Perenniality induces high inbreeding depression in self-fertilising species

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ABSTRACT

When predicting the fate and consequences of recurring deleterious mutations in self-fertilising populations most models developed make the assumption that populations have discrete non-overlapping generations. This makes them biologically irrelevant when considering perennial species with overlapping generations and where mating occurs independently of the age group. The few models studying the effect of perennial life-histories on the genetic properties of populations in the presence of self-fertilisation have done so considering age-dependent selection. They find low levels of inbreeding depression in perennial populations that do not explain empirical observations. Here we propose a simple deterministic model in continuous time with selection at different fitness traits and feedback between population fitness and size. We find that a perennial life-history can result in high levels of inbreeding depression in spite of inbreeding, due to higher frequencies of heterozygous individuals at the adult stage. We also propose that there may be demographic advantages for self-fertilisation that are independent of reproductive success.

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1. Introduction

The prevalence of outcrossing in phylogenies where self-fertilisation has evolved independently several times (and with no detected returns to outcrossing Igic and Busch, 2013) is a long-running question in evolutionary biology. Though it has been suggested that self-fertilisation is an evolutionary dead-end (Takebayashi and Morrell, 2001; Wright et al., 2013), with self-fertilising lineages suffering from higher extinction rates (Goldberg et al., 2010), the short-sightedness of natural selection makes it seem unlikely that only long-term disadvantages are responsible for the maintenance of outcrossing. Furthermore, there exists a correlation between longevity and the evolution of self-fertilisation, with annual species tending to be self-fertilising and perennials outcrossing (see Morgan et al., 1997). This implies that life-history may play an important part in the evolution of reproductive systems. Short-term disadvantages or barriers to the spreading of self-fertilisation related to perenniality must therefore exist.

The most evident short-term barrier to the evolution of self-fertilisation is inbreeding depression, a lower relative fitness of selfed versus outcrossed progeny due to the expression of partially recessive deleterious mutations (Charlesworth and Charlesworth, 1987). It is generally accepted that if inbreeding depression is not too high, Fisher's automatic advantage will favour the spreading of an allele promoting self-fertilisation (Fisher, 1941). As self-fertilisation increases, this should lead to a purge of deleterious alleles (Glémin, 2003), lowering the observed level of inbreeding depression. Indeed, it has been suggested that the observed correlation between perenniality and outcrossing is due to higher observed levels of inbreeding depression in perennial species even in species with mixed mating systems (Morgan et al., 1997; Byers and Waller, 1999; Winn et al., 2011). This phenomenon has been attributed to selective interference (Winn et al., 2011), a consequence of linkage and identity disequilibria brought on by self-fertilisation that results in the inability to purge deleterious mutations in spite of selfing (Lande et al., 1994). Though perenniality is expected to lead to higher per generation mutation rates than would be observed in annual species (due to a higher number of mitoses Scofield and Schultz, 2006), therefore favouring selective interference, it seems unlikely that the observed levels of inbreeding maintained

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in perennial populations be due solely to this phenomenon as selective interference requires a high mutation rate to very recessive deleterious mutations (independently of their coefficient of selection), and most deleterious mutations are only partially recessive (see Kelly, 2007).

The higher than expected levels of inbreeding depression in perennials have been associated with a less efficient purging of the genetic load compared to annual species (Byers and Waller, 1999). This is further supported by the observation that self-fertilising perennials seem to maintain higher than expected heterozygocity at loci under selection (Spigler et al., 2009) compared to predictions from discrete-time models with non-overlapping generations (Charlesworth and Charlesworth, 1987; Glémin, 2003). Life-history may therefore be a non-negligible trait when studying the evolution and the evolutionary consequences of self-fertilisation. Most conventional population genetics models studying the consequences of the evolution of self-fertilisation have done so assuming discrete-time and non-overlapping generations (Lande and Schemske, 1985; Charlesworth et al., 1990; Porcher and Lande, 2005; Glémin and Ronfort, 2013). Such models therefore neglect the potential effect of life-history traits on the maintenance of inbreeding depression.

Previous works on the relationship between life-histories and self-fertilisation have found that perenniality may actually facilitate the evolution to high selfing rates due to lowered levels of inbreeding depression at later stages (Morgan, 2001). However, Morgan's (Morgan, 2001) model considered selection to occur on longevity, with each generation presenting the opportunity for less fit genotypes to be purged from the population. Though this is not an implausible definition of fitness, it does not take into account other possible components that can contribute to both mean fitness and inbreeding depression.

