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Geographic parthenogenesis in a consumer-resource model for sexual reproduction

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ABSTRACT

The phenomenon of geographic parthenogenesis is closely tied to the question of why sexual reproduction is the dominant mode of reproduction in animals and plants. Geographic parthenogenesis describes the fact that many species reproduce asexually at the boundaries of their range. We present a mathematical model that derives the dominance of sexuals at the center and the dominance of asexuals at the boundary of a species' range from exactly the same mechanism. Our model is based on a set of resources that regrow slowly and that can be consumed only by those individuals that have a suitable genotype. Genotype is implemented by a multilocus model with two alleles at each locus, and with free recombination during production of sexual offspring. The model is tailored to seasonal species with intermittent mixis and low survival of offspring, such as *Daphnia* and aphids. Several patches of resources are arranged in a row, with a gradient of those parameters that typically vary through the range of species. By letting sexually and asexually reproducing populations compete, we obtain the typical patterns of geographic parthenogenesis.

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1. Introduction

Any theory that aims at explaining why sexual reproduction prevails in most organisms, must be in agreement with the general patterns of parthenogenesis, in particular geographic parthenogenesis. Geographic parthenogenesis describes the fact that many species reproduce asexually at the boundaries of their range, i.e. in northern regions, at high elevations, or at the transition to deserts, while they reproduce sexually closer to the center of their range (Vandel, 1928; Glesener and Tilman, 1978; Bell, 1982; Hebert et al., 1988). For both phenomena, sexual reproduction and geographic parthenogenesis, exist a variety of explanations and models, however, these cannot easily be linked.

Theories for sexual reproduction argue that it can purge the genome more efficiently from deleterious mutations under the appropriate conditions (Muller, 1932; Charlesworth and Charlesworth, 1987; Morran et al., 2009), and that it facilitates adaptation to a novel environment when sex leads to an increased variance in fitness (Morran et al., 2009). A variation of the latter hypothesis, when the environment of a species is dominated by the negative influence of another species, is the Red Queen hypothesis (Van Valen, 1973; Hamilton, 1980; Lively and Dybdahl, 2000; Lively, 2009). Furthermore, sex can restore genetic combinations

that become lost due to drift but that are favored in temporally or spatially fluctuating environments (Otto and Lenormand, 2002). In particular, environmental heterogeneity facilitates sexual reproduction, as stated in the Tangled Bank hypothesis (Bell, 1982), and as confirmed by a recent experimental study (Becks and Agrawal, 2010). Natural environments are usually heterogeneous, as demonstrated by experiments that show that genetically diverse populations can better exploit resources than genetically homogeneous populations (Doncaster et al., 2000). Generally, it is increasingly recognized that genetic diversity affects the performance of communities in various ways including e.g., competition for resources and community productivity (Hughes et al., 2008).

Theories for geographic parthenogenesis propose that parthenogenesis is a side effect of hybridization in boundary regions (Kearney, 2005) or of selection for polyploidy (Otto and Whitton, 2000). Other authors emphasize that asexuals are capable of colonizing new habitats faster (Cuellar, 1977; Law and Crespi, 2002) or that asexual reproduction arises whenever environmental changes may have provided opportunities for shifts to asexuality (Hörandl, 2009). In the only spatially extended mathematical model for geographic parthenogenesis that exists so far, Peck et al. (1998), showed explicitly that a sufficiently strong source-sink effect (Dias, 1996) can lead to a dominance of parthenogenetic reproduction in boundary regions, because sexual cannot establish the phenotype that is optimal for this region. In this model, asexuals are assigned a lower fitness than sexuals, given the same degree of adaptation to their environment, which changes along the spatial gradient. The fitness of the sexuals in the boundary

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region is even lower than that of the asexuals because of the inflow of maladapted genotypes due to migration. The immigrating sexual individuals mate with the local sexual population and thus prevent it from becoming adapted to the local environment. In contrast, the local asexual genotypes can be perfectly adapted to the environment. An alternative scenario is envisaged by Gaggiotti (1994) who has pointed out that geographic parthenogenesis could occur as an equilibrium phenomenon if parthenogenetic reproduction was selectively favored against sexual reproduction in the boundary regions, while sexual reproduction was favored elsewhere.

In this paper, we pursue the latter idea that the mode of reproduction prevailing at a certain location should be the one that has a selective advantage at this location. This idea has been most forcefully put forward by Bell (1982) in his book “The masterpiece of nature”, and it is justified by the observation that many organisms have the ability to switch between different modes of reproduction. In particular, situations of crowding and starvation elicit sexuality in organisms that reproduce asexually at other times. Because of this observation, we assume furthermore that resource availability is the main determinant of the fitness of an individual. Indeed, Glesener and Tilman (1978), citing the book of Chiselin (1974), pointed out that the depletion of resources favors those individuals that switch to a currently underutilized resource. Thus, sexual reproduction should be favored in heterogeneous environments with a broad spectrum of resources that have a limited availability, while parthenogenetic reproduction should prevail where the resource limitation is not important or affects both modes of reproduction in the same way, as is the case in new habitats or in habitats with high mortality or small resource richness. This is the essence of the argument put forward in Bell (1982).

