# The opposing effects of genetic drift and Haldane's sieve on floral-morph frequencies in tristylous metapopulations

## Camille Roux[1] and John R. Pannell[2] (iD)

[1]CNRS, UMR 8198 – Evo-Eco-Paleo, Univ. Lille, Lille F-59000, France; [2]Department of Ecology and Evolution, University of Lausanne, Lausanne 1015, Switzerland

Author for correspondence:
*John R. Pannell*
*Tel: +41 21 692 41 70*
*Email: john.pannell@unil.ch*

## Summary

• Tristyly is a genetic floral polymorphism in which three floral morphs are maintained at equal frequencies by negative frequency-dependent selection on alleles at two interacting loci. Because dominant alleles at these loci are maintained at a lower frequency than their recessive counterparts, they are more likely to be lost by founder events and genetic drift.

• Here we examine the hypothesis that dominant alleles under negative frequency-dependent selection should also be more likely to re-invade populations than recessive alleles, due to Haldane's Sieve, because recessive alleles not expressed in a heterozygote state cannot benefit from positive selection when rare.

• We used computer simulations of tristylous metapopulations to verify that Haldane's Sieve acting on migrants into occupied demes can indeed reverse the bias in allele frequencies expected for small single tristylous populations, particularly in situations of rapid population growth following colonisation. This effect is manifest both locally and at the metapopulation level.

• Our study illustrates the potential effect of Haldane's Sieve in the novel context of an iconic plant sexual-system polymorphism under the influence of metapopulation dynamics.

## Introduction

Many flowering plants have evolved sexual systems that involve floral polymorphisms, with populations comprised of two or three classes of individual that produce flowers differing in morphology, sex allocation or compatibility type (Barrett, 2002). These polymorphic species have long fascinated botanists and indeed were the subject of one of Charles Darwin's books about plants (Darwin, 1877; Barrett, 2010). Apart from posing interesting questions regarding the maintenance of morphological variation in floral strategies within populations, floral polymorphisms have also provided useful model systems for testing general theories in evolutionary ecology and ecological and population genetics. These include: the fitness consequences of different allocation strategies (Lloyd, 1983; Ashman, 1999; Sakai *et al.*, 2008); the consequences of interactions between flowers and pollinators for pollen transfer and mating (Harder & Barrett, 1995; Barrett & Harder, 2005); and the evolutionary forces that regulate the maintenance of genetic variation in natural populations, particularly negative frequency-dependent selection, which maintains variation, and genetic drift, which allows variation to be lost. Tristyly, a genetic polymorphism in which individuals adopt one of three different floral morphologies, is particularly noteworthy in this latter context, because biases in the frequency of the three morphs may be informative on the relative roles of genetic drift and selection.

Tristylous populations are typically comprised of three floral morphs that differ reciprocally in stigma and anther height (Darwin, 1877; Barrett, 1993) and that may vary nonrandomly in their relative frequencies within populations. The three floral morphs are referred to as the long-, mid- and short-styled morphs (hereafter L-, M- and S-morph), with a reciprocal correspondence of anther and stigma positions, a condition referred to as reciprocal herkogamy (Lloyd & Webb, 1992); see Fig. 1. Reciprocal herkogamy promotes disassortative mating as a result of segregated pollen deposition on the bodies of pollinators (Barrett & Glover, 1985; Costa *et al.*, 2017), a situation that gives rise to strong negative frequency-dependent selection because individuals of the rarest morph enjoy greater mating opportunities and higher fitness. In large populations, morph frequencies should therefore be maintained at roughly equal frequencies (isoplethy) (Heuch, 1979; Barrett *et al.*, 1987), but they can deviate from isoplethy in small populations as a result of genetic drift. For example, although large populations of the aquatic annual plant *Eichhornia paniculata* tend to be isoplethic in large populations, morph frequencies often deviate from isoplethy in small populations as a result of genetic drift, even to the extent that one or two morphs may be entirely absent (Barrett, 1985; Barrett *et al.*, 1989). Similar deviations from isoplethy have been observed in small populations of other tristylous systems (Heuch, 1980; Eckert & Barrett, 1992; Eckert *et al.*, 1996; Balogh & Barrett, 2016).

Markedly, the observed deviations from isoplethy in tristylous morph frequencies are not random, but tend to be biased in favour of the L- and M-morphs, with the S-morph often absent
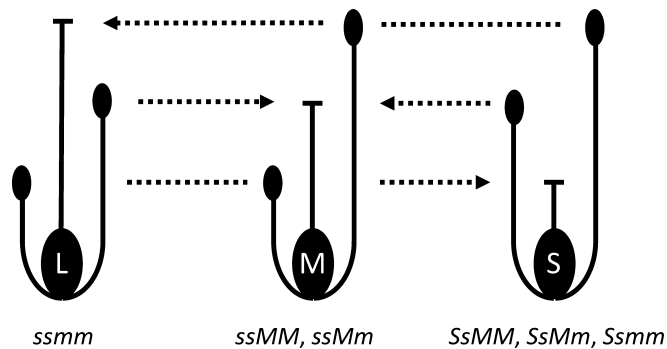
**Fig. 1** Schematic depiction of the three floral morphs in tristylous populations, the long morph (L), the mid morph (M) and the short morph (S). Shown are the central pistil with short, midlevel or long styles and two stamens per flower, each with its anther at one of the two other possible heights. Arrows indicate the directions of pollen transfer between anthers and stigmas of the same height. The genotypes for each morph are shown under each diagram; these represent the typical genetic architecture of tristly, as expressed in *Eichhornia paniculata* (see text for details).

(Heuch, 1980; Barrett, 1988; Barrett *et al.*, 1989; Eckert & Barrett, 1992; Husband & Barrett, 1992; Eckert *et al.*, 1996; Balogh & Barrett, 2016; da Cunha & Barrett, 2019). These biases are thought to arise because the interaction of genetic drift with natural selection depends on the underlying genetics of tristyly. For instance, tristyly in *E. paniculata* is the result of the segregation of recessive vs dominant alleles at two interacting loci (Barrett, 1988), a mode of inheritance that also occurs in other tristylous species in Lythraceae and Oxalidaceae (reviewed in Lewis & Jones, 1992); see Fig. 1. Possession of a dominant *S* allele at the *S* locus underlies expression of the S-morph, irrespective of the genotype at the *M* locus (i.e. genotypes $S-/-$). Individuals lacking the dominant *S* allele (and therefore homozygous for the *s* allele) produce either L-morph flowers if they are also homozygous for the recessive *m* allele at the *M* locus (i.e. genotype *ss/mm*), or M-morph flowers if they possess the dominant *M* allele at the *M* locus (i.e. genotype *ss/M-*) (Fig. 1). Importantly, even though tristylous morph frequencies may be equal at equilibrium, the genetic architecture of tristyly implies that the dominant *S* and *M* alleles will be maintained at substantially lower frequencies than their recessive counterparts *s* and *m*; see fig. 1 in Pannell *et al.* (2005). They are accordingly also more likely to be lost by drift, as observed in several tristylous species (Barrett, 1977; Heuch, 1980; Eckert *et al.*, 1996). Barrett *et al.* (1989) specifically modelled the combined effects of drift and frequency-dependent selection on tristyly, and used their results to attribute the biased loss of the S-morph in *Eichhornia paniculata* to the greater role played by genetic drift in geographic regions in which populations are smaller and more subject to population turnover. Similar reasoning was invoked to explain deviations in morph frequencies in *E. crassipes* (Barrett, 1977) and *L. salicaria* (Heuch, 1980; Eckert *et al.*, 1996).

