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The effective size of bryophyte populations

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Abstract

Bryophytes with their dominant haploid stage conform poorly to the life cycles generally treated in population genetical models. Here we make a detailed analysis of what effective sizes bryophyte model populations have as a function of their breeding system. It is found that the effective size is rarely much smaller than the scored number of haploid gametophytic individuals, even when the limited number of diploids (sporophytes) formed is taken into account. The most severe decrease in effective size occurs when unisexual gametophytic females produce only a small number of fertile diploid sporophytes in male biased populations; this effect is due to the restricted sampling of male gametophytic individuals that then occurs. It is shown that the harmonic mean of diploid sporophytes formed per haploid gametophytic individuals is the relevant measure in these calculations and not the standard (and generally larger) arithmetic mean.

Keywords: Breeding system; Intragametophytic selfing; Asexuality; Coalescence

1. Introduction

In this article, our aim is to present analyses of how the effective size of bryophyte populations is to be calculated and understood. The problem has – as far as we know – never been properly tackled before, and has become acute in the face of more and better assembled demographic and genetic data. A short introduction is first given to the concept of “an effective population size” and then an explanation is given of why bryophytes need to be given a particular study. The important question about what constitutes a bryophyte population is brought to discussion at the end of the paper.

In every population of limited size, variability is lost due to genetic drift. The rate of loss depends on the size of the population and on its breeding system; the loss is rapid in small populations and slow in large populations. Variability is generally restored by mutation, but the effect of drift is noticeable even in its presence. The standing genetic variability is for example more reduced in small than in large populations, even when the mutation rate is the same in the two cases. Similarly, the difference between two homologous gene sequences taken from two individuals in a small population is, on average, smaller than the difference between sequences taken from a large population. One way of understanding this is to consider the time required to go back to the last common progenitor of the sequences (the coalescence time). This time is on average smaller in a small population than in a large one, and fewer mutations will therefore have hit the sequences in the first than in the second case. In mathematical population genetics a number of functional relationships between genetic variability, coalescence time, mutation rate and population size have been worked out (see e.g. Hein et al., 2005, for a useful introduction to coalescence theory).

Generally, these relationships have been calculated for populations with an ideal reproductive system (at least from a mathematical point of view). It is assumed that N diploid

individuals produce an infinite number of haploid gametes that join at random and generate a new generation with again N individuals. It is easy to show that the drift properties of this population is the same as that of a population with $2N$ haploid individuals that produce an infinite number of asexual propagules that found a new generation with again $2N$ members. In both cases it is assumed that chance alone determines who genders what number of individuals in the next generation. A common name for populations with these drift properties is ‘Wright-Fisher populations’, following these authors’ classical work on the role of chance in genetic transmission (Wright, 1931, 1950; Fisher, 1930).

Many organisms have life cycles or breeding systems that fit the assumptions underlying Wright-Fisher populations only poorly. Extensive research has therefore gone into characterizing the ‘effective size’ of such populations, i.e. the size of a Wright-Fisher population with the same rate of loss of genetic variation as the population under consideration. Most of this work (summarized by Crow and Kimura, 1970, but see also e.g. Orive, 1993, and Yonezawa, 1997) has been directed towards organisms where the diploid phase dominates – a pattern that obviously does not fit bryophytes (i.e. mosses, liverworts and hornworts), where the haploid life stage is predominant. Bryophytes are different also in that they can be said to have three natural life cycle stages: first a vegetatively growing haploid gametophytic phase – the commonly observable ‘individuals’ in the population – of limited size; then a diploid sporophytic phase that is also limited in number; and finally a phase with haploid spores produced in very great number by the diploids after meiosis and from which the vegetative individuals in the new generation are drawn.

Within this framework, the bryophytes display certain flexibility with respect to their breeding system. It is estimated that about 57% of the mosses and 68% of the liverworts are unisexual, having male and female structures on separate gametophytes (Wyatt and Anderson, 1984). In theory, this makes the *unisexual bryophytes* obligate outbreeders (though

as noted by Shaw (2000), fertilizations between gametophytes produced by spores from the same diploid are genetically comparable to self-fertilizations in seed plants). With respect to *bisexual bryophytes*, fertilizations involving male and female gametes produced by the same gametophytic individual ('intragametophytic selfing' *sensu* Klekowski, 1972), gives rise to a completely homozygous diploid. The spores produced by such a sporophyte will be genetically identical (ignoring mutations), as well as identical to the parental gametophyte, thereby resembling asexual propagules produced by the haploid gametophyte (Mishler, 1988). So, given these different complications, what effective size do bryophyte populations have?

