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## Geographic parthenogenesis in a consumer-resource model for sexual reproduction

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### Abstract

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

*Key words:* Asexual reproduction, Migration, Resource limitation, Spatial modeling,  
Structured resources

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## 14 1. Introduction

16 Any theory that aims at explaining why sexual reproduction prevails in most organisms, must  
18 be in agreement with the general patterns of parthenogenesis, in particular geographic partheno-  
20 genesis. Geographic parthenogenesis describes the fact that many species reproduce asexually  
22 at the boundaries of their range, i.e. in northern regions, at high elevations, or at the transition to  
24 deserts, while they reproduce sexually closer to the center of their range [46, 16, 4, 20]. For both  
26 phenomena, sexual reproduction and geographic parthenogenesis, exist a variety of explanations  
28 and models, however, these cannot easily be linked.

22 Theories for sexual reproduction argue that it can purge the genome more efficiently from  
24 deleterious mutations under the appropriate conditions [36, 8, 35], and that it facilitates adapta-  
26 tion to a novel environment when sex leads to an increased variance in fitness [35]. A variation  
28 of the latter hypothesis, when the environment of a species is dominated by the negative influ-  
30 ence of another species, is the Red Queen hypothesis [45, 19, 31, 33]. Furthermore, sex can  
32 restore genetic combinations that become lost due to drift but that are favored in temporally  
34 or spatially fluctuating environments [38]. In particular, environmental heterogeneity facilitates  
sexual reproduction, as stated in the Tangled Bank hypothesis [4], and as confirmed by a re-  
cent experimental study [3]. Natural environments are usually heterogeneous, as demonstrated  
by experiments that show that genetically diverse populations can better exploit resources than  
genetically homogeneous populations [11]. 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 [23].

36 Theories for geographic parthenogenesis propose that parthenogenesis is a side effect of hy-  
38 bridization in boundary regions [26] or of selection for polyploidy [37]. Other authors emphasize  
40 that asexuals are capable of colonizing new habitats faster [9, 30] or that asexual reproduction  
42 arises whenever environmental changes may have provided opportunities for shifts to asexuality  
44 [21]. In the only spatially extended mathematical model for geographic parthenogenesis that  
46 exists so far, Peck(1998) [40], showed explicitly that a sufficiently strong source-sink effect [10]  
48 can lead to a dominance of parthenogenetic reproduction in boundary regions, because sexuals  
50 cannot establish the phenotype that is optimal for this region. In this model, asexuals are as-  
signed 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 region is  
even lower than that of the asexuals because of the inflow of maladapted genotypes due to migra-  
tion. 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)  
[13] who has pointed out that geographic parthenogenesis could occur as an equilibrium phe-  
nomenon if parthenogenetic reproduction was selectively favored against sexual reproduction in  
the boundary regions, while sexual reproduction was favored elsewhere.

52 In this paper, we pursue the latter idea that the mode of reproduction prevailing at a certain  
54 location should be the one that has a selective advantage at this location. This idea has been  
56 most forcefully put forward by Bell(1982) [4] in his book “The masterpiece of nature”, and it  
is justified by the observation that many organisms have the ability to switch between differ-  
ent 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  
58 furthermore that resource availability is the main determinant of the fitness of an individual. In-  
deed, Glesener(1978) [16], citing the book of Ghiselin(1974) [15], pointed out that the depletion

60 of resources favors those individuals that switch to a currently underutilized resource. Thus,  
62 sexual reproduction should be favored in heterogeneous environments with a broad spectrum  
64 of resources that have a limited availability, while parthenogenetic reproduction should prevail  
66 where the resource limitation is not important or affects both modes of reproduction in the same  
68 way, as is the case in new habitats or in habitats with high mortality or small resource richness.  
70 This is the essence of the argument put forward in Bell(1982) [4].

72 However, older mathematical implementations of the tangled bank hypothesis [6] that in-  
74 clude a broad spectrum of resources, while leading to the persistence of sexual reproduction  
76 despite the twofold cost of males, result in the coexistence of both modes of reproduction and  
78 can neither tolerate a continuous creation of new asexual clones, nor do they lead to the phe-  
80 nomenon of geographic parthenogenesis. The tangled bank hypothesis was also rejected due to  
82 the lack of empirical evidence. When interpreted as predicting a greater advantage to sexual re-  
84 production when numbers of offspring and thus sib competition are larger, it does not agree with  
86 empirical investigations [12, 27]. Burt & Bell(1987) [5] rejected the tangled bank hypothesis  
88 on similar grounds, as mammal species that have more offspring do not have increased rates of  
90 recombination. However, these arguments have been questioned by other authors [7, 28, 18].