The concept of fitness is essential in any work determining how natural selection influences a population's genetic and demographic state. In very general terms, the consensus is that individual fitness is its ability not only to survive but also to reproduce in a given environment (Orr, 2009). In population genetics models, this remains true, though the exact definition of fitness may vary depending on how selection has been introduced (see Haldane, 1924, Chapter 7 of Roughgarden, 1979 and Parsons et al., 2010 for examples of how fitness was accounted for). The very widely used discrete models with non-overlapping generations make biological assumptions that cannot be universally applied and mainly represent annual plant populations (Nagylaki and Crow, 1974). In such models definitions of fitness i.e. survival or fecundity are interchangeable (Haldane, 1924; Bodmer, 1965). As individuals are present for only one generation this does indeed seem plausible (if an individual does not survive to reproduce or simply does not reproduce the outcome is the same), but what of populations that are not as compartmentalised as annual plants? Do different components have the same influence on population equilibria as in the discrete case?

When modelling perenniality, two approaches can be considered: discrete-time age-structured models (see Charlesworth, 1994) or continuous-time models (Fisher, 1930, Chapter 5.3 of Crow and Kimura, 1970, and Nagylaki and Crow, 1974). In the latter case, age-structure is of little importance if selection is considered to be age-independent as genic and genotypic frequencies in a population evolve towards time-persistent forms independently of the initial conditions considered (Vlad, 1988). The use of continuous-time models without age-structure provides a simpler alternative to modelling overlapping generations, there are however two main consequences: (1) The effect of age on reproductive capacity and survival is ignored and (2) Certain individuals can live for a very long time due to the variability of life-spans. How age influences

fecundity and survival is not clear-cut (see Baudisch, 2008), therefore considering age-independent selection is not wholly unrealistic.

Most continuous-time models stem from Fisher's Fundamental Theorem of Natural Selection (Fisher, 1930) wherein he introduced the notion of Malthusian fitness, defined as the growth rate. However, simultaneously introducing mutation, selection and non-random mating in such models can prove to be challenging and simpler models in continuous time seem to be lacking. For there to be demographic equilibrium, all genotypes must have the same Malthusian fitness, making it an inappropriate indicator of differences between genotypes in this scenario (Charlesworth, 1970). Other definitions of fitness are therefore to be preferred when examining population equilibrium, all the more so if they facilitate the comparison to definitions of fitness in discrete-time models.

Another aspect that is often ignored in conventional population genetics models is that of the demographic consequences of the genetic load. Works that have addressed the potential genotypic effects of deleterious mutations on population size have done so by considering density-dependent selection, usually with a trade-off between r- and K-selection (for example Charlesworth, 1971; Clarke, 1972; Roughgarden, 1979, but in Charlesworth, 1971 see section on density-independent selection). And in cases where mutations are unconditionally deleterious, the ecological and genetic aspects of the models were dissociated (Clarke, 1973; Agrawal and Whitlock, 2012, but see the extreme case of the mutational meltdown Lande, 1994; Lynch et al., 1995). By considering that the ecological and genetic properties vary independently, any potential feed-back between the two may be missed. That different components of fitness have different effects on population size has been suggested by different models (Clarke, 1973; Agrawal and Whitlock, 2012), but could the mating system further influence the consequences of selection on population demography?

Here we introduce a simple model in continuous time where both the demographic and genetic equilibria are emerging properties and not pre-defined parameters. We study how the rate of self-fertilisation, in interaction with different components of fitness, influences population size and the genetic properties of populations at mutation–selection balance. We compare our results to expectations from conventional population genetics models in discrete time so as to evaluate whether perenniality may play a role in the maintenance of outcrossing.

2. Model

We consider the evolution of a population with a varying population size and a single bi-allelic locus, where A is the wild type and a is a deleterious mutant allele influencing individual fitness. The population is made up of sexually reproducing hermaphrodite individuals, who self-fertilise at a fixed rate α (with $\alpha = 0$ being panmictic and $\alpha = 1$ strictly self-fertilising). The environment is stable, and the population is isolated and spatially unstructured. Three genotypes can be found in the population, aa, Aa and AA, which, from here onwards, are denoted X, Y, and Z respectively. At a given time t, the population is made up of three kinds of individuals, X_t, Y_t and Z_t representing the number of individuals carrying the respective genotype. We denote the population size $N_t = X_t + Y_t + Z_t$. In a large population setting, these quantities can be considered as continuous, and the evolution of the number of individuals of each genotype is described in continuous time using ordinary differential equations. Three processes affect the change in the number of individuals of each genotype, births (occurring with rate R_t^V, where V can be either X, Y or Z), deaths (at a rate M_t^V) and mutation. Selection and density dependence are introduced