

A new hypothesis to explain geographic parthenogenesis

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In many plants and animal species, asexuals are more common in marginal habitats such as high latitudes or altitudes than their closely related sexual counterparts. Here we propose a new hypothesis to explain this pattern called “geographic parthenogenesis”. In marginal habitats, populations may often exist as metapopulations with high degrees of subdivision and local extinction and recolonization, resulting in genetic bottlenecks during colonization. Our hypothesis states that such dynamics could play a key role in geographic parthenogenesis. Genetic bottlenecks and subsequent drift have stronger negative fitness consequences in sexuals than in asexuals because genetic drift leads to increased homozygosity and inbreeding depression in sexual but not in asexual populations. Migration, leading to inter-population hybridisation, may induce temporary fitness recovery in sexuals. Asexuals arising from such hybrids have an increased likelihood of invading sexual populations because they keep their high fitness, whereas the fitness of sexuals is doomed to decrease due to subsequent inbreeding and inbreeding depression. Therefore, asexuals may replace sexuals in subdivided habitats with local extinction and recolonization while they would not succeed in unstructured habitats without local turnover dynamics.

The pattern of geographic parthenogenesis and hypotheses for its explanation

Geographic parthenogenesis is the geographically distinct distribution of closely related sexual and asexual organisms (Vandel 1928). More specifically, it is well documented that asexual, or parthenogenetic, organisms occur more often at higher latitudes and altitudes, on islands or in island-like habitat, in xeric environments, and in environments variously classified as marginal,

extreme, stressful, transient, or disturbed (Cuelar 1977, Glesener & Tilman 1978, Bell 1982, Lynch 1984, Bierzychudek 1985, Suomalainen *et al.* 1987). The ecological correlates of asexual reproduction have received much attention because they may provide insights about the advantages and disadvantages of sexual reproduction (Bell 1982).

There are four main, non-exclusive classes of hypotheses to explain geographic parthenogenesis. Firstly, asexual organisms may be better able to colonize marginal habitat because they do

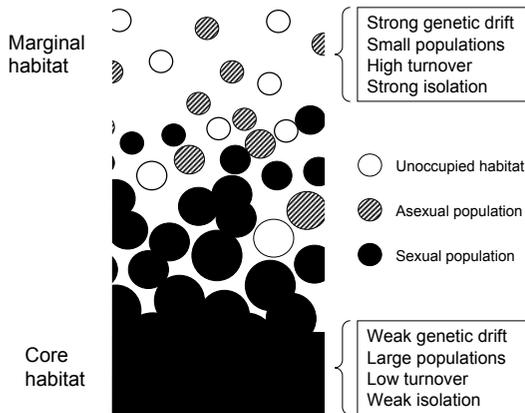


Fig. 1. Illustration of the hypothetical distribution of sexual and asexual populations in core habitats and marginal habitats. The black area and black circles indicate habitat patches occupied by sexual populations, dashed circles indicate habitat patches occupied by asexual populations, and unfilled circles indicate unoccupied habitat patches. The size of a patch indicates (potential) population size. When moving from core to marginal habitat genetic drift increases because the populations become smaller, more isolated, and have a high extinction-colonization dynamic (turnover).

not need to find a mate for reproduction: “reproductive assurance” (Baker 1955, Gerritsen 1980, Cuellar 1994). Secondly, sexual organisms living in marginal habitats may be permanently maladapted because of gene-flow from core-habitat, whereas any well-adapted asexual genotypes that may exist are isolated from non-adapted immigrants and can thus maintain adaptation (Antonovics 1968, Peck *et al.* 1998). Thirdly, sexual reproduction may be most advantageous in habitats that involve many biotic interactions because co-evolutionary arms races with parasites, predators, and competitors favour sexual reproduction (Jaenike 1978, Hamilton 1980, Lively *et al.* 1990). Asexuals, on the other hand, would occur more often in sparsely inhabited habitat, where these interactions are rare and where environmental factors are dominating (Levin 1975, Glesener & Tilman 1978, Hamilton *et al.* 1990). The fourth class of hypotheses states that asexual species may occupy a broader range of environments because of selection for generalist clones (Parker *et al.* 1977, Lynch 1984), because of their hybrid origin (Bulger & Schultz 1979), or because they have many differentially

adapted clonal “microspecies” (Roughgarden 1972, Vrijenhoek 1984).

The metapopulation hypothesis: A new hypothesis to explain geographic parthenogenesis

Here we suggest a further, non-exclusive hypothesis, which may contribute to explaining geographic parthenogenesis. Populations in marginal habitats may often exist as metapopulations with a high degree of population subdivision and frequent events of local extinction and recolonization (Fig. 1). Recolonization events will often lead to genetic bottlenecks, which may have stronger negative fitness consequences in sexual organisms than in asexual organisms. Genetic bottlenecks cause genetic drift in both sexual and asexual organisms, but the consequences of drift differ between them. In sexual organisms, genetic drift leads to increased identity by descent, causing inbreeding, which may reduce fitness (Charlesworth & Charlesworth 1987, Keller & Waller 2002). In asexual organisms, in contrast, drift does not lead to increased homozygosity because there is no mating and no segregation. Thus, due to metapopulation dynamics, genetic bottlenecks lead to inbreeding depression in sexual populations but not in asexuals.