92 A different approach to the mathematical modelling of ideas related to the tangled bank  
94 hypothesis was taken by Scheu & Drossel(2007) [42], where the number of locally coexisting  
96 genotypes was limited and drift was assigned an important role. The model is tailored to  $r$ -  
98 strategists with intermittent mixis and includes explicitly the interaction of the consumers with  
100 their resources. Resources are structured, and one consumer genotype therefore can only exploit  
102 a small part of the resources. Similar to older tangled bank models, it relies on quantitative  
104 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 [42, 1]. 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 & Drossel(2007) [42]. 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 di-  
mension, 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 partheno-  
genesis. 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

106 Twenty resource patches are arranged along a one-dimensional chain. A gradient of up to  
 108 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  $L = 256$  dif-  
 110 ferent "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  
 112 genotype of the consumers is represented by a set of 8 diallelic loci. When the two alleles at each  
 locus are labelled 0 and 1, the genotype can be represented by a binary number with 8 bits. A  
 114 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 Gavrilets  
 116 (2005) [14]. 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 re-  
 118 spect. 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  
 120 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., dif-  
 122 ferent individuals exploit resources in different ways. Indeed, experiments show that genetically  
 diverse populations can better exploit resources than genetically homogeneous populations [11].  
 124 Svanbäck and Bolnick (2005) [44] 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 *Daphnia* [4, 20]. Thus,  
 the biomass  $P_i$  of consumer number  $i$ , which is best adapted to the niche  $i$  increases from the  
 initial value  $P_i = 1$  by parthenogenetic reproduction during the season according to the equation

$$\dot{P}_i = \lambda \sum_{j=1}^L \alpha_{ij} P_i R_j - d P_i, \quad (1)$$

while the resource biomass decreases according to

$$\dot{R}_j = - \sum_i \alpha_{ij} P_i R_j, \quad (2)$$

126 where the sum is taken over all consumers in the same patch. The ecological efficiency  $\lambda$  was  
 chosen to be 0.2 [43]. The coupling strength  $\alpha_{ij}$  between consumer and resource was set equal  
 128 to 1 for  $i = j$  and equal  $e^{-k}$  (with  $k$  being 0, 0.5 or 1) when  $i$  and  $j$  differ in one bit. Otherwise  
 it was set to zero. In most of the simulations reported below, we used  $k = 0$ , which means that  
 130 each consumer uses with equal efficiency all 9 resources available to it.

In order to mimic increasing harshness of the environment as the patch index increases from  
 132 center to the boundary of a species' range, we let the death rate  $d$  increase linearly with increasing  
 patch index, or we let the number of resources  $L$  decrease linearly. Variation in the number of  
 134 resources was implemented such that the resources with the largest labels were removed.

Population dynamics (1) is applied for each consumer until  $\dot{P}_i$  becomes zero, when the con-  
 sumer stops feeding and growing. After all consumers have stopped growing, the season is ended.

We assume that sexual individuals mate at random within the patch, where there is an equal number of males and females, and all females lay the same large number of eggs per biomass. Thus the number of eggs per parent biomass laid by asexuals is twice as large as that of sexuals. The precise number of eggs per female is irrelevant for the following, since the number of eggs that give rise to a surviving individual is small and independent of the total egg number. Next, the starting configuration for the next season is calculated: Resources regrow partially according to the equation

$$\Delta R_j = G(1 - R_j/R_{\max}) = \frac{G}{R_{\max}} \underbrace{(R_{\max} - R_j)}_{R_j^{\text{consumed}}}, \quad (3)$$

with the regrowth percentage  $G \leq R_{\max}$ , which can vary between patches. The number of consumer individuals in each patch at the beginning of a new season is chosen from a Poisson distribution with mean value  $n$ . Each egg is chosen with the same probability to give rise to such a surviving individual. Therefore, the mode of reproduction of each individual at the beginning of the new season is sexual with probability

$$p_s = \frac{\sum_{i \text{ sex.}} P_i}{\sum_{i \text{ sex.}} P_i + 2 \sum_{i \text{ parthenog.}} P_i}, \quad (4)$$