From the studies cited above, it is clear how the combination of genetic drift and selection can bring about the biased loss of the L-morph in small populations of tristylous species, but the question remains as to how drift and selection might interaction

with migration in species subject to metapopulation dynamics. This question is important for two reasons. First, metapopulation dynamics have been implicated as an important feature of the population biology of both *E. paniculata* and *L. salicaria*, and as a possible contributor to the small effective sizes of their local and regional populations (Morgan & Barrett, 1988; Husband & Barrett, 1991, 1995; Eckert *et al.*, 1996; Barrett & Husband, 1997). Second, we might expect migration to bring about bias in tristylous morph frequencies in a way that is very different from the effects of drift (Pannell *et al.*, 2005). Simulation modelling of the biased loss of the S-morph in tristylous populations, while motivated to some extent by the metapopulation structure of species and the importance of population turnover due to the balance between local population extinction and colonisation (Husband & Barrett, 1998), has focused largely on the effects of drift in single populations (Barrett *et al.*, 1989), although see Eckert *et al.* (1996) and Morgan & Barrett (1988). Yet the fate of dominant vs recessive alleles following their immigration into a population in which the immigrant allele is not yet present should also be influenced by the phenomenon of 'Haldane's Sieve' (Haldane, 1924; Orr & Betancourt, 2001), for which previous work has not accounted.

The idea of Haldane's Sieve derives from theory on the influence of dominance on probability of fixation of new mutations in a population (Haldane, 1924; Crow & Kimura, 1970), but it should also have effects on standing genetic variation (Orr & Betancourt, 2001) as well as on new variants that immigrate into local populations from elsewhere (Pannell *et al.*, 2005). Theory predicts that the probability of ultimate fixation of a new weakly advantageous mutation is approximately equal to twice the product of its selective advantage (or selection coefficient, *s*) and its dominance coefficient, *h* (Haldane, 1924; Crow & Kimura, 1970). This means that an advantageous allele that is at least partially dominant will fix with a greater probability than a purely recessive allele, because dominant or partly dominant alleles are immediately expressed and positively selected, whereas the fate of a recessive mutation while it is still rare in a population (and therefore carried only by heterozygotes and therefore not expressed) is determined almost entirely by genetic drift and is very likely to be lost. Although this prediction applies to the fixation probability of new mutations subject to weak directional positive selection (Haldane, 1924; Whitlock, 2003), the principle should also apply to alleles that migrate into a population and are then subject to negative frequency dependency (or other modes of balancing selection) that ultimately maintain them at an intermediate frequency (Pannell *et al.*, 2005). Therefore, dominant alleles under frequency-dependent selection should be more likely to spread towards an expected intermediate equilibrium frequency than their recessive counterparts. In tristylous metapopulations, specifically, we predict that the dominant *S* allele should have an advantage as an immigrant allele into populations that lack them than the recessive *s* allele (with a similar prediction made for the *M* and *m* alleles). If so, then Haldane's Sieve should contribute to a bias in morph frequencies in precisely the opposite direction to that predicted for

small single populations subject to the local effects of drift (Pannell *et al.*, 2005).

Pannell *et al.* (2005) raised the possibility that the effect of Haldane's Sieve on plant reproductive polymorphisms in a metapopulation might oppose the effect of local drift. They specifically speculated that Haldane's Sieve should favour dominant alleles in a metapopulation as long as local populations grow rapidly to a large size following colonisation, but not when population sizes remain small. They proposed two reasons why this may occur. First, homozygosity should be increased by inbreeding in small populations, so that advantageous recessive alleles would be immediately selected, reducing the advantage that dominant alleles might otherwise have (Whitlock, 2003). Second, dominant alleles should be lost more often from established populations, as explained above, because their local equilibrium frequencies should be lower (Bateman, 1952; Barrett *et al.*, 1989).

Here, we investigate the opposing forces of genetic drift in established populations vs Haldane's sieve during migration in metapopulations of tristylous plants, drawing inspiration from studies of the effects of drift on tristylous morph frequencies (Heuch, 1980; Barrett *et al.*, 1989; Eckert *et al.*, 1996) and broadening its focus from the fate of alleles in single finite populations to metapopulations governed by population turnover and interdeme migration. Our model is especially pertinent to the case of *E. paniculata*, in that we assume the same genetics (see Materials and Methods) as well as self- and intramorph compatibility that allow deviations from disassortative mating. If the effect of Haldane's Sieve is considerable, thereby reversing the expected bias in morph ratios for a broad range of metapopulation scenarios, we would expect the regional metapopulation dynamics inferred for species such as *E. paniculata* to be weak compared with the local effects of drift in small populations. Such a conclusion would be significant not only for our understanding of variation in morph variation in *E. paniculata*, but also because *E. paniculata* has been cited as one of the few examples of a true metapopulation (Freckleton & Watkinson, 2002) and also as one of the only plausible instances of key phases of Wright's 'shifting balance' theory (Coyne *et al.*, 1997). Alternatively, if Haldane's Sieve acts in a metapopulation only under a narrow range of conditions or is incapable of reversing the well established effects on morph frequencies of population size on its own, we would have reason to be satisfied by the simpler single-population models (Heuch, 1980; Barrett *et al.*, 1989; Eckert *et al.*, 1996).

We first apply our specific model to the case of individual populations, establishing a basis for comparison with earlier work and confirming that dominant alleles are lost more frequently from small populations than recessive alleles. We then test the prediction that dominant migrant alleles at the *S* and *M* loci should be more frequently established in individual demes than recessive alleles as a result of Haldane's Sieve than their recessive counterparts. Next, we compare the establishment success of dominant vs recessive alleles as migrants into an entire metapopulation, as might occur through dispersal linking geographical regions of a species in which populations maintain tristly with those in which populations have lost the polymorphism. Finally,

we explore the combined effects on morph frequencies of drift, frequency-dependent selection and Haldane's Sieve in a dynamic metapopulation with population turnover and interdeme migration. Here, we specifically test the prediction that the effect of Haldane's Sieve might be relaxed or even reversed in metapopulations with small subpopulations compared with those whose demes are larger or grow very rapidly (Pannell *et al.*, 2005).

## Materials and Methods

### Overview of approach taken

We assumed a metapopulation with demes linked by gene flow via seed dispersal (and not pollen dispersal), and subject to population turnover as a result of stochastic local extinctions and recolonisation. To understand the outcome of the complex interactions between drift, migration and frequency-dependent selection, we conducted our simulations in three phases. First, considered the effects of drift and migration on the composition of single isolated demes in which mating followed the same rules as for simulations of the metapopulation as a whole, but in which migration was ignored. This phase essentially replicated previous work (Barrett *et al.*, 1989) to establish a common base for the new work. Second, to examine the effects of Haldane's Sieve within single populations, we considered the invasion of dominant or recessive alleles into populations fixed for the alternative allele. Third, we conducted simulations combining local genetic drift, selection and migration between populations within the context of a metapopulation with population turnover. We provide details of these three phases below, after describing the assumed genetics and dynamics of mating within each deme.

### Genetics and within-deme mating

We assumed a tristylous metapopulation composed of habitat patches populated by individuals belonging to one, two or three of the tristylous morphs, with style morph determined by the expression of genes at two loci according to the genetics established for *Eichhornia paniculata* (Barrett *et al.*, 1989). For simplicity, we assume that the two loci are completely unlinked in our model, as is the case in *Decodon verticillatus* (Eckert & Barrett, 1993), *Lythrum salicaria* (Fisher & Mather, 1943) and *Pontederia cordata* (Gettys & Wofford, 2008), although not in *E. paniculata* (reviewed in Barrett & Shore, 2008). With this genetic system of morph determination, the following phenotype-genotype map applies, where '−' can be either allele: S-morph: genotypes $S$-, −; L-morph: $ss$, $mm$; M-morph: $ss$, $M$- (see Fig. 1).