After a general introduction to the assumptions that normally underlie studies of effective population sizes, we consider two archetypical bryophyte model populations (for their relevancy, see e.g. Cronberg et al., 2006, and Eppley et al., 2007). In the first model all haploid gametophytic individuals are bisexual with a certain frequency of intragametophytic selfing. This case turns out to be mathematically identical to a mixed model where the haploid individuals produce one proportion of haploid propagules asexually and another proportion of haploid spores after random union of gametes followed by meiosis.

In the second model population, all haploid individuals are unisexual, *i.e.* they produce either male or female gametes but never both (those that produce neither are not scored in the analysis). In both model situations we assume that all haploid gametophytes with female functions produce the same number of diploid sporophytic structures; the effect of this assumption is reconsidered in the last result subsection. The calculations on which the results are based are arithmetically cumbersome but scientifically trivial. They are summarily described in appendices at the end of the paper.

The background to our work is the increased interest in bryophyte demography that has grown out of the attempts to conserve their biodiversity and which has led to the collection of increasing amounts of high-quality molecular data (see e.g. the review by Shaw

et al., 2002). However, before this molecular information can be turned into any genuine understanding of bryophyte evolution, a proper analysis of their specific transmission genetics is needed.

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2. General assumptions and the simplest asexual model

2.1 Outline of the life cycle

In most discussions of the effective size of a population it is assumed that it is relevant to consider discrete generations. The number of individuals in the population is scored at a specific developmental moment and it is normally assumed – as here – that in the next generation the number of individuals is the same when scored at the identical moment in the organism's life. The size of the population is denoted N , and the task is to find the effective size of the population, N_e , which is the number of individuals in the 'ideal' Wright-Fisher population that would lose genetic variation at the same rate as the one under consideration. The difference between the two populations is that the one under consideration uses a mode of reproduction that makes it function as if it had a different size from a population with the ideal mode of reproduction (there is no value judgment in this notation; 'ideal' does not mean 'the best' but only the mode with the simplest mathematical properties).

The ideal mode of reproduction can in the bryophyte case be taken to be asexual haploid reproduction – in one way or another – without any formation of sporophytic diploids. Thus, assume a population with N haploid individuals at the time of maturity, *i.e.* when the process of reproduction is about to begin. All individuals produce a very large number (which we treat as infinite) of haploid propagules (vegetative reproductive structures or similar). The next generation is derived from this pool of infinitely many haploid propagules. A more or less large number of them may germinate and/or start to grow, but at the time of maturity, *i.e.* at the same time as when the earlier generation was scored, exactly N individuals remain. No element of selection based on genotype is assumed to play any role in this process from N over ∞ to N again.

2.2 Loss of genetic variability

In this ideal population, genetic variability is lost at rate $1/N$ per generation, as is standard in Wright-Fisher populations of haploid size N . Thus, if the genetic variation in the parental population is measured by the standard diversity measure H , generally called ‘heterozygosity’, then the expected change in genetic variability due to chance – genetic drift – in the transition between two generations is given by

$$H' = (1 - 1/N)H, \quad (1)$$

where the prime sign is used to denote the expected value in the next generation. (See Appendix A for a derivation of this result.) The formula shows, as expected, that the rate of loss of genetic variation is rapid in small populations and slow in large populations.

(The measure H of genetic diversity can in a haploid population be thought of as one minus the probability that two randomly drawn gametophytic individuals (without replacement) are identical by descent for the genetic region under consideration. The notion of identity between gene copies due to their parentage goes back to work published by Malécot in 1941; see Gillois, 2002.)

2.3 Comment

It should be noted that every individual in the parental generation leaves between zero and N offspring to the next generation. It is the element of chance that here intervenes which causes the gradual loss of genetic variation to the population. If every individual in the parental generation produced exactly one offspring, then there would be no change over time in genetic diversity, *i.e.* instead of (1) we would have $H' = H$.

