that will be either selfed or outcrossed, which is realistic if selection is a result of inherent differences in gamete production or viability (e.g. ovule number or size). However, when selection arises from gamete performance or loss during outcrossed matings only (e.g. via sperm competition or sperm digestion by the mating partner), polymorphic parameter space is also predicted to be reduced by selfing, but remains symmetric for both sex-functions [31]. To determine which assumption is applicable in a given system, it is necessary to measure sex-specific selection on selfed and outcrossed gametes separately. Manipulations that enforce selfing or outcrossing would be of value here.

Our second key prediction is that with unequal selection on male and female fitness, higher self-fertilization rates cause fitness though the female sex-function to become increasingly important relative to the male sex-function, and that this creates more stringent conditions for the maintenance of sexually antagonistic polymorphism for partial selfers in heterogeneous environments. Reliable measurements of sex-specific selection pressures are critical for testing this prediction. This is a non-trivial task, because tracking paternity (a more accurate measure of male reproductive success) is difficult in most natural populations [73,107]. We recommend increasing efforts to measure male fitness (even crudely) in future studies of natural populations of hermaphrodites; for example, anther number/mass and pollen removal in plants or mating rate in animals. Again, manipulative approaches should also be valuable, in the context of both sex allocation and expression of traits thought to be under sexually antagonistic selection. For example, hand pollination (and/or emasculation) experiments could be used to manipulate maternal/paternal investment while monitoring sex-specific fitness. As noted earlier, direct manipulation of traits thought to be subject to sexually antagonistic selection, coupled with estimation of sex-specific fitness and other pleiotropically linked traits offers another promising approach (e.g. [83]). Such manipulations may be easier in plants than animals, at least in the field. Nevertheless, simple measures of sex-specific fitness can be incorporated into many common experimental designs, including reciprocal transplants, resource manipulation experiments and studies of resource use and/or allocation. Despite these many challenges, our theoretical predictions offer some encouragement for empiricists studying spatially variable sex-specific selection in hermaphrodites or separate-sexed species: insofar as simple Levene-type models can be used to draw inference about natural populations, our results suggest that even basic estimates of average selection through each sex-function across sites or habitats can still provide valuable information about the invasion of rare alleles and the maintenance of sexually antagonistic genetic variation.

Our final key prediction is that spatially heterogeneous selection promotes the maintenance of sexually antagonistic polymorphism in predominantly outcrossing populations but constrains it in predominantly selfing ones. Testing this prediction will be challenging. A first step is of course to measure sex-specific *selection* across multiple populations, scaling up the approaches suggested above for key prediction one. Second, estimating the amount of standing sexually antagonistic *genetic variation* in multiple populations is critical. This requires either replicated genotypes (clones or inbred lines), or detailed information about genetic structure (a pedigree) from each population. From this information, the variance in male and female fitness can be partitioned into genetic and environmental components, and a genetic correlation for fitness can be estimated, where a negative genetic correlation would be indicative of substantial sexually antagonistic genetic variation. Simply measuring phenotypic correlations between male and female reproductive success is informative but not sufficient, because variation in resource acquisition can result in a positive correlation even when there is an energetic trade-off between the sex-functions [108–110]. Measuring population differences in sexually antagonistic genetic variation is therefore a large undertaking, but the predictions presented at least give us some guidelines where we expect the variation to be substantial. Given that almost nothing is currently known about sexually antagonistic genetic variation in hermaphrodites—not even whether they generally harbour more or less variation than separate-sexed species—this is fertile ground for future research.

5. Conclusion

Although interactions between sex-specific selection and environmental heterogeneity have received some attention in separate-sexed species (e.g. [30,91,92]), they have yet to be examined in hermaphrodites. To guide intuition and future research, we have developed a simple theoretical model of spatially variable sex-specific selection in hermaphrodites, emphasizing the effects of self-fertilization on the invasion of rare alleles and the maintenance of genetic variation. Our model makes several novel predictions compared to models for separate-sexed species or constant environmental conditions. While the available literature appears to support some parts of the model, empirical tests of our predictions await additional studies examining both female and male fitness components, and the genetic basis of fitness trade-offs between the sex-functions, in multiple contexts.

Data accessibility. Mathematica code necessary to reproduce the model and key analytic result is provided in electronic supplementary material, appendix B. Additional R code necessary to reproduce simulation results is available at https://github.com/colin-olito/SA-SexSystem-LocalAdapt.

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