and parthenogenetic with probability  $1 - p_s$ , with the  $P_i$  being the biomasses at the end of the previous season. The factor 2 in the denominator takes into account the twofold cost of sex, due to half of the sexual individuals being male. The genotype of a parthenogenetic individual is randomly chosen among the genotypes of parthenogens present at the end of the previous season, with weights proportional to their final biomass, and with each bit of the genotype being mutated with a small probability  $\mu$ . The genotype of a sexual individual is determined by randomly choosing two sexual parent genotypes with probabilities proportional to their biomass at the end of the previous season, and by generating the offspring by free recombination at every locus. Just as for asexual offspring, each bit of the genotype is then mutated with a small probability  $\mu$ . Finally, with a small probability  $u = 0.001$ , the offspring of sexual individuals becomes parthenogenetic, implementing the 'frozen niche variation hypothesis' of Vrijenhoek(1979) [47], which is based on the fact that parthenogenetic lineages can arise in sexual populations.

Before onset of resource consumption, each individual is allowed to migrate to each neighboring patch with a migration probability  $\eta$ . Alternatively, we also implemented the case of egg dispersal, where "migration" occurs before selection of the surviving eggs.

We iterated this process for 200 seasons and averaged the resulting final proportion of sexuals in each patch over 1000 runs of the computer simulation.

### 152 3. Results

154 Fig. 1 shows the average proportion of sexuals in each patch that was obtained after 200 seasons, when an equilibrium had been reached. In the first graph (Fig. 1A), the death rate  $d$  was increased with increasing patch index, varying in total by a factor of 3.5; in the second graph (Fig. 1B) the number of different resources,  $L$ , was decreased from 256 to 66 with increasing patch index, in the third (Fig. 1C) and fourth graph (Fig. 1D) the percentage  $G$  of consumed resource biomass that regrows between subsequent seasons was decreased from 40 to 11.5, together with a change in  $d$  or  $L$ . In each of the four cases, the proportion of sexuals decreases

160 from (almost) 100% to (almost) 0% with increasing patch index, i.e., with increasing harshness  
162 of the environment. The model thus reproduces the phenomenon of geographic parthenogenesis.

162 These results are independent of the initial distribution of genotypes and modes of reproduc-  
164 tion. We obtained the same graphs when we tested the following four initial situations: (a) 25  
164 asexual and 25 sexual genotypes in random niches in each patch, (b) 50 sexual genotypes and no  
166 asexuals in random niches in each patch, (c) 25 sexual and 25 asexual genotypes in random niches  
166 in the first patch, with all other patches being empty, (d) 50 sexual genotypes in random niches  
168 in the first patch, with all other patches being empty. The first case imposes no bias towards one  
168 mode of reproduction, the second case shows the long-term effect of the rare production of asex-  
168 ual clones within sexual populations, the third and fourth case simulate the colonization of a new  
170 habitat by a population that initially displays either both modes of reproduction or reproduces  
170 only sexually.

172 The pattern of geographic parthenogenesis is robust against changes in other ecological fac-  
172 tors, which are investigated in the following.

174 Fig. 2 shows the influence of the migration rate  $\eta$  and of the mutation rate per locus  $\mu$ . The  
174 advantage of sexuals increases at first with increasing migration rate (Fig. 2A), because new  
176 genetic variance is brought in from neighboring patches, thus preventing a decline of genetic  
176 variance of the local sexual populations. When the migration rate becomes even larger, the  
178 proportion of sexuals decreases more and more, because the asexual genotypes can be present  
178 in several patches at the same time, which decreases their extinction rate and enables them to  
180 benefit from the twofold cost per season incurred by the sexuals. We also investigated the case  
180 where migration happens before determining the genotypes of the individuals at the beginning  
182 of a new season (which can be interpreted as egg dispersal). The curves changed only little with  
182 this modification. In Fig. 2B,  $\mu$  is increased from the first to the last patch reflecting the fact  
184 that stressful environment can elicit a high mutation rate [17, 2]. In this case, the proportion  
184 of sexuals decreases from (almost) 100% to (almost) 0% with increasing patch index, i.e., with  
186 increasing environmental stress.