We assumed that mating in each deme was disassortative, with the probability of intramorph mating in general being lower than that expected under random mating. We generated progeny for the next generation in two ways. In most simulations, we assumed stochastic reproduction, with parents chosen at random from within a given deme, constrained by rules for assortative vs disassortative mating, governed by parameter $P$ (see below).

Here, we used the following protocol (see the Supporting Information Notes S1 for further details):

(**1**) We sampled a potential female and male parent at random from the population (with the possibility of choosing the same individual as both the male and female parents). If the chosen parents were both of the same morph (or were the same individual) in a polymorphic deme, we accepted the pair with a probability $P$; if the pair was rejected, we resampled a new pair by returning to (1).

(**2**) In monomorphic demes, all pairs were accepted, that is, we did not allow demes to become extinct because of a local lack of mates. This scheme therefore rules out complete disassortative mating.

(**3**) We created a progeny individual by sampling an ovule from the female parent and a pollen grain from the male parent with haplotypes determined by meiosis at each locus and free recombination between loci.

Steps (1) and (2) were repeated until a suitable pair was chosen. Steps (1) to (3) were repeated until the deme was populated to carrying capacity $N$. A scenario with $P = 0$, which we did not simulate, would corresponded to complete disassortative mating, as one would expect for a population in which intramorph mating is not possible because of strong trimorphic incompatibility. For $0 < P < 1$, disassortative mating was intermediate, with morphs expected to be maintained by (weaker) frequency-dependent mating. $P = 1$ (simulations not shown) corresponds to a population in which mating is entirely random, and in which allele change in frequency simply by genetic drift and fix with a probability given by their starting frequency.

## Drift and selection in isolated populations

We first considered the effects of population size and frequency-dependent selection by simulating our model for individual populations, recording the allele, genotype and corresponding morph frequencies over time and the proportion of simulations in which morph loss or fixation occurred.

## Invasion of a monomorphic population by a new morph

We compared the ability of a dominant allele ($S$ allele, determining the S-morph and $M$ allele, determining the M-morph) vs a recessive allele (alleles $s$ and $m$, respectively) to invade populations monomorphic for the S-morph (genotypes $SSMM$ or $SSmm$), the M-morph (genotype $ssMM$) and the L-morph (genotype $ssmm$). Specifically, we considered mutations that arise in a heterozygous state in a population (or, equivalently, the arrival of immigrants that are heterozygous at a floral-morph locus), and determined the probability with which they could invade and be maintained for substantial periods of time under negative frequency-dependent selection. According to expectations for Haldane's Sieve, new dominant $S$ alleles that occur in a population monomorphic for the recessive $s$ allele (i.e. fixed for either $ssmm$ or $ssMM$) should therefore immediately generate dimorphism in the population, with the S-morph enjoying a strong early benefit of frequency-dependent selection, whereas recessive $s$ alleles that occur in a $SSmm$

or $SSMM$ background will not be immediately expressed and should therefore not experience immediate selection.

While it is difficult to obtain analytical predictions for the probability that a new allele invades and remains in a polymorphic state in a metapopulation subject to population turnover (or, alternatively, that is fails to invade or is fixed), we derived expressions for the invasion and maintenance of floral-morph alleles into single populations as a function of the local effective size $N$ and the degree of disassortative mating allowed, governed by $P$. We compared the predictions of these calculations with the results of simulations for individual populations of the metapopulation model, thereby allowing us to verify good behaviour of the critical module of our metapopulation simulations.

## Drift, selection and migration in a dynamic metapopulation

For multideme simulations, we assumed a metapopulation of 100 demes, each occupied by $N$ individuals at the local carrying capacity. Each generation, each deme could become extinct with a probability $E$. Extinct demes were immediately recolonised by $k$ individuals chosen randomly from elsewhere in the metapopulation. At this point, all other demes received $I$ immigrants similarly sampled randomly from the metapopulation at large, such that the $I$ immigrants replaced the same number of local individuals in the deme, also chosen randomly. We assumed that $I$ was Poisson-distributed, with parameter $M = Nm$, that is, $m$ here is the migration rate, or the probability that a given individual was an immigrant the previous generation. Following extinction, colonisation and/or migration, all demes underwent a round of reproduction, with the same mating protocol applying to all demes. Reproduction maintained extant demes at their carrying capacity, whereas it returned recolonised demes to their local carrying capacity in a single generation.

## Exploration of parameter space

To study the evolution of a single stable isoplethic population, we considered that the three floral morphs were each initially at frequencies of 1/3. In the first generation, individuals of the S-morph, M-morph and L-morph were all of genotypes $SsMm$, $ssMm$ and $ssmm$, respectively. We determined the loss, maintenance or fixation of the different morphs by recording the population status at each generation over 10 000 generations. This was done for each of the nine parameter combinations ($N$ in (10, 40, 100); $P$ in (0, 0.1, 1)), with each combination simulated independently 1000 times.

To investigate the invasion of a single monomorphic population by a new recessive or dominant allele, we introduced a single allele (dominant or recessive) into a population that was monomorphic for its counterpart, that is the allele was introduced in a heterozygous individual. Two population sizes were explored ($N$ in (10, 40)), with values for $P$ stepped from 0 to 1.0 at intervals of 0.1. We performed 2000 independent simulations for each combination of $N$ and $P$.

Our simulations of a metapopulation commenced with all demes either at isoplethy or monomorphic for the relevant allele and morph. Here, we assumed metapopulations of 100 demes,

each of 500 individuals. The average number of migrants per deme and generation, *M*, was varied from 0 to 1 at intervals of 0.2. We examined dynamics under extinction rates *E* of 0, 0.01 or 0.1. We performed 1000 simulations for each parameter combination.

We examined the effects of carrying capacity, *N*, on floral-morph frequencies for metapopulations of 100 demes, with *N* in (10, 20, 40, 100, 250, 375, 500, 625, 750, 875, 1000). For these simulations, we assumed $P = 0.1$, $E = 0.05$ and *M* in (0.1, 0.5, 1).

In each generation, we recorded the number of trimorphic demes, the number of demes that had lost only the S-, M- and L-morphs and the number of demes that had fixed the S-, M- or L-morph. The global frequencies of the different morphs were also recorded each generation. The model was implemented in C, using the GNU Scientific Library for all functions related to random sampling, and is freely available at https://github.com/popgenomics/triStyle.

## Results

### Morph loss from individual demes

Our simulations of single finite populations confirm previous results that genetic drift leads to the destabilisation of tristyly, and that this loss can be rapid for small *N*. Importantly, our results confirm that the dominant *S* allele is more rapidly lost than the recessive *s* allele, such that the S-morph is most frequently lost first, followed by the frequent fixation of the L-morph (Fig. 2). As expected, the details of these trajectories are sensitive to the degree of disassortative mating. The tristylous polymorphism was more strongly maintained in small populations when strong disassortative mating ($P = 0.1$) largely prevents within-morph mating and selfing, with very slow loss of tristyly in populations of $N = 100$ (Fig. 2e), and the L-morph or, less frequently, the M-morph fixed only in very small populations ($N = 10$; Fig. 2a). While the equilibrium was reached rapidly for $N = 10$ (0.3% short fixation, 10.7% mid fixation, 89% long fixation), the simulations for $N = 40$ and $N = 100$ tended towards the same equilibrium, but over periods too long to be explored exhaustively by our forward individual-based approach. However, the dynamics of frequency change for the three morphs is expected to occur over ecological time scales (over a duration well below $10N$ generations) than over longer evolutionary periods (i.e. $> 1000N$ generations), so the long equilibration times in these simulations are probably not biologically insightful.

