Temporal patterns of resource use in an ecological model of sexual reproduction and geographic parthenogenesis

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ABSTRACT

Questions: How are the prevalence of sexual reproduction and the phenomenon of geographic parthenogenesis related to resource availability? What is the pattern in space of resource and consumer dynamics?

Mathematical methods: A population dynamics model with structured resources in short supply, including a spatial gradient of consumer mortality and resource diversity. Species are modelled using quantitative genetics, combined with random mating for sexuals and clonal reproduction for asexuals.

Key assumptions: Resources are limited and re-grow slowly. Only a few consumer genotypes can co-exist locally. The twofold cost of sex is incurred once per season.

Conclusions: The advantage of sexual reproduction is due to the ability of the sexual population to generate offspring that can use resources that have not been exploited for some time. Resource use of the sexual population, therefore, changes continuously. This advantage is most significant at the centre of a species' range.

Keywords: genetic variance, Red Queen, resource dynamics, spatial variation, tangled bank.

INTRODUCTION

The importance of ecology for evolution is widely acknowledged, although it is not always included explicitly in mathematical models. Theories about the evolution and maintenance of sexual reproduction focus on genetic mechanisms (De Visser and Elena, 2007; Otto, 2009) and on predator–prey (Salathe *et al.*, 2008; Tobler and Schlupp, 2008) or host–pathogen interactions (Van Valen, 1973; Hamilton, 1980; Lively and Dybdahl, 2000; Lively, 2009). However, considering the high costs of sexual reproduction (Williams, 1975; Maynard Smith, 1978), it remains unclear whether these mechanisms are

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sufficient to explain the maintenance of sexual reproduction (West *et al.*, 1999; Otto, 2009). Ecological processes other than predator–prey or host–pathogen interactions, such as the role of resources and their dynamics, are rarely taken into account, despite early and also recent studies stressing their importance (Williams, 1975; Bell, 1982, 1988; Olofsson and Lundberg, 2007). In the lottery models of Williams (1975), different resource patches in space matching respective genotypes are more likely to be exploited by sexual than by asexual progeny as the latter are assumed to be genetically homogeneous with all progeny matching the same resource patch. These arguments resemble the ideas of Ghiselin (1974) paralleling economic and ecological resource use and using resource use scenarios to explain the maintenance of genetic diversity and sexual reproduction. Bell (1982) elaborated this hypothesis, calling it 'tangled bank'. Later, however, tangled bank models became discredited because of lack of empirical evidence (Bell, 1987; Bierzychudek, 1987; Burt and Bell, 1987). However, previous resource-based models did not incorporate feedback mechanisms between resource use and the fitness of progeny with the genotypes adapted to use certain fractions of the resources available. Recently, Scheu and Drossel (2007) introduced such a model for the maintenance of sexual reproduction. In this model, resources are structured, with one consumer genotype being able to exploit only a fraction of the resources. The dynamic of resource abundance is explicitly taken into account, so that resource use effectively feeds back to the fitness of progeny. Slow re-growth of resources combined with stochastic effects due to restrictions on the number of locally co-existing genotypes leads to the prevalence of sexual reproduction over a broad parameter range in spite of the costs of producing males. In contrast, it leads to the prevalence of asexual reproduction when mortality is high or when there are no resources that are exploited considerably more than other resources. The model of Scheu and Drossel (2007), however, falls short in that it does not consider the distribution of resources in space and therefore its conclusions necessarily are limited to local resource patches. The model therefore could not explain variations in sexual or parthenogenetic reproduction in space. Variations in sexual reproduction in space, termed geographic parthenogenesis, were first documented by Vandel in 1928, but resisted a convincing explanation based on evolutionary theory (Gaggiotti, 1994; Peck *et al.*, 1998; Kearney, 2006). In a recent model (Song *et al.*, 2011), feedback between resource use and fitness of progeny has been combined with variations in