3. Model population 1A: Bisexual bryophytes with partial selfing

3.1 Outline of the life cycle

The population is scored at ‘maturity’ when it consists of N haploid individuals. All these individuals are bisexual and produce both male and female gametes. Every individual haploid gametophyte produces an infinite number of male gametes, while only k of its egg cells get fertilized and develop into full-grown diploids (sporophytes). We assume k to be a fixed number but will later weaken this assumption. The proportion of diploids formed through intragametophytic selfing is s , the rest of the diploids are formed by random union of male and female gametes (selfing may occur also here but then due to pure chance alone). All diploids produce an infinite number of haploid spores. There is no selection on either haploid or diploid genotypes.

3.2 The effective population size

The effective size of this population is (see Appendix B):

$$N_e = N/[1 + (1 - s^2)(1 - 1/N)/4k]. \quad (2a)$$

In Table 1 are given some values for N_e based on numerical assumptions for N , k and s . For all but the smallest values on N the formula is closely approximated by

$$N_e = N/[1 + (1 - s^2)/4k]. \quad (2b)$$

3.3 Comments

(i) This differs from the standard Wright-Fisher model in that a limited number of individuals exist both at the haploid *and* the diploid state. If k is allowed to grow unboundedly, which implies that infinitely many diploid sporophytes are formed per haploid gametophyte, then the effective population size becomes exactly equal to N . This is as expected, since the population will then behave in a typical Wright-Fisher manner. The effective size of the population is smaller than the directly scored size N for all parameter values except when $s = 1$ or $N = 1$. (The last result is trivial: in a population consisting of a single haploid individual there is never any loss of genetic variability due to drift.)

(ii) However, the decrease in effective size due to the restricted number of diploid sporophytes formed is comparatively small (see Table 1; based on formula 2a). At most the reduction is 20%, which occurs for $s = 0$, N large and $k = 1$.

(iii) This implies that intragametophytic selfing does not have any large effect on the effective population size. In haploids selfing is identical to asexuality, and – as expected from the introductory ideal model – complete selfing leads to the standard effective size (as long as a Poisson variance in offspring numbers is assumed). In general, the effective size increases with the amount of intragametophytic selfing, which follows from the way that selfing reduces the possibilities for chance to affect the next generation's genetic composition.

4. Model population 1B: Bisexual bryophytes with partial asexuality

Assume that the haploid propagules that start the new generation have been produced either asexually, with rate a , or sexually via random union of gametes (thus without any direct intragametophytic selfing except due to chance alone) with rate $1 - a$. Note that asexual reproduction is here occurring in the haploid phase, unlike for example in vascular plants where it occurs in the diploid phase, when it occurs.

It is easy to see that this population will have exactly the same drift properties as the case considered above (Model population 1A), with the simple substitution of a for s in expressions (2a) and (2b). This is, in effect, just a restatement of the preceding comment (iii).

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5. Model population 2: Unisexual bryophytes

5.1 Outline of the life cycle

Assume that infinitely many haploid spores have been produced by the earlier generation. These spores form the new generation. From the germinated haploid spores N_f haploid female individuals develop. Each gametophytic female produces exactly k diploid sporophytic structures, each of which produces a very large (infinite) number of haploid spores. The female individuals are fertilized by gametes from the male gametophytic individuals in the population (one randomly chosen male gamete per diploid structure). There are N_m male haploid individuals in the population, all equally productive with respect to male gametes. Sexes are separate, so that a haploid gametophytic individual is either male or female (sterile individuals are not scored). The sex of an individual is determined independently of the genetic material considered here.

5.2 The effective population size

The effective size of this population, N_e , is given by

$$1/N_e = (1/4N_f) + (1/4kN_f) + (1/4N_m) - (1/4kN_fN_m), \quad (3a)$$

as outlined in Appendix C. For all but the smallest values on both N_f and N_m the formula is closely approximated by

$$1/N_e = (1/4N_f) + (1/4kN_f) + (1/4N_m). \quad (3b)$$

5.3 Comments

(i) The number of diploid sporophytes, k , produced by female gametophytic individuals becomes in this case directly important, as seen particularly clearly in formula (3b). This is because the male gamete pool is sampled through these structures. When few diploids are formed (k small), there is not much effect of an abundance of males in the population, since most of them will never participate in any fertilization.