### Invasion of a monomorphic population by a new morph

Our numerical calculations for the invasion of dominant vs recessive alleles into single populations (Fig. 2) closely match the results from Monte Carlo implementation of our model (Table 1). This conformity lends further confidence that the code on which our metapopulation modelling is appropriately implemented. As predicted, our numerical calculations show that in a single population of size *N*, a floral-morph polymorphism should become established substantially more frequently after the introduction of a dominant than after than of a recessive allele. For
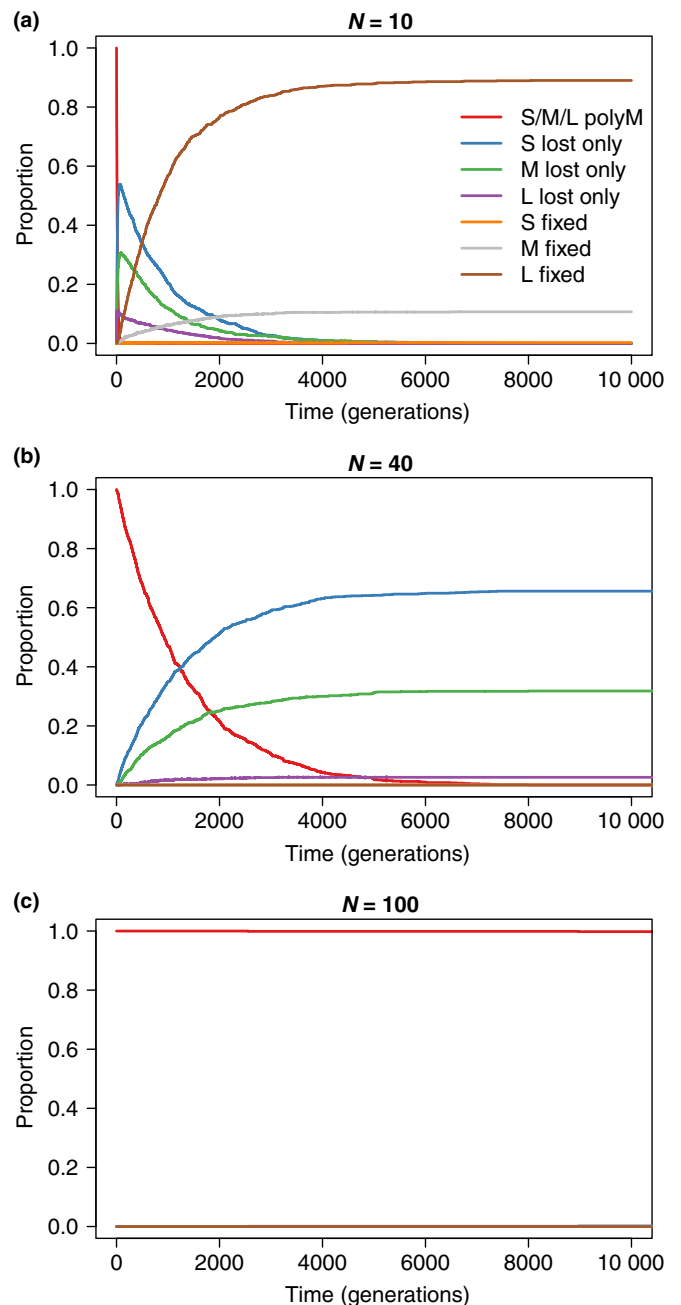


**Fig. 2** Expected morph composition in demes subject to drift as a function of time from starting under isoplethy. Curves show the proportion over 1000 independent simulations of populations at a given time point that had fixed or lost particular morphs, as indicated in the inset legend. The ancestral population contains all three morphs in similar proportions. The effects of drift and frequency-dependent selection are recorded at each generation over a period of 1000*N* generations, for populations of size (a) *N* = 10, (b) *N* = 40 and (c) *N* = 100. All simulations assumed *P* = 0 (i.e. strong disassortative mating).

example, polymorphism is established and maintained over 6*N* generations after introduction of a dominant allele with a probability of 0.95 for *N* = 10 and *P* = 0), whereas this probability drops to 0.22 for a recessive allele (Fig. 3a). Also as expected, these probabilities decline with reductions in the degree of disassortative mating in the population, reaching 0 for *P* = 1 (i.e.

random mating). For larger populations, the difference between the establishment rates of dominant vs recessive alleles is even more pronounced.

Importantly, the lower probability of the maintenance of floral polymorphism after introduction of a recessive allele $s$ is not attributable to a higher fixation rate, as is the case for small isoplethic populations (Fig. 3b). Rather, the predicted difference in the maintenance of floral polymorphism following the introduction of dominant vs recessive alleles is explained by more rapid loss of the recessive than the dominant allele while still rare, as expected under Haldane's Sieve (Fig. 3c). This difference is enhanced in large outcrossing populations, because recessive allele remain hidden in heterozygotes for longer and have a greater chance of being lost by drift. Conversely, the larger the population, the less likely it is for dominant alleles to be lost by drift (Fig. 3c).

## Invasion of a monomorphic population by a new morph

We compared the ability of a dominant allele ($S$ allele, determining the S-morph and $M$ allele, determining the M-morph) vs a recessive allele (alleles $s$ and $m$, respectively) to invade populations monomorphic for the S-morph (genotypes $SSMM$ or $SSmm$), the M-morph (genotype $ssMM$) and the L-morph (genotype $ssmm$). Here, we permitted mutations to arise at a heterozygous state, and to have an immediate effect on morphology depending on their level of dominance.

New S alleles occurring in a $ssmm$ or $ssMM$ genomic background should therefore immediately generate dimorphism in the population, with the S-morph enjoying a strong early benefit of frequency-dependent selection. Accordingly, we found that the S-morph was maintained $6N$ generations after the introduction of the $S$ allele in c. 95% of the simulations for small population of $N = 10$ (Table 1), and in all simulations for $N = 40$ and $N = 100$. Similarly, the introduction of an $M$ allele into a population monomorphic for the L-morph ($ssmm$) led to its long-term maintenance with the L-morph in 93.4% of simulations for $N = 10$ and all simulations for the larger populations we explored (Table 1).