186 A decrease of the regrowth percentage  $G$  without a simultaneous increase in the death rate or  
188 decrease in the number of the different resources, leads to an increase in the percentage of sexuals  
188 instead of a decrease. A large value of  $G$  favors parthenogenetic reproduction, since there is no  
190 advantage of exploring new niches when resources grow very fast. A change of  $n$  (either between  
190 patches or overall) does not change qualitatively our results, as long as  $n$  is considerably smaller  
192 than  $L$  even at the center, i.e., as long as there are enough unexploited niches that can be used by  
192 sexual offspring, and as long as  $n$  is large enough to support a significant genetic variance.

194 We also investigated the effect of a different coupling strength to neighboring resources.  
194 For  $k = 0.5$  or  $1$ , the parameter region where sexual reproduction dominates becomes different  
196 (because a larger  $k$  has a similar effect to a larger  $d$  (Eq. 1)), but geographic parthenogenesis  
196 is also observed. When the number of resources on which a genotype can feed is extended to  
198 a larger neighborhood, there is no longer any advantage to sexual reproduction, because there  
198 are no unexploited resources left even for smaller values of  $n$ . We also varied the number of  
200 loci. When we performed our simulations with 9 loci and up to  $L = 512$  different resources, the  
200 parameter interval where sexual reproduction dominates became larger. With 5 or less loci, we  
202 could not obtain a proportion of sexuals close to 1, because the advantage to sexuals of having a  
202 larger genetic variance is not strong enough. With 7 loci, we could obtain results similar to those  
204 with 8 loci only with sufficiently large  $k$ , i.e. when an individual could not feed on neighboring  
204 resources. With smaller  $k$ , each genotype would be able to exploit 8 resources, which is roughly  
206 1/11 of all resources. In order to have unused resources that could be exploited by the sexual



208 offspring, the population size would have to be very small - and then the genetic variance would  
be lost so quickly that sexuals have no advantage. With 6 loci, the parameter range for which we  
found a dominance of sexual reproduction was much smaller.

#### 210 4. Analysis

In order to understand the simulation results in greater depth, let us first consider the case of  
212 a single patch (or, equivalently, a set of isolated patches). Due to the twofold cost of producing  
males incurred once per season, sexuals can only have an advantage when there is sufficient ge-  
214 netic variance in the patch so that offspring can be generated that are capable of exploiting unused  
resources. We therefore evaluate in the following the genetic variance of sexuals and asexuals  
216 under different conditions. If there was no selection, the genetic variance would be independent  
at each locus and fully determined by drift. With a population size of  $n$  and an initial frequency  
218 of 50 percent of each of the two alleles, the probability of not having lost one of the two alleles  
after  $g$  seasons can be estimated to be roughly of the order  $e^{-g/n}$  (since the number of individuals  
220 with a given allele changes per generation by the order of  $\sqrt{n}/2$ , and since the number of random  
steps of this size required to cover the distance  $n/2$  is of the order of  $n$ ). One can therefore expect  
222 the number of loci with two alleles to become very small within 100 seasons. This is indeed  
the case, as shown in Fig. 3. Without mutations, the genetic variance eventually declines to zero  
224 (Fig. 3A). We performed the simulation once for a purely sexual population and once for a purely  
asexual population, without taking into account selection, i.e., with each individual having the  
226 same chance of being the parent of a child in the next season. While the number of diallelic loci  
behaves exactly in the same way in both cases, the number of genotypes is considerably larger  
228 for the sexuals, due to recombination. When the mutation rate is nonzero (Fig. 3B), the genetic  
variance reaches a nonzero stationary value. As long as the mutation rate is small, the sexuals  
230 have a clear advantage over the asexuals in terms of genetic variance. A single mutation in a  
sexual individual at a locus that has lost one of the two alleles can generate many new genotypes  
232 through recombination with all the other genotypes. In contrast, a mutation in an asexual individ-  
ual generates only one new genotype. If the mutation rate is higher, this advantage of the sexuals  
234 becomes smaller. Fig. 3B shows the result obtained with  $\mu = 0.016$ , where the number of sexual  
genotypes is less than twice the number of asexual genotypes, which means that the two-fold  
236 cost of sex cannot be compensated (remember that this simulation was performed without taking  
into account differences in resource availability). Therefore, the patches with high mutation rate  
238  $\mu$  are dominated by parthenogenetic reproduction (Fig. 2B). When resource dynamics are taken  
into account, rare alleles will in fact have a considerable advantage in sexual species due to being  
240 able of exploiting unused resources. The loss of an allele becomes therefore less likely. This is  
shown in Fig. 4A and Fig. 4B for a zero and a nonzero mutation rate, respectively. A comparison  
242 with Fig. 3 demonstrates a large difference between sexuals and asexuals: Even without muta-  
tion, the sexuals usually lose none of their alleles, because rare alleles can recombine with other  
244 genotypes to exploit underutilized resources. Mutation does not confer an additional advantage.  
In contrast, the number of asexual genotypes depends strongly on the mutation rate. Neverthe-  
246 less, just as for the sexuals, resource dynamics prevents the loss of rare alleles. The reason is that  
asexual lineages that had plenty of food in the previous season and lay many eggs, produce off-  
248 spring that feed all on the same (limited) resource in the present season. At the end of the season,  
the number of individuals of this genotype will be approximately the same as when there initially  
250 had only been one individual, meaning that additional individuals of the same genotype at the  
beginning of the season do not lead to a larger number of individuals at the end of the season. The