(ii) With a large number of diploids formed (k large) and an equal sex ratio ($N_f = N_m$) the effective size of the population becomes the sum of male and female gametophytic individuals ($N_e = N_f + N_m$), as expected.

(iii) The effective population size for some numerical values on the parameters is given in Table 2 (based on formula 3a). In Figure 1 the different possibilities for a population of size 10 are described for small values on k . Comments (i) and (ii) are well illustrated.

(iv) Any amount of haploid asexual reproduction will increase the effective population size towards N , just as in the preceding case. This follows from the more equal representation of individuals in the next generation that asexuality entails; since it does not lead to any new important structural insights no exact analysis of its effect has been made.

6. Variance in number of diploid sporophytes formed

6.1 Harmonic mean

In the preceding sections it has for simplicity been assumed that every bisexual gametophyte or female unisexual gametophyte produces exactly k diploid sporophytes. What happens when this simplifying restriction is removed and instead it is assumed that the number of diploids per egg-producing gametophytic individual follows a distribution where the probability of producing exactly k diploids is taken to be p_k ($k \geq 1$)?

The answer is simple. The results described in expressions (2) and (3) remain unchanged, with the exception that k^* should be inserted instead of k , where k^* is the harmonic mean of the distribution of k -values, i.e.

$$1 / k^* = \sum (p_k / k) . \quad (4)$$

In Appendix D is described how this result comes about for the most relevant case, the situation with separate sexes.

6.2 Comments

(i) For all nontrivial cases, the harmonic mean is smaller than the standard arithmetic mean, which implies that the reducing effect of a restricted k -value is more pronounced than if the arithmetic mean is used.

(ii) This effect can be illustrated by a numerical example. As seen in Table 2, the effective population size under the bisexual case for $N_f = 10$, $N_m = 100$, $k = 3$ is 30.0. If instead the population is separated into five equal lots producing 1, 2, 3, 4 or 5 diploids each

(arithmetic mean 3 but harmonic mean 2.2), then the effective size of the population becomes 25.8.

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7. Discussion

Our results are clear and easy to interpret and use. From the point of view of genetic drift, the effective size of a bryophyte population is rarely much smaller than the scored number of reproductively active gametophytic haploids. Only in the case with bisexual individuals and a strong male-bias will the effective size be considerably smaller than the scored number of haploid individuals, particularly so if the number of diploid sporophytes produced by females is low. In unisexual bryophytes the sex determination is considered to be chromosomal and a sex ratio of 1:1 is therefore expected (Ramsay and Berrie, 1982). However, female-biased sex ratios seem to be the rule for bryophyte populations (Bowker et al., 2000). In most cases the mechanism behind this bias is unknown, but in our context it is notable that a female bias reduces the effective population size less than a similar male bias.

Thus, the bryophytes' unusual combination of a limited number of haploid gametophytic individuals *plus* a limited number of diploid sporophytic individuals does not in itself induce drift effects of any drastically increased magnitude. This is an important result, because it has earlier been assumed that the characteristics of the bryophyte life cycle (a long haploid life stage with predominating asexual reproduction) would automatically lead to strong drift effects and therefore to populations depleted in genetic variation (cf. Cummins and Wyatt, 1981, for a discussion). However, molecular studies – in better agreement with our theoretical results – have revealed that moss populations on average contain levels of genetic diversity similar to tracheophytes (Shaw, 2000). Inter-population differences indicative of drift, as measured by G_{ST} for example, range all the way from almost zero (no differentiation among populations) to unity (all genetic variation among populations) for different species (Shaw, 2000). The position of species along this dimension appears to be correlated with life-history characteristics and breeding system. For example, studies of widespread perennial and

sexually reproducing bryophytes (cf. Cronberg, 2002) have often revealed comparatively high levels of variation and low inter-population differentiation, suggesting that effects of genetic drift are limited. In cases where populations with contrasting levels of population polymorphism have been detected in such species, reduced levels of variation appear to be associated with founder events during range expansion in combination with clonal propagation (Cronberg, 2002; Wyatt et al., 2005; Grundmann et al., 2008).