The immigration of recessive alleles into a monomorphic population showed a very different pattern. The introduction of the $s$ allele into a population monomorphic for the S-morph (genotype $SSMM$) led to the maintenance of dimorphism for the S- and M-morph in only 22% of the simulations for $N = 10$ (Table 1). Also by contrast with the immigration of dominant alleles, the rate of establishment of recessive allele migrants decreased with population size, for example, polymorphism was maintained in only 11% of simulations for $N = 100$. A very similar pattern was observed for migration of the $s$ allele into a population monomorphic for the S-morph, but with genotype $SSmm$. Comparable establishment rates were observed for migration of an $m$ allele into a $ssMM$ population, for example, the maintenance of a mid/long dimorphism in 21% ($N = 10$), 12% ($N = 40$) and 10% ($N = 100$) of the simulations.

| Ancestral genotype | New allele | N | Proportion of polymorphism | | | Proportion of fixation | | |
|---|---|---|---|---|---|---|---|---|
| | | | Short/Mid | Short/Long | Mid/Long | Short | Mid | Long |
| ssmm (long) | S | 10 | 0 | 0.947 | 0 | 0.001 | 0 | 0.052 |
| | | 40 | 0 | 1 | 0 | 0 | 0 | 0 |
| | | 100 | 0 | 1 | 0 | 0 | 0 | 0 |
| | M | 10 | 0 | 0 | 0.934 | 0 | 0.001 | 0.065 |
| | | 40 | 0 | 0 | 1 | 0 | 0 | 0 |
| | | 100 | 0 | 0 | 1 | 0 | 0 | 0 |
| SSMM (short) | s | 10 | 0.22 | 0 | 0 | 0.773 | 0.011 | 0 |
| | | 40 | 0.15 | 0 | 0 | 0.847 | 0 | 0 |
| | | 100 | 0.11 | 0 | 0 | 0.888 | 0 | 0 |
| | m | 10 | 0 | 0 | 0 | 1 | 0 | 0 |
| | | 40 | 0 | 0 | 0 | 1 | 0 | 0 |
| | | 100 | 0 | 0 | 0 | 1 | 0 | 0 |
| SSmm (short) | s | 10 | 0 | 0.233 | 0 | 0.757 | 0 | 0.01 |
| | | 40 | 0 | 0.136 | 0 | 0.864 | 0 | 0 |
| | | 100 | 0 | 0.096 | 0 | 0.904 | 0 | 0 |
| | M | 10 | 0 | 0 | 0 | 1 | 0 | 0 |
| | | 40 | 0 | 0 | 0 | 1 | 0 | 0 |
| | | 100 | 0 | 0 | 0 | 1 | 0 | 0 |
| ssMM (mid) | S | 10 | 0.953 | 0 | 0 | 0.001 | 0.046 | 0 |
| | | 40 | 1 | 0 | 0 | 0 | 0 | 0 |
| | | 100 | 1 | 0 | 0 | 0 | 0 | 0 |
| | m | 10 | 0 | 0 | 0.213 | 0 | 0.772 | 0.015 |
| | | 40 | 0 | 0 | 0.124 | 0 | 0.876 | 0 |
| | | 100 | 0 | 0 | 0.116 | 0 | 0.884 | 0 |

**Table 1** The polymorphic state of populations initially monomorphic for the given ancestral genotypes following migration of either dominant or recessive alleles at the $S$ and $M$ loci.

Ancestral genotypes were $ssmm$ (L-morph), $SSmm$ (S-morph), $ssMM$ (M-morph) or $SSMM$ (S-morph). Proportions are measured in terms of the number of 1000 replicate simulations in which the stated polymorphism still persisted after $6N$ generations from the time of introduction of the immigrant individual. Simulations are shown for populations with $N = 10$, 40 and 100 individuals.

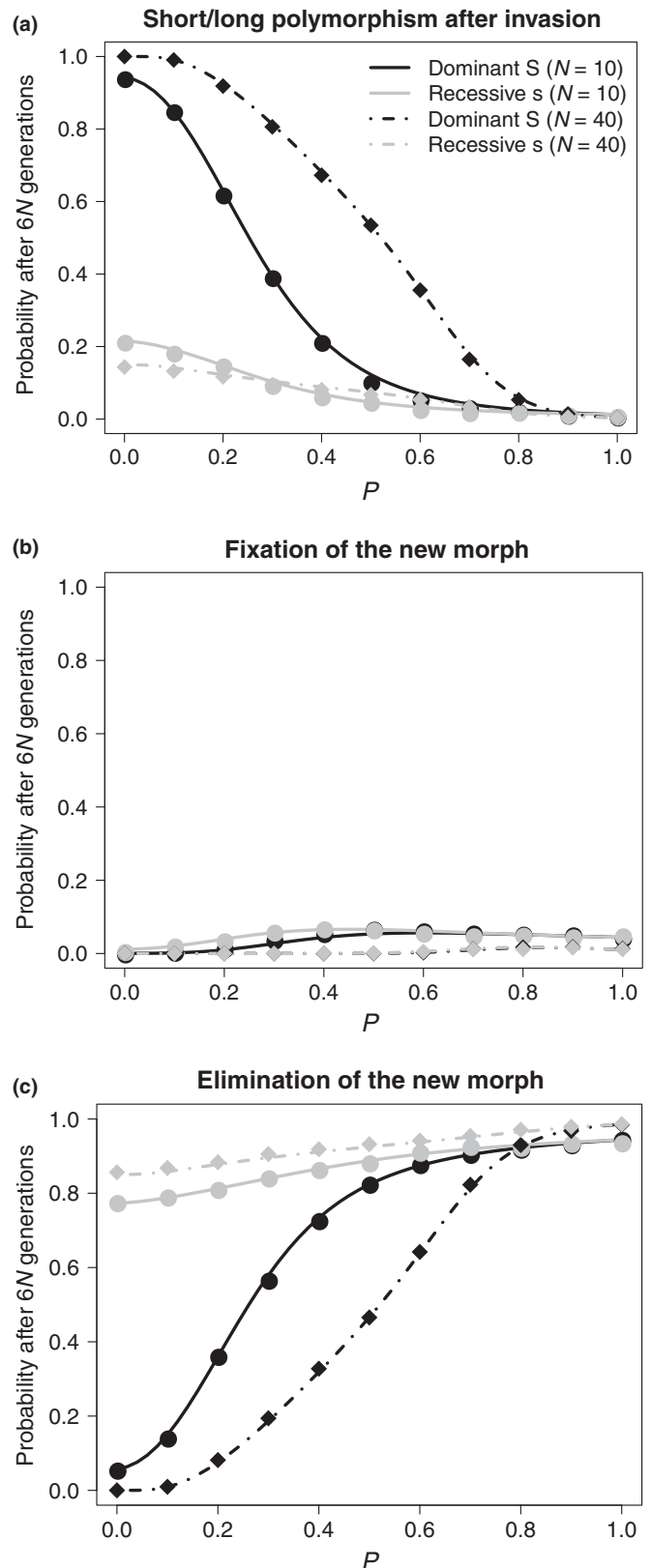## Effect of metapopulation dynamics on morph frequencies

As predicted, isoplethy was maintained effectively indefinitely in all simulations of a metapopulation in the absence of local deme extinction ($E=0$), irrespective of the rate of migration assumed (Fig. 4). However, population turnover via extinction and recolonisation dynamics tended to reduce the relative frequency of the S-morph over the entire metapopulation. therefore, for $E=0.1$, the S-morph was completely lost from the entire metapopulation when the average number of immigrants per generation $<0.5$ (Fig. 4a). A greater migration pressure should maintain trimorphism for longer, while maintaining the S-morph at frequencies $<0.33$. For the same extinction rate, the M-morph was also lost from the metapopulation for low migration rates (e.g. $I=0$ and $I=0.1$), that is, the metapopulation became monomorphic for the L-morph. Accordingly, population turnover generally favoured the L-morph, with frequencies at the metapopulation level always being $>0.47$ for $E=0.1$ for all parameter values explored.