252 total number of asexual genotypes decreases in the absence of mutations to a single-digit number  
253 because genotypes with overlapping resources have a disadvantage compared to those without  
254 resource overlap, and the number of different genotypes declines until the remaining individuals  
have (almost) no overlap.

256 Finally, we evaluated the number of loci  $N_{di}$  for which both alleles are present in the popula-  
257 tion, and the number of different genotypes  $N_{ge}$  for the full model, for the simulation parameters  
258 of Fig. 2A. The results are shown in Fig. 5. One can see that the sexuals quickly lose their genetic  
259 variance in patch number 20, where death rate is high, and where asexuals have the advantage of  
260 having more offspring. On the other hand, the sexuals can maintain their genetic variance in the  
261 first patch, where they succeed at producing more offspring than the asexuals, due to being capa-  
262 ble of utilizing more resources. In both cases, the winning mode of reproduction can already be  
263 identified during the first few season, due to the rapid decline of the other mode of reproduction.  
264 This means that in the central patches sexual reproduction is not only a long-term advantage, but  
also a short-term advantage.

266 One can also see that migration can further increase the genetic variance of sexuals as long as  
267 the migration rate is not too large. Interestingly, over the entire set of patches, almost all alleles  
268 are present irrespective of the mode of reproduction ( $N_{di}$  in Fig. 5C). This proves once again that  
structured resources prevent the decline of genetic variance in general, by preferring rare alleles.

## 270 5. Conclusions

271 In this paper, we have modified and extended a mathematical model for sexual reproduction  
272 that is based on a broad spectrum of limited resources that regrow slowly [42], in order to ob-  
273 tain the phenomenon of geographic parthenogenesis. In this model, the number of genotypes  
274 that can coexist at the same place is limited, thus providing an advantage to sexuals whenever  
275 the offspring can acquire a genotype that enables it to exploit unused resources. In contrast to  
276 the original model [42], which was based on quantitative genetics, we now used a genetically  
277 explicit model. This permitted us to generate sexual offspring via recombination, and to evaluate  
278 explicitly the number of different alleles present in the populations. The two different imple-  
279 mentations used in the two models, represent two limiting cases: The quantitative genetic model  
280 includes only two parameters to specify a resource and a genotype, both of which are continuous  
281 and Gaussian distributed with a constant genetic variance, which implies that they result from  
282 the superposition of the effects of many genes that contribute additively to it. The genetically  
283 explicit model uses eight parameters to specify a resource and a genotype, with each parameter  
284 taking only two values. Both genetic implementations lead to a prevalence of sexual reproduction  
285 when there is a sufficient amount of unexploited resources and when the ability to exploit these  
286 resources leads to an increase in the number of offspring. This demonstrates that the outcome  
287 of the model is sufficiently generic and does not rely on the precise way in which genetics is  
288 implemented. If only the following three requirements are met, sexual reproduction can prevail  
289 over a wide parameter range: (i) the number of locally coexisting genotypes is so small that they  
290 can use only part of the resources with good efficiency. (ii) Sexual parents can have offspring that  
291 can efficiently use resources that their parents could not efficiently use. (iii) Resources regrow  
292 slowly.