To assess whether this process contributes to fitness differences between sexuals and asexuals, it is important to consider the origin of asexual clones. It is thought that most asexual clones repeatedly arise from sexual ancestors (Bell 1982, Simon *et al.* 2003) and that only a subset of all new clones are able to invade sexual populations (Innes *et al.* 2000). The successful asexual invaders may be those clones that arise from sexual ancestors with high fitness. In metapopulations, local sexual populations go through phases of extreme variation in fitness. Hybridisation with unrelated immigrants leads to temporary outcrossing and may cause a strong temporary increase in fitness (“heterosis”, Whitlock *et al.* 2000, Ebert *et al.* 2002, Saccheri & Brakefield 2002). Asexuals can be of high fitness if they originate from these occasional outbred sexuals. Unlike sexuals, which will decline in

fitness due to subsequent inbreeding when populations go through a new bottleneck, asexuals may retain their high fitness and may therefore be able to invade.

The fitness difference between sexuals and asexuals due to inbreeding may give asexuals an advantage at two levels of competition. First, high fitness asexual genotypes may invade inbred sexual populations and drive sexuals to local extinction. Second, asexual populations may produce more dispersing offspring than inbred sexual populations, and asexuals may therefore have an advantage in the recolonization of empty habitat patches, which are commonly found in marginal habitats. These two factors may explain why asexuals are more frequently found in subdivided habitats with local extinction and recolonization.

Our hypothesis makes two assumptions. First, it can only explain geographic parthenogenesis if populations in marginal habitats are subdivided and more likely to exist as metapopulations with increased levels of genetic drift than populations in core habitats. There are several reasons to believe that this may indeed be the case: marginal habitats may offer less favourable conditions, may be environmentally less predictable, and may be more patchily distributed than core habitats (Fig. 1). These factors may lead to increased probabilities of local extinction, and bottlenecks will then occur when recolonization takes place by a small number of individuals. The most extreme bottleneck is a single founder, as can be the case with hermaphroditic species. In contrast in core habitats, populations are usually large and stable and consequently have low extinction probabilities and experience much less genetic drift (Fig. 1).

The second assumption is that selection against deleterious mutations after a genetic bottleneck ("purging by drift", Glémin 2003) is inefficient. Because homozygosity exposes recessive or partially recessive mutations to selection, a genetic bottleneck can lead to increased selection against deleterious alleles in sexual populations. In sexual populations, a bottleneck may thus lead to an initial fitness decrease, but this decrease may be reversed by selection. In certain cases selection may lead to higher fitness than before the bottleneck (Kirkpatrick & Jarne 2000). If

purging is effective, the negative fitness consequences of genetic bottlenecks for sexual populations would thus be transitory. However, in many situations, purging is expected to be ineffective (Byers & Waller 1999, Wang *et al.* 1999, Wang 2000, Glémin 2003). First, many mutations seem to have only slightly deleterious effects (e.g., Willis 1999), and as long as the selection coefficient, s , is smaller than $1/2N$ (where N is the effective population size), drift affects the frequency of these alleles more strongly than selection. In other words, alleles with $s < 1/2N$ are virtually invisible for selection and are therefore not purged (Wright 1977). Second, if several deleterious alleles occur within the same genome, linkage between them may lead to selective interference among loci, an effect that increases with increasing homozygosity and renders selection less efficient (Hill & Robertson 1966). Third, genetic drift and, in particular, strong genetic bottlenecks, can lead to local fixation of deleterious alleles, and fixed alleles cannot be purged by selection (Lynch *et al.* 1995, Whitlock 2003). It thus seems that our second assumption of weak purging of the genetic load, applies particularly well to metapopulations, in which local effective population size is small, genetic bottlenecks during colonization are severe and migration is limited. However, because of these complicating effects of purging, and because drift also affects the fitness of asexual organisms through mutation accumulation (Muller 1964, Charlesworth & Charlesworth 1997), explicit mathematical modelling is necessary to identify the circumstances most favourable for our hypothesis.

A case in which geographic parthenogenesis may be a consequence of metapopulation structure is the European distribution of *Daphnia pulex*. In central Europe and southern Scandinavia *D. pulex* reproduces by cyclical parthenogenesis ("sexual") whereas populations in northern Scandinavia predominantly reproduce by obligate parthenogenesis ("asexual", Ward *et al.* 1994). Central European populations occur mostly in stable medium-sized ponds or small lakes (e.g., Michels *et al.* 2003), but in Scandinavia, the populations often occur in very small rock pools with frequent extinction and recolonization (e.g. Pajunen 1986, Bengtsson 1989, Pajunen & Pajunen 2003). In central Scandina-

via, where the distributions of sexual and asexual *D. pulex* overlap, the genetic population structure of sexual populations shows signs of frequent genetic bottlenecks, evidenced by strong genetic differentiation at short distances and by higher than expected variance in microsatellite allele sizes (Palsson 2000). For another sympatric *Daphnia* species (*D. magna*), living under the same unstable environmental conditions, genetic bottlenecks are due to a small number of colonizers and lead to high inbreeding depression and to hybrid vigour after hybridisation with unrelated immigrants (Ebert *et al.* 2002, Haag *et al.* 2002).