Our results can also be taken as a reminder that the genetic variation in a population is primarily determined by the interplay of neutral mutations and the size of the population. The breeding system enters this relationship only via its effect on the effective size of the population. The same point has been clearly made by Stenøien and S  stad (2001) in their review of genetic variability in bryophytes. There is also every reason to stress with these authors the difference between *genetic* diversity, as measured at single locus level, and *genotypic* diversity. The second is determined not only by the genetic variation at single loci but by the pattern of recombination between them. Thus, in a population with much genetic variation at the sequence level, the number of scored genotypes may nevertheless be highly restricted, if reproduction is exclusively asexual (or via intragametophytic selfing alone) leading to no effective recombination between loci. Compared to most other eukaryotes, bryophytes have actually a great technical advantage in being easy to genotype at the haploid level, making it comparatively easy to estimate the amount of linkage disequilibria between loci. We hope to see many such studies in the future.

Finally we wish to state where we believe the greatest limitation of our work resides. It is in the presumption of a closed ‘population’ that has been used throughout. Behind the idea of ascribing an effective size to a group of organisms underlies the notion that this group functions as a (reasonably) distinct reproductive unit for at least a certain amount of time (many generations). This assumption cannot always be taken for true.

In bryophytes, with their tendency to a long life span and facility for clonal reproduction, the balance between re-sampling of local genetic material through various reproductive mechanisms and the inflow of new genetic variants via migration must always be given particular attention. Many bryophytes are dispersed by wind-borne spores over long distances, thereby obliterating any pattern of ‘isolation by distance’ (see e.g. Crow and Kimura, 1970). For example, gene flow in *Hylocomium splendens* among islands in a Baltic archipelago appeared essentially random (*i.e.* as without any clear geographic component), when investigated by allozyme variation (Cronberg, 2002). This case may be contrasted to the situation in such bryophytes that produce spores that are not actively dispersed (cf. Dewey, 1989), illustrated for example by the genus *Riccia*, where spores are released only when the gametophyte disintegrates. Accordingly, Dewey (1989) found evidence, when studying local populations of three cryptic species belonging to the formal species *Riccia dictyospora*, that each population evolved apparently independent of the rest and primarily due to local genetic drift.

To be relevant, any estimate of the effective size of a bryophyte population must therefore always be accompanied by studies that clarify what population dynamics exist in the species and ascertain that it is relevant to speak of a ‘local population size’. Thus, we warn against all unquestioned use of the formulae described in this article, but hope that they may turn out useful in the analysis of relevant situations.

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Appendix A. Rate of change of genetic diversity in the ideal asexual case

Assume that at the start of the population, a number of generations ago, every haploid gametophytic individual had its own unique allele at the locus under consideration. At the moment the population is studied, some of the haploid individuals in the population will carry alleles that are identical by descent, while others will carry different alleles. Let the probability that the alleles from two randomly drawn individuals are identical by descent be I . This makes the probability that they are different $1 - I$; this probability is normally called the genetic diversity index ('heterozygosity') for the locus and is denoted H .

Take two individuals at random from the next generation. With probability $1/N$ they derive from the same haploid gametophytic individual in the studied generation and their alleles are thereby, by necessity, identical by descent. With probability $1 - 1/N$ they derive from two different individuals in the studied generation, and the probability that their alleles at the locus under consideration are identical by descent is then I .

Thus, if we let the prime sign ($'$) denote the expected value in the next generation, then we have

$$I' = (1/N) 1 + (1 - 1/N) I,$$

which leads to

$$H' = (1 - 1/N) H$$

as in expression (1).

Appendix B. Bisexual bryophytes with partial selfing

The same logic as above is used for this case, but due to many more possible relationships between the two haploid gametophytic individuals drawn from the later generation, much greater complexity arises.

An example: The outcome (O) of the drawing of two individuals may be that their alleles at the locus under consideration both derive from the same haploid gametophytic individual in the parental generation, that they come from two different diploid sporophytes produced by this individual, and that both were transmitted via the egg (or more correctly: that both haploids now drawn have genetic material that were transmitted into the parental diploid via the egg). The probability (P) of this outcome is $(1/N) (1 - 1/k) (1/4)$. The expected identity EI of these two individuals is exactly 1, since even if they derive from different diploid individuals (sporophytes) their genetic material must be identical since it in both cases is derived from the same ‘mother-haploid’.