## Migration of a new morph in a monomorphic metapopulation

The fate of migrants invading a monomorphic metapopulation (or network of populations within a larger metapopulation) were to some extent qualitatively similar to their fate as migrants into individual demes. We illustrate the immigration of a dominant $S$ allele in individuals of genotype $SsMM$ (single-locus heterozygotes of the S-morph) into a metapopulation that was ancestrally monomorphic for the M-morph (fixed for genotype $ssMM$), and compare it to a scenario in which the recessive $s$ allele migrates into a population, again as an $SsMM$ heterozygote, that was monomorphic for the S-morph (fixed for genotype $SSMM$). The results are presented in Fig. 5 in terms of the rate of establishment of the immigrant allele and the median time of its ultimate establishment as a function of the extinction rate $E$ and the average number of immigrants $I$ per deme and per generation. We arbitrarily define establishment as its presence in at least 75% of the metapopulation's demes. For each explored combination of $E$ and $I$, the dominant $S$ allele never established less frequently in a metapopulation initially fixed for the genotype $ssMM$ than the $s$ allele into its counterpart metapopulation fixed for genotype $SSMM$ (Figs 4b, 5a). The establishment rates of the $S$ and $s$ alleles

were zero for $E=0$ and $I=0$, as expected (for there was no possible gene flow among demes). For nonzero migration values, and for each combination of $E$ and $I$ explored, the difference in the establishment rate between the $S$ and $s$ alleles varied from 0.126



**Fig. 3** The predicted fate of dominant vs recessive floral-morph alleles following their introduction into finite populations. Shown are the probabilities of a given state after $6N$ generations, where $N$ is the local population size. (a) Probability that a floral polymorphism is maintained. (b) Probability that the introduced allele reaches fixation. (c) Probability that the introduced allele is lost from the population. Probabilities are obtained either by recursions of Eqns 3–5 in the Supporting Information Notes S1 or by individual-based simulations (2000 independent simulations per combination of parameters; discrete symbols). Expectations and simulations are shown for the case where the introduced morph is determined by a dominant allele $S$ (in black) or by a recessive allele, $s$ (in grey). Scenarios are shown for $N=10$ (solid lines and filled circles) and $N=40$ (dotted lines and filled diamonds).
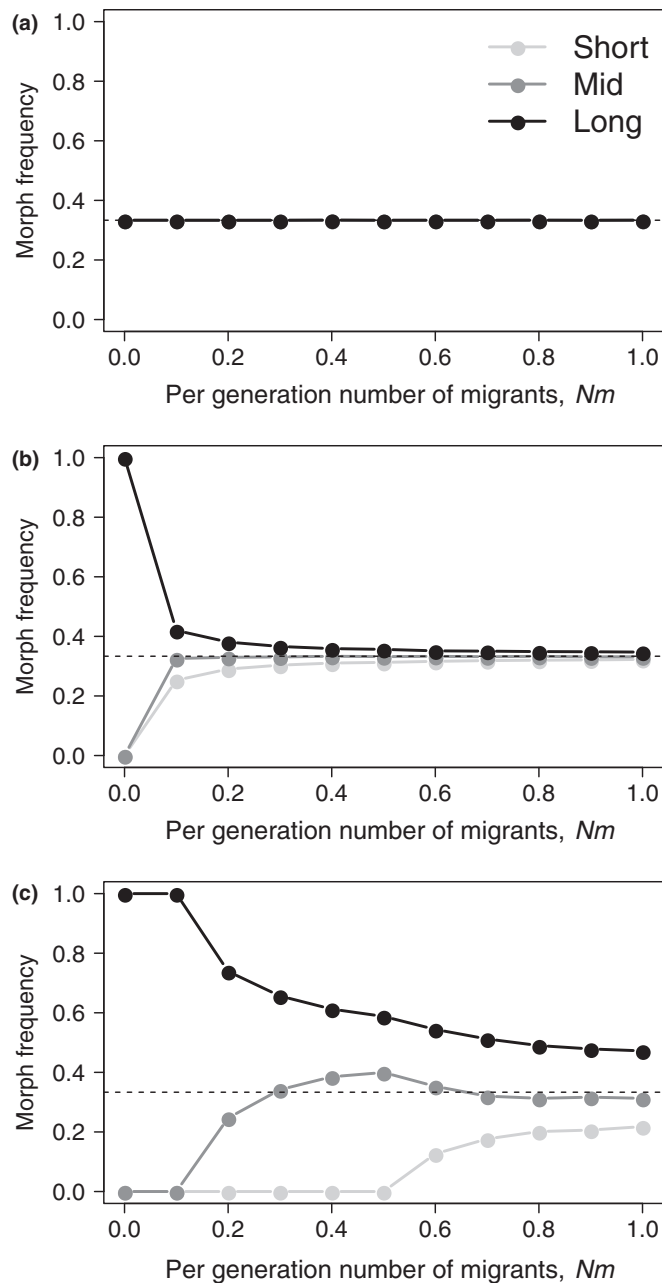
**Fig. 4** Effect of population turnover and rates of immigration on the frequency of morphs across a metapopulation. The metapopulation comprised 100 demes of 500 individuals. All simulations were started with all demes in a state of isoplethy. Metapopulation-wide morph frequencies are plotted for a range of different rates of migration (in terms of the mean number of immigrants per generation), and for three different extinction rates : $E = 0$ (a), $E = 0.01$ (b) and $E = 0.1$ (c). Results are shown after 10 000 generations. The dashed line indicates the expected frequency of the three morphs at equilibrium (isoplethy).

(establishment rate of 0.0454 for the $s$ allele, and 0.1719 for the $S$ allele for $E = 0.1$ and $I = 0.2$) to 0.944 (establishment rate of 0.056 for the $s$ allele, and 1 for the $S$ allele for $E = 0$ and $I = 1$; Fig. 5). The establishment of the dominant $S$ allele was favoured by migration rather than by extinction and recolonisation dynamics, with an establishment rate that decreased with $E$ for the same value of $I$.

The median time taken for a new mutation to be present in at least 75% of demes decreased with increases in migration between demes, as expected. Also as expected, this establishment time was shorter for greater $E$ (because population turnover indirectly brought about a further component of interdeme migration; Fig. 5d). Interestingly, greater population turnover (greater $E$) tended to slow the invasion of a metapopulation by a dominant $S$ allele, whereas greater population turnover increased the rate of establishment of the recessive $s$ allele (compare Fig. 4c and d). This pattern of easier and faster establishment of the recessive $s$ compared with the dominant $S$ allele was also found for the corresponding alleles at the $M$ locus (Fig. S1).

### Effect of population carrying capacity on morph frequencies in a metapopulation

We finally assessed the effects of both drift within local demes and the potential establishment advantage of dominant vs recessive migrant alleles in a dynamic metapopulation with population turnover through local extinctions and recolonisations. In simulations with low migration pressure ($I = 0.1$), we found that metapopulation dynamics tended to maintain the L-morph at a higher frequency than the other two morphs for a wide range of local population carrying capacities, with the M-morph maintained at an intermediate frequency and the S-morph rare (Fig. 6a). In simulations of a metapopulation with high migrant pressure ($I = 1$), the morph frequencies were less strongly skewed, being closer to isoplethy across the metapopulation (Fig. 6c). However, although the frequency ranking observed for simulations with a low migrant pressure (i.e. L > M > S) was conserved for metapopulations with demes of small carrying capacity, the ranking was reversed for metapopulations in which the carrying capacity of demes was higher (Fig. 6c). This pattern of the reversal of style morph frequency rankings was accentuated in simulations with an intermediate number of immigrants ($I = 0.5$), with the L-morph maintained at substantially lower frequencies that that other two morphs (i.e. < 0.33), the M-morph most frequent, and the S-morph at a frequency > 0.33 (Fig. 6b).