However, older mathematical implementations of the tangled bank hypothesis (Case and Taper, 1986) that include a broad spectrum of resources, while leading to the persistence of sexual reproduction despite the twofold cost of males, result in the coexistence of both modes of reproduction and can neither tolerate a continuous creation of new asexual clones nor do they lead to the phenomenon of geographic parthenogenesis. The tangled bank hypothesis was also rejected due to the lack of empirical evidence. When interpreted as predicting a greater advantage to sexual reproduction when numbers of offspring and thus sib competition are larger, it does not agree with empirical investigations (Ellstrand and Antonovics, 1985; Kelley, 1989). Burt and Bell (1987) rejected the tangled bank hypothesis on similar grounds, as mammal species that have more offspring do not have increased rates of recombination. However, these arguments have been questioned by other authors (Charlesworth, 1987; Koella, 1987; Greenwood, 1987).

A different approach to the mathematical modeling of ideas related to the tangled bank hypothesis was taken by Scheu and Drossel (2007), where the number of locally coexisting genotypes was limited and drift was assigned an important role. The model is tailored to r -strategists with intermittent mixis and includes explicitly the interaction of the consumers with their resources. Resources are structured, and one consumer genotype therefore can only exploit a small part of the resources. Similar to older tangled bank models, it relies on quantitative genetics with a fixed genetic variance of sexuals. Slow regrowth of resources combined with stochastic effects due to restrictions on the number of locally coexisting genotypes, leads to the prevalence of sexual reproduction in spite of the cost of producing males. Interestingly, in this model the advantage of sexual reproduction does not increase with increasing density, since this would decrease the stochastic effects due to different resources being exploited at different times. The mentioned results hold for a wide range of parameters (Scheu and Drossel, 2007; Ament et al., 2008). However, with increasing

mortality or decreasing resource richness, the dominant mode of reproduction becomes asexual. This finding suggests that the model can also be used to generate a scenario that shows geographic parthenogenesis.

In the following, we will investigate a modified model that differs in two respects from the one by Scheu and Drossel (2007). First, instead of using quantitative genetics, the modified model is genetically explicit and uses several diallelic loci with free recombination. This feature permits to study the effect of recombination on the genetic diversity of the population, which was not possible in the quantitative genetic model. Second, the modified model includes a spatial dimension, in order to generate a setup that can show geographic parthenogenesis. By arranging patches of resources along a habitat that stretches from regions of low consumer mortality to regions of high consumer mortality or from regions of large resource richness to regions of small resource richness, we will find a pattern resembling the phenomenon of geographic parthenogenesis. The model thus shows that the dominance of sexuals at the center and the dominance of asexuals at the boundary of a species' range can be caused by exactly the same mechanism.

In the next section, we will define the rules of the model in more detail. In the following two sections, we will present the results of computer simulations and explain how they follow from the rules of the model. We conclude this paper by placing the results in a wider context.

2. The model

Twenty resource patches are arranged along an one-dimensional chain. A gradient of up to three patch features (specified below) reflects the change in habitat properties from the center (patch 1) to the boundary (patch 20) of a species' range. Each patch contains up to $L=256$ different “resources”, which are labeled by binary numbers from 0 to 255, and which we will also name “niches” in the following. Consumers are characterized by their mode of reproduction and by their genotype, which for simplicity is denoted by the same numbers as the resources. The genotype of the consumers is represented by a set of eight diallelic loci. When the two alleles at each locus are labeled 0 and 1, the genotype can be represented by a binary number with 8 bits. A consumer is best adapted to the resource the label of which matches its genotype. This method of implementing a genotype and matching it with resources is similar to the one chosen by Gavrillets and Vose (2005). The resources in this model do not necessarily represent different species, but the different possible ways in which consumers can specialize on resources that differ in some respect. The eight degrees of freedom can thus represent different location (humid, less humid, more or less shady), different manifestation (producing certain defenses or not, having a harder surface), or different parts (upper or lower leaves) and so on of the same type of resource. Due to different search patterns, different digestive abilities, different morphological features, etc., different individuals exploit resources in different ways. Indeed, experiments show that genetically diverse populations can better exploit resources than genetically homogeneous populations (Doncaster et al., 2000). Svanbäck and Bolnick (2005) argue that individuals that differ in their ability to find, handle or digest alternative resources may have different diets.

The model is initiated with a maximum resource biomass $R_j=R_{\max}=100$ for each resource, and with some niches being occupied by sexual or asexual individuals. The life cycle of the consumers is tailored to that of species with intermittent mixes such as *Daphne* (Bell, 1982; Hebert et al., 1988). Thus, the biomass P_i of consumer number i , which is best adapted to the niche i increases

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