All possible outcomes with their corresponding probabilities and expected identities can be enumerated in the same way. An abbreviated summary looks like this (where the example just analysed is number 10):

The alleles at the locus under consideration of the two drawn individuals derive

- O: From the same individual, from the same diploid, both transmitted via egg; $P = (1/N) (1/k) (1/4)$; $EI = 1$.
- O: From the same individual, from the same diploid, one transmitted by egg, this egg was fertilized by selfing; $P = (1/N) (1/k) (1/2) s$; $EI = 1$.

- O: From the same individual, from the same diploid, one transmitted by egg, this egg was fertilized by outcrossing; $P = (1/N) (1/k) (1/2) (1-s)$; $EI = (1/N) + (1 - 1/N)I$.
- O: From the same individual, from the same diploid, none transmitted via egg; $P = (1/N) (1/k) (1/4)$; $EI = 1$.
- O: From different individuals, both transmitted via egg; $P = (1 - 1/N) (1/4)$; $EI = I$.
- O: From different individuals, one transmitted via egg, this egg was fertilized by selfing; $P = (1 - 1/N) (1/2) s$; $EI = I$.
- O: From different individuals, one transmitted via egg, this egg was fertilized by outcrossing; $P = (1 - 1/N) (1/2) (1 - s)$; $EI = (1/N) + (1 - 1/N)I$.
- O: From different individuals, none transmitted via egg, both produced by selfing; $P = (1 - 1/N) (1/4) s^2$; $EI = I$.
- O: From different individuals, none transmitted via egg, at least one produced by outcrossing; $P = (1 - 1/N) (1/4) (1 - s^2)$; $EI = (1/N) + (1 - 1/N)I$.
- O: From the same individual, but from different diploids, both transmitted via egg; $P = (1/N) (1 - 1/k) (1/4)$; $EI = 1$.
- O: From the same individual, but from different diploids, one transmitted via male gamete, this gamete participated in a direct selfing; $P = (1/N) (1 - 1/k) (1/2) s$; $EI = 1$.
- O: From the same individual, but from different diploids, one transmitted via male gamete, this gamete participated in outbreeding; $P = (1/N) (1 - 1/k) (1/2) (1 - s)$; $EI = (1/N) + (1 - 1/N)I$.
- O: From the same individual, but from different diploids, none transmitted via egg, both produced by selfing; $P = (1/N) (1 - 1/k) (1/4) s^2$; $EI = 1$;
- O: From the same individual, but from different diploids, none transmitted via egg, at least one produced by outcrossing; $P = (1/N) (1 - 1/k) (1/4) (1 - s^2)$; $EI = (1/N) + (1 - 1/N)I$.

In accordance with the formula in Appendix A we can write

I' = the sum of the products between the respective probabilities P and the expected identities EI for these fourteen outcomes.

After simplification and substitution ($H = 1 - I$) this expression becomes

$$H' = (1/N_e) + (1 - 1/N_e) H,$$

where N_e is as given by expression (2a), making this by definition the variance effective size of the population (using the same logic as outlined in the Introduction in Orive, 1993).

Appendix C. Unisexual bryophytes

In this case we do not outline the different possibilities but only write the relevant equation. The interested reader will be able to deduce the underlying analysis.

$$\begin{aligned} I' &= (1/kN_f) [(1/2) 1 + (1/2) I] + \\ &+ (1 - 1/k) (1/N_f) [(1/4) 1 + (1/2) I + (1/4) \{(1/N_m) + (1 - 1/N_m) I\}] + \\ &+ (1 - 1/N_f) [(1/4) I + (1/2) I + (1/4) \{1/N_m + (1 - 1/N_m) I\}]. \end{aligned}$$

After simplification and substitution ($H = 1 - I$), the same formula as above is reached, but where now the definition of N_e is as given by expression (3a).