293 One can imagine various other variants of the model that satisfy these requirements when  
294 parameter values are chosen in an appropriate range. For instance, we performed simulations of  
295 a genetically explicit version of the quantitative genetic model, where each trait value resulted  
296 from the addition of the values at 20 diallelic loci. This version of the model displays similar

298 results when there is a sufficiently large number of patches that are coupled by migration, so that  
alleles do not get lost too quickly. We also performed simulations with a fourth version of the  
300 model: Instead of letting each individual feed on the resource(s) it is best adapted to, we placed  
each individual directly into a niche, where it could feed with an efficiency that depends on the  
302 extent of agreement between the trait value of the individual and the niche value. This version  
of the model permits using much larger population sizes, since only part of the individuals feed  
with maximum efficiency; again it displays the prevalence of sexual reproduction.

304 In the present paper, we have extended our previous model [42] such that it is composed  
of several patches, which are arranged as a one-dimensional chain extending from the center  
306 to the boundary of a species' range, with migration between neighboring patches, and with a  
spatial gradient of those parameters that may vary as the environment becomes harsher towards  
308 the boundary. Parameters were chosen such that sexual reproduction would prevail at the center  
and that asexual reproduction would prevail at the boundary if there was no migration. Our  
310 simulations have shown that the spatially extended system with migration reaches an equilibrium  
distribution of sexual and asexual individuals such that no asexuals are at the center and no  
312 sexuals are at the boundary, as long as the migration is not too large. While we have demonstrated  
this pattern of geographic parthenogenesis by using the genetically explicit model, it occurs  
314 also for the quantitative genetic model and the other modifications mentioned in the previous  
paragraph, when patches are arranged in a similar way. We have thus found a class of models  
316 that can produce the phenomenon of sexual reproduction and the phenomenon of geographic  
parthenogenesis by exactly the same mechanisms.

318 The finding that mortality has a strong influence on the reproductive mode is in agreement  
with the observation that asexual organisms are more frequent in transient, ecotonal, disturbed  
320 or marginal environments, like deserts [25], which are associated with high mortality.

322 We have explained the results of the computer simulations by considering the genetic vari-  
ance of the sexuals as function of the parameters. Whenever recombination, mutation and mi-  
324 gration together allow for many more sexual than asexual genotypes, sexual reproduction wins  
over parthenogenetic reproduction when resources are scarce, despite the twofold cost of males  
that sexuals incur once per season.

326 The model used in this paper, of course, is only a simplified description of sexual reproduc-  
tion in a spatially inhomogeneous environment. In the simulations, we used 20 patches with up  
328 to 256 different resources each, and the consumers were represented by a genotype of 8 bits and  
an average population size of 50, which can barely capture the extent and importance of overall  
330 spatial variation and local restriction of resources and consumer genotypes. Nevertheless, the  
model demonstrates nicely the advantage of sexual reproduction wherever it enables consumers  
332 to exploit the resources more efficiently, and the transition to parthenogenesis wherever there is  
no advantage of consumers switching to other resources.

334 Other theories for the evolution of sex cannot easily be extended to generate geographic  
parthenogenesis. Contrary to geographic parthenogenesis, lottery models [48] predict that sexual  
336 reproduction is favored at the boundary of a species' range, where the habitat is capricious and  
unpredictable. A spatially extended model by Salathe(2006) [41], which is based on Muller's  
338 ratchet decreasing the fitness of asexuals while they invade a sexual population, predicts the  
dominance of asexuals in marginal habitats, with small populations that can be invaded rapidly.  
340 However, such an asexual invader could persist only temporarily, until its fitness has decreased  
to the point where it dies out or a sexual invader replaces it again. Geographic parthenogenesis  
342 therefore cannot be an equilibrium phenomenon in that model. Models based on the Red Queen  
mechanism [24, 19] require a decreasing impact of parasites on their host towards the boundary