By focussing on population structure rather than on geographical correlates (e.g., latitude), our hypothesis has the potential to explain geographic distribution patterns of sexual and asexual organisms that have previously not been recognised as cases of geographic parthenogenesis. For instance, sexual populations of *Daphnia pulex* in North America seem to be encircled by asexual populations on a continent-wide scale rather than to follow a classical latitudinal pattern (Hebert & Finston 2001). Our hypothesis does not predict that the occurrence of parthenogens is causally linked to latitude, but rather to habitats in which populations are more likely to exist as metapopulations. Moreover, our hypothesis predicts that due to increasing habitat fragmentation by human activity, the advantage of asexual reproduction may become more and more widespread. This may be especially important because invasive species, which cause enormous economic costs, are often asexual (Baker 1974, Ellstrand & Schierenbeck 2000, Sakai *et al.* 2001). For instance, Niemelä and Matheson (1996) found that among introduced and successfully spreading forest insects in North America, parthenogenetic reproduction was four times more common than among natives.

Besides the prediction that asexuals should be more common in habitats with metapopulation dynamics, our hypothesis would be supported by the following observations. First, observed asexuals (i.e., asexuals that successfully invade sexual populations) should be more heterozygous than sexuals because they arise from inter-population hybrids. High heterozygosity is indeed commonly observed in asexuals (e.g., Innes *et al.* 1986, Ward *et al.* 1994, Del-

motte *et al.* 2002), although the reason for this is currently unclear. Second, sexual populations at the edge of their distribution should be more homozygous and consequently have a lower fitness than in central parts of their distribution. A lower fitness, measured by germination success in isolated as compared with central populations was indeed found in the plant *Silene alba* (Richards 2000). Third, sexual populations at the edge of their distribution should exhibit hybrid vigour as a consequence of inter-population crosses, that is, after immigration. These hybrid individuals should also have a fitness equal to or superior to asexuals. Fourth, sexual populations at the edge of their distribution should be characterized by low local genetic diversity and high genetic differentiation among populations because the distribution of genetic diversity is strongly affected by colonization bottlenecks. These observations apply mainly to the contact zones of sexuals and asexuals. Empirical support for these observations would be consistent with our hypothesis although they may also be consistent with other hypotheses for geographic parthenogenesis.

Our hypothesis does not deal with the evolution of sexual reproduction because it does not explain how the two-fold cost of sex can be overcome. Instead, it predicts that in marginal, subdivided habitats sexual reproduction has a particularly high cost due to inbreeding depression, and that this is why asexual organisms are more often found in such habitats. Several recent models for the evolution of sexual reproduction have considered the effect of population subdivision (Chasnov 2000, Agrawal & Chasnov 2001, Otto & Lenormand 2002). They found that in equilibrium conditions recessivity of deleterious mutations and population structure favour sexual reproduction because sexual reproduction leads to more efficient purging. As discussed before, our hypothesis applies only to situations in which purging is ineffective. It is possible that moderate population structure with large demes prevents asexuals from invading because purging allows sexuals to keep a high fitness. Asexuals may, however, invade highly subdivided metapopulations with local extinction and recolonization, because in these situations purging is inefficient and sexual reproduction leads to inbreeding depression.

Another hypothesis states that sexual populations are more likely to be found in more variable environments, where the extinction rates of asexual populations are relatively high because asexual clones can exploit a smaller spectrum of resources than genetically diverse sexual populations (“demographic balance hypothesis”, Getz 2001). However, the simulations which supported this hypothesis assumed large populations, in which genetic drift is relatively unimportant. These conditions therefore apply again more to metapopulations with large demes rather than to the highly subdivided metapopulations with a strong impact of genetic drift envisaged here.

Our hypothesis does not oppose the idea that asexual clones are relatively short lived (thousands rather than millions of years, Bell 1982). Even though asexuals may initially be favoured in metapopulations, their fitness may in the long term fall below that of the sexuals because of mutation accumulation (Peck *et al.* 1999). But if new high-fitness clones repeatedly arise from outbred (inter-population hybrid) sexual ancestors, the mechanisms described here may lead to asexuals being more common in marginal habitat with metapopulation dynamics and sexuals being more common in core habitat without metapopulation dynamics.

In conclusion, our hypothesis states that asexual organisms should more often occur in habitats in which populations exist as metapopulations because genetic drift caused by bottlenecks during colonization has different consequences for the fitness of sexual and asexual organisms. Our hypothesis does not exclude other factors like reproductive assurance or gene-flow from core habitat to contribute to geographic parthenogenesis. However, the new aspect is that we identified consequences of metapopulation dynamics, which to our knowledge have not been included in previous ideas on the evolution of geographic parthenogenesis.

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