D. Variance in number of diploid sporophytes formed

Assume that in the preceding case not every haploid gametophyte produces exactly k diploid sporophytes, but that the haploids produce a random number of diploids where the probability that k is produced is given by p_k ($k \geq 1$). It is then easy to see that the preceding formula should be written

$$\begin{aligned}
 I' = & \sum p_k (1/kN_f) [(1/2) 1 + (1/2) I] + \\
 & + \sum p_k (1 - 1/k) (1/N_f) [(1/4) 1 + (1/2) I + (1/4) \{(1/N_m) + (1 - 1/N_m) I\}] + \\
 & + (1 - 1/N_f) [(1/4) I + (1/2) I + (1/4) \{1/N_m\} + (1 - 1/N_m) I],
 \end{aligned}$$

where the sums are taken over all possible values for k .

Again, this equation leads to expression (3a), but with the substitution given by (4).

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Table 1

The effective size of a population, N_e , given numerical assumptions on the scored population size of haploid gametophytes, N , the number of diploid sporophytes produced by every haploid gametophytic individual, k , and the proportion of diploid sporophytes produced by intragametophytic selfing, s

N	k	s	N_e
10	1	0	8.2
10	1	0.5	8.6
10	1	0.9	9.6
10	3	0	9.3
10	3	0.5	9.5
10	3	0.9	9.9
10	10	0	9.8
10	10	0.5	9.8
10	10	0.9	10.0
100	1	0	80.2
100	1	0.5	84.3
100	1	0.9	95.5
100	3	0	92.4
100	3	0.5	94.2
100	3	0.9	98.5
100	10	0	97.6
100	10	0.5	98.2
100	10	0.9	99.5

Table 2

The effective size of a population, N_e , given numerical assumptions on N_f (the number of female haploid gametophytic individuals in the population), N_m (the number of male haploid gametophytic individuals in the population), and k (the number of diploid sporophytes produced by every female haploid gametophytic individual)

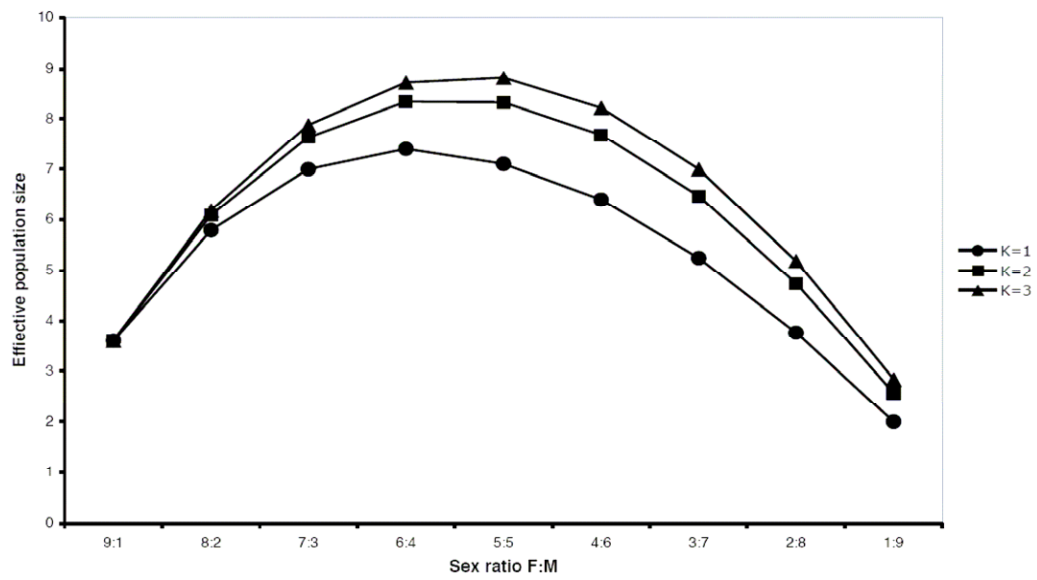
N_f	N_m	k	N_e
10	10	1	13.8
10	100	1	19.1
100	10	1	33.6
100	100	1	133.8
10	10	3	17.4
10	100	3	30.0
100	10	3	35.4
100	100	3	171.7
10	10	10	19.1
10	100	10	33.4
100	10	10	36.1
100	100	10	190.6

Figure legend

Fig. 1. The effective size of a population, N_e , consisting of ten haploid gametophytic individuals with different proportions of males (M) and females (F). The number of diploid sporophytes produced by every female haploid gametophyte, k , is varied from 1 to 3.

Accepted manuscript

Figure 1



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