### Discussion

Under near disassortative mating in tristylous populations, we expect the three style morphs to be maintained at equal frequency (isoplethy) as a result of strong frequency-dependent selection (Heuch, 1979; Heuch & Lie, 1985; Barrett *et al.*, 1987). However, previous work has shown that because dominant alleles for style length will be maintained at a lower frequency than recessive alleles at the same locus, they are more susceptible to being lost from small populations by drift. In the case of tristyly, as exemplified by *Eichhornia paniculata* (Barrett, 1988; Barrett *et al.*, 1989; Husband & Barrett, 1992), but also in a number of other tristylous species with essentially the same genetic architecture (Heuch, 1980; Eckert & Barrett, 1992; Eckert *et al.*, 1996), this tendency for the loss by drift of dominant alleles means that, within local demes, the S-morph is more likely to be missing than the L- or M-morphs. At the metapopulation level, this biased loss of the S-
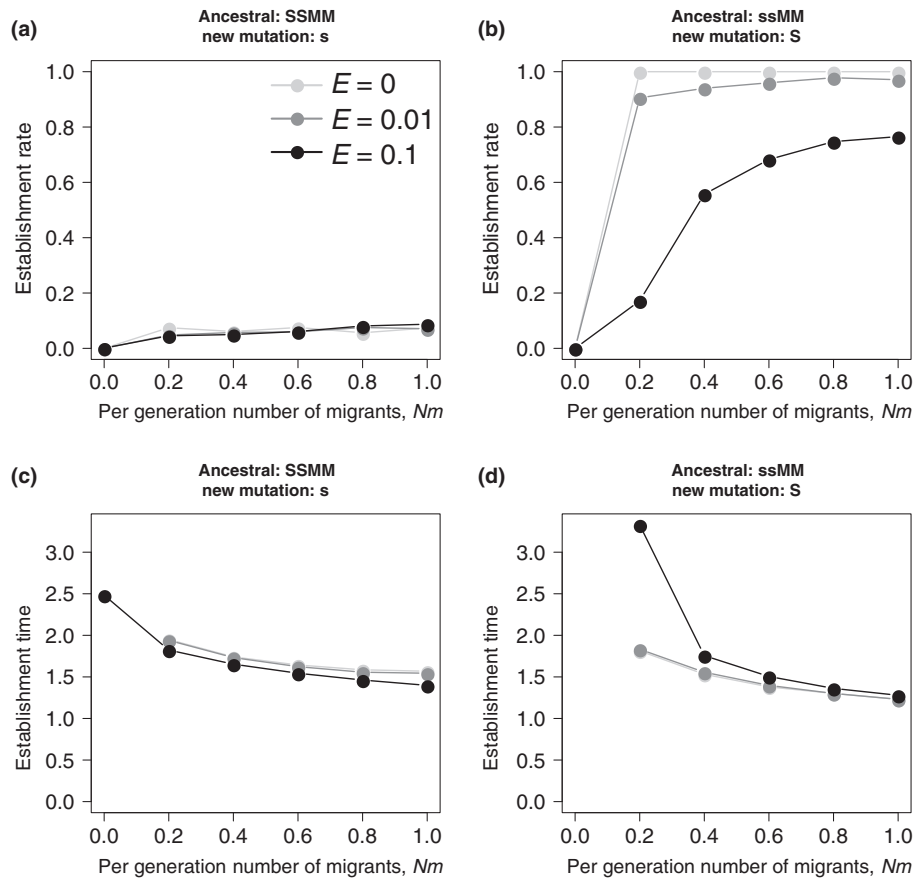
**Fig. 5** Migration of dominant vs recessive alleles into a metapopulation. The establishment rate (a, b) corresponds to the proportion of 1000 replicate simulations in which the migrant allele because established in at least 75% of the demes after 5000 generations. The establishment time (c, d) is the number of generations ($\log_{10}$) required for the new allele to become established in 75% of the demes.

morph locally will mean that the effects of drift will tend to reduce the frequency of the S-morph below its isoplethic expectation of 0.33. Our simulations largely confirm this intuition.

Beyond confirming previous results for single isolated population, our study supports the hypothesis that tristylous morph frequencies should be affected not only by the biased effects of local drift, but also by Haldane's Sieve, as hypothesised by Pannell *et al.* (2005). Indeed, the results of our simulations demonstrate the favoured establishment of dominant over recessive alleles that immigrate via seed dispersal, as predicted. Although Haldane's Sieve is usually invoked to explain the biased fixation of dominant mutations in a population (Haldane, 1924; Crow & Kimura, 1970), migration into a deme is in important respects similar to mutation, so our result should not be surprising. Nevertheless, it demonstrates that a process invoked to understand the biased fixation of new mutations under positive directional selection is also relevant to alleles under negative frequency-dependent selection that are not destined to fix in a population but rather to be maintained at an equilibrium frequency. The reason is that Haldane's Sieve still operates on such mutations that end up under balancing selection because, when they are rare (after immigration), they are positively selected (Pannell *et al.*, 2005). Haldane's Sieve helps to protect dominant alleles from stochastic loss in the early stages of establishment in a deme, whereas

recessive alleles are not protected from loss until they become sufficiently numerous to be found in homozygotes.

The idea that Haldane's Sieve might apply to migrant alleles is not entirely new. Referring to this effect as 'dominance drive', Mallet (1986) modelled the frequencies of dominant vs recessive alleles underlying wing-colour variation in a hybrid zone between butterfly mimics subject to frequency-dependent selection. He found that '[e]ven if the two phenotypes are equally fit "dominance drive" tends to increase the area in which the dominant allele is present' (Mallet, 1986). Schierup *et al.* (1997, 2000) modelled the frequency of sporophytic self-incompatibility alleles with different levels of dominance and showed that population fragmentation and migration biased allele frequencies in ways consistent with expectations for Haldane's Sieve or dominance drive. Pannell (1997) considered the maintenance of sexual systems in a metapopulation in which hermaphrodites co-occurred with individuals expressing either male- or female-sterility mutations. They found that the equilibrium frequency of these mutations and the resulting phenotypes depended on whether they were recessive or dominant, with dominant sterility mutations more likely to be maintained globally when rare, implying an effect of Haldane's Sieve. Finally, Craze (2009) presented a computational model of these effects for polymorphisms maintained by frequency-dependent selection in metapopulations generally,
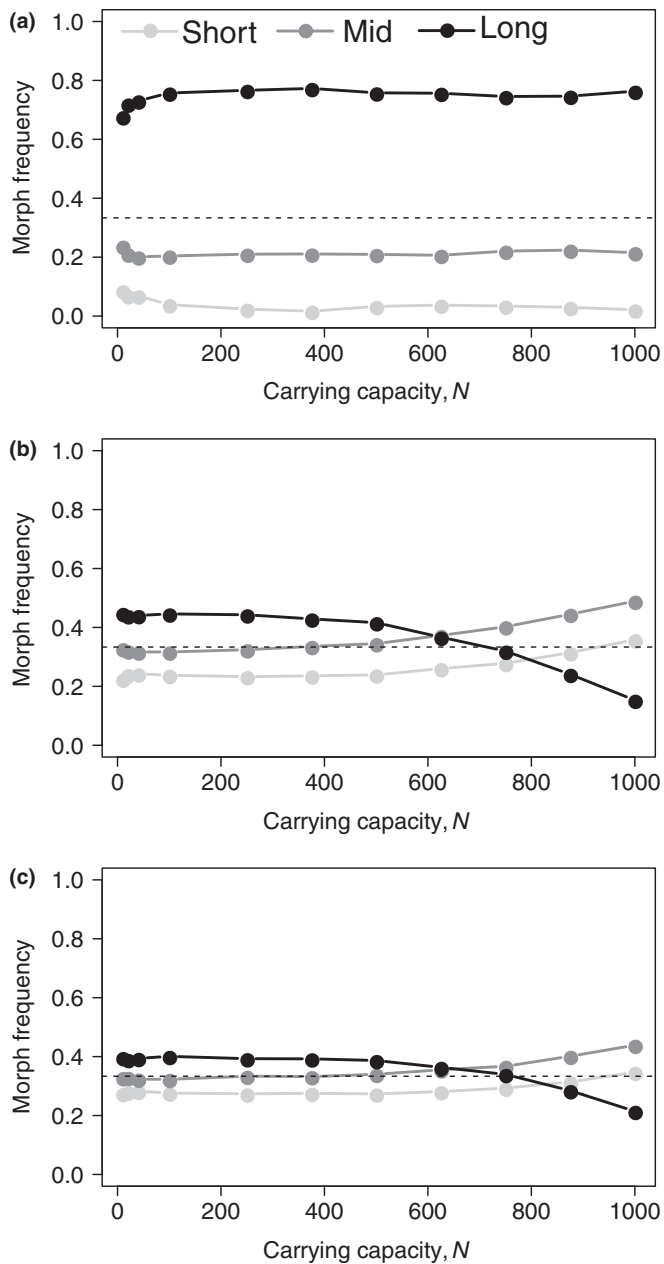
**Fig. 6** Effect of population carrying capacity on morph frequencies in a dynamic metapopulation. The morph frequencies maintained in a metapopulation averaged over 1000 replicate simulations, each run for $10N$ generations. The metapopulation comprised 100 demes liable for extinction at a probability $E = 0.05$, with immediate recolonisation by a single founder sampled randomly from the rest of the metapopulation. Mating assumed strong (but incomplete) disassortative mating ($P = 0.1$), and an average number of immigrants per generation and demes of 0.1 (a), 0.5 (b) and 1 (c).