344 of the host's range in order to produce geographic parthenogenesis. Such models require as-  
 346 sumptions about how host and parasite change with the geographic location [32]. Indeed, hosts  
 are more likely to be exposed to a larger number of parasites in the center of their range which  
 weakens the Red Queen mechanism [29] and therefore the advantage of sexual reproduction.  
 348 Further, Howard(1994) [22] demonstrated that a model that only includes the effect of parasites  
 reducing the fitness of the host, is not sufficient to explain the maintenance of sex. Finally,  
 350 many mathematical models on the maintenance of sexual reproduction are based on population  
 genetics [34, 39], where fitness values are assigned to genotypes. Since such models do not  
 352 consider explicitly the ecological environment, there is no straightforward way to extend them to  
 explain geographic parthenogenesis. Overall, processes such as Muller's ratchet, interaction with  
 354 parasites, and interactions between genes, may all affect the mode of reproduction. However, re-  
 sources are fundamental and universal, no living organism can survive or even reproduce without  
 356 resources. Our model including a broad spectrum of limited resources, together with stochastic  
 effects (drift) is unique in providing a generally satisfying explanation for the phenomenon of  
 358 geographic parthenogenesis and for the general dominance of sexual reproduction.

Our model is limited by the fact that it is based on equilibrium dynamics and therefore does  
 360 not take into account the ever continuing change of the biotic and abiotic environment. The set  
 of resources used in our model is the same in every patch and over the duration of the simulation.  
 362 Recent work on the advantages of sexual reproduction [35, 39] focuses more on the ability of  
 sexually reproducing organisms to adapt to new challenges. A combination of these approaches  
 364 with an explicit modelling of structured resources could be an important step towards a synthesis  
 of the different theories of evolution and maintenance of sex.

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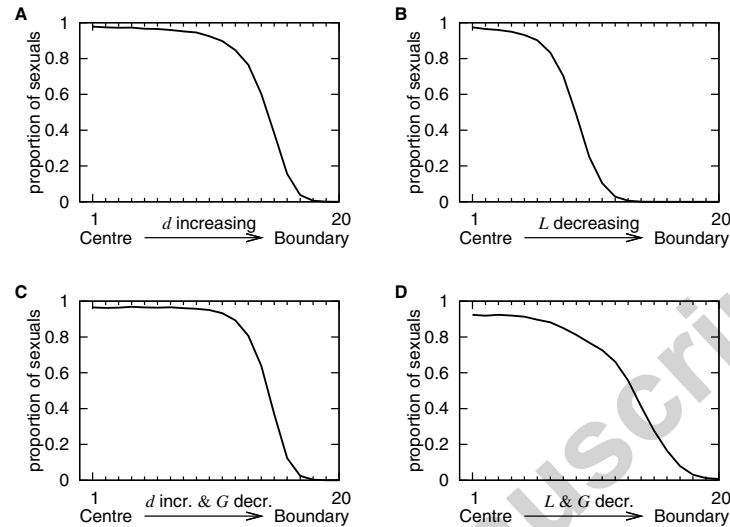


Figure 1: Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the consumer death rate  $d$ , (B) the number of different resources  $L$ , (C) the death rate  $d$  and the regrowth percentage of resources  $G$ , (D)  $G$  and  $L$ . The death rate  $d$  is increased in constant steps from 30 to 106, the number of different resources  $L$  is decreased from 256 to 66 in (B) and to 142 in (D), and the regrowth percentage of resources  $G$  is decreased from 40 to 11.5 in (C) and (D). The parameters that are not varied between patches are  $d = 30$ ,  $L = 256$ ,  $G = 20$ . The remaining parameters are: average number of initial individuals per patch  $n = 50$ , mutation rate per locus  $\mu = 0.002$ , sexual-to-asexual mutation rate  $u = 0.001$ , migration rate  $\eta = 0.01$ , and equal coupling strength to all 9 resources available to a genotype (i.e.,  $k = 0$ ).

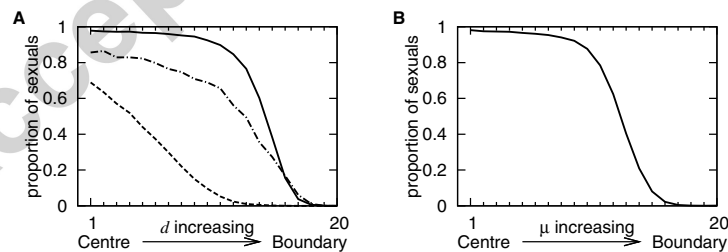


Figure 2: Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the consumer death rate  $d$  (in constant steps from 30 to 106) for three different values of the migration rate  $\eta = 0$  (dot-dashed),  $\eta = 0.01$  (solid),  $\eta = 0.1$  (dashed), (B) the mutation rate per locus  $\mu$  (increasing from 0 to 0.019). The parameters that are not varied between patches are  $d = 30$ ,  $\mu = 0.002$ ,  $L = 256$ ,  $G = 20$ ,  $n = 50$ ,  $u = 0.001$ ,  $k = 0$ .