although with a focus on the effects of local drift, as in Barrett *et al.* (1989). Our study now shows that the same sort of process may contribute to biasing allele and morph frequencies in tristylous species in which both genetic drift and between-population migration plays an important role.

Our simulations have not only demonstrated the hypothesised effect of Haldane's Sieve on dominant migrant alleles into demes

locally, but also on their establishment across a metapopulation as a whole. Again, here the dominant allele for the S-morph of the tristylous sexual system is evidently more likely to invade and spread into a metapopulation in which it has previously been lost than the recessive allele for the L-morph. In principle, this finding runs counter to the idea that metapopulations composed of demes with small effective population sizes are more likely to be missing the S- than the L- (or M-) morphs. The fact that in tristylous metapopulations it is in fact the S-morph that tends to be lost from entire regions of a metapopulation would seem to suggest that the effect we have observed here does not occur commonly in the wild, at least not in the metapopulations of *Eichhornia paniculata* or, for example, *Lythrum salicaria*, which has also been studied so extensively by Barrett and colleagues (see Introduction).

In the absence of evidence for the favoured invasion of the short morph into populations or metapopulations, we might still ask under what circumstances the positive effect of Haldane's Sieve on the dominant alleles *could* overwhelm the negative effects of local population drift in causing its biased loss? We addressed this question by simulating tristylous metapopulations with processes occurring together. For a wide range of the parameter values assessed, the effects of Haldane's Sieve were indeed unable to overwhelm those of local drift. therefore, for a wide range of parameter values, population turnover, which tends to reduce the effective size of both the metapopulation and local demes (Maruyama & Kimura, 1980; Lande, 1992; Whitlock & Barton, 1997; Pannell & Charlesworth, 1999), ultimately overwhelms the smaller effect of Haldane's Sieve by bringing about the loss of the S-morph more frequently than the L or M-morphs. In small populations, particularly those in which one or two of the morphs have been lost, we might expect a corresponding increase in selfing rates (Barrett *et al.*, 1989) to diminish the potential effect of Haldane's Sieve further still. In this broad sense, the original suggestions of Pannell *et al.* (2005) were overly optimistic about the effect that Haldane's Sieve might have on the composition of a floral polymorphism such as tristyly in a metapopulation. Nevertheless, Pannell *et al.* (2005) also advanced the narrower hypothesis that the balance between Haldane's sieve in a metapopulation and the effect of local drift within demes should be most sensitive to the local demes' carrying capacity, as well as on their growth rate. Our simulations confirm this intuition. Whereas the local effects of drift appear to hold sway in metapopulations in which local demes remain small, with the biased loss of the S-morph and an elevated metapopulation-wide frequency of the L-morph, this pattern was reversed in metapopulations in which the local carrying capacity was high (implying rapid growth in our simulations from the initial number of colonists). The reason for this result is that, in metapopulations with large demes that nonetheless suffer stochastic extinction, particularly if population growth is rapid, drift will be minimised locally, removing the likelihood that the S-morph will be lost, but Haldane's Sieve still operates, and does so more effectively, because inbreeding and homozygosity are reduced.

Our most important conclusion is that Haldane's Sieve is likely to rescue dominant alleles from loss through local drift only

under conditions in which demes grow rapidly to large size after their establishment by colonists. We expect that these conditions will rarely be met in plant metapopulations, except during biological invasion where introduced populations of tristylous species can in fact be much larger than the native range (e.g. *Lythrum salicaria*; Eckert *et al.*, 1996). The importance of metapopulation dynamics for plants has been the focus of heated disagreement in the past (Freckleton & Watkinson, 2002; Ehrlén & Eriksson, 2003; Pannell & Obbard, 2003; Alexander *et al.*, 2012). A review of the literature by Freckleton & Watkinson (2002) concluded that while most plants claimed to be subject to metapopulation dynamics were better described in terms of other spatial structures, *Eichhornia paniculata* was one of the most likely systems to conform to metapopulation expectations. Importantly for the current discussion, regions of the geographical range of *E. paniculata* in northeastern Brazil most prone to population turnover were also those in which populations tended to be small (Barrett *et al.*, 1989; Husband & Barrett, 1998). Similarly, metapopulations of the plant *Mercurialis annua* subject to elevated rates of local population extinction (and presumably turnover; Dorken *et al.*, 2017) also tended to have smaller demes (Eppley & Pannell, 2007). According to the results of our study, these are evidently not conditions optimal for an overwhelming effect of Haldane's Sieve.

The conditions under which Haldane's Sieve is likely to overwhelm local drift appear quite restrictive in the context of the maintenance of dominant vs recessive alleles underlying wild tristylous metapopulations. Nevertheless, the process might be important in reducing morph-ratio biases from what they might be in its absence. Unfortunately, this conjecture is very difficult to test with the sorts of data that might be available from field studies. However, the processes that we have investigated illustrate the importance that the details of a trait's genetic architecture might have on its frequency in natural populations. Phenotypic selection models will not always be sufficient to predict phenotype frequencies when these are effectively the result of a sum over evolutionary trajectories that depend on the underlying genetics of polymorphism. The importance of details of inheritance for tristylous morph frequencies was already apparent in previous work that explained the biased loss of the S-morph in terms of drift in small populations, as discussed above. Our study has now demonstrated the extent to which phenotype frequencies in plant sexual polymorphisms might also be sensitive to the interaction between genetics and demography, particularly involving migration and population turnover in metapopulations.

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## Author contributions

JRP conceived the project. CR performed the simulations. JRP and CR wrote the manuscript.

## ORCID

John R. Pannell (iD) https://orcid.org/0000-0002-0098-7074

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Expected morph composition in demes subject to drift as a function of time from starting under isoplethy.

**Notes S1** Simulation protocol for reproduction within the demes, data from runs for the establishment of a migrant allele in a metapopulation, and numerical calculations based on transition probabilities.

**Table S1** Establishment probabilities of dominant vs recessive migrant alleles into a metapopulation.

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