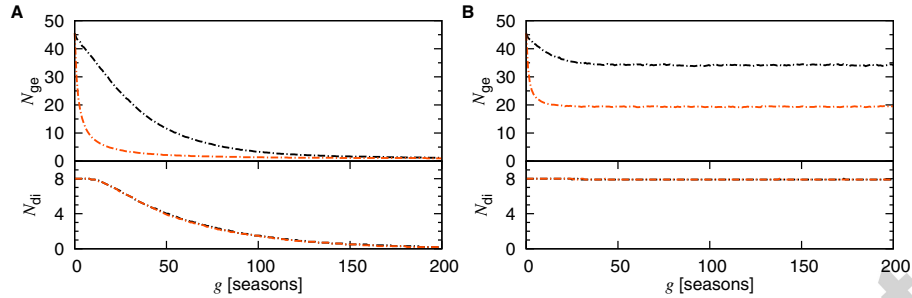


Figure 3: Average number of diallelic loci  $N_{di}$  and genotypes  $N_{ge}$  for a sexual (black lines) or parthenogenetic population (red lines) of average size  $n = 50$  at the beginning of each season as function of time. The graphs are evaluated for a null-model, i.e., only with drift and without selection, and the two reproductive modes are considered independently from each other. The mutation rate per locus is (A)  $\mu = 0$  and (B)  $\mu = 0.016$ . The average number of diallelic loci evolves in the same way for both sexual and parthenogenetic reproduction.

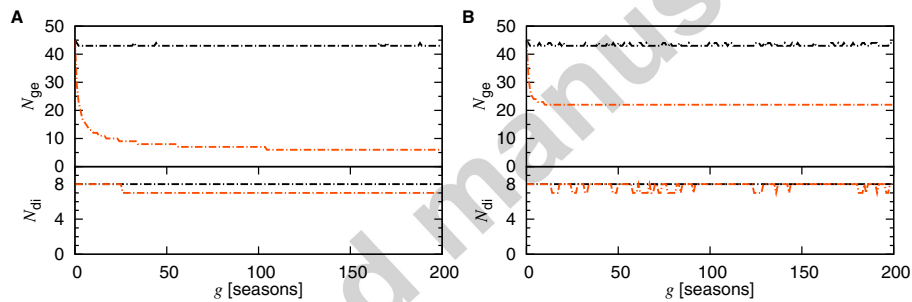


Figure 4: Same as Fig. 3, but with resource dynamics. The additional parameters are: death rate  $d = 30$ , number of different resources  $L = 256$ , regrowth percentage of resources  $G = 20$ , average number of initial individuals per patch  $n = 50$ , and equal coupling strength to all 9 resources available to a genotype (i.e.,  $k = 0$ ).

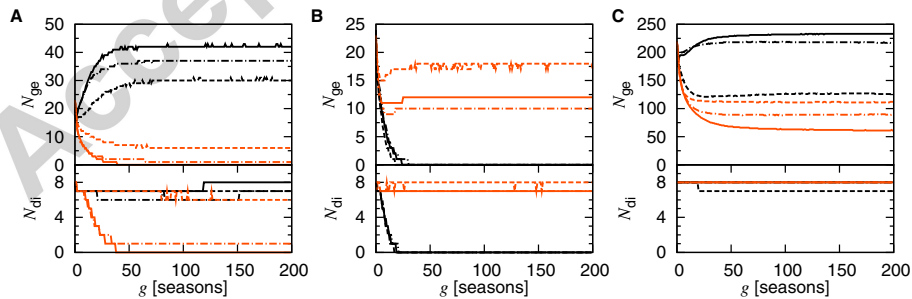


Figure 5: Average number of loci  $N_{di}$  with two alleles and of different genotypes  $N_{ge}$  for a situation where sexual (black lines) and parthenogenetic reproduction (red lines) compete with each other, as function of time. The simulations were performed for the parameter set of Fig. 2A. (A) first patch  $m = 1$ , (B)  $m = 20$ . (C) all 20 patches. Dot-dash line:  $\eta = 0$ ; solid lines:  $\eta = 0.01$ ; dash line:  $\eta = 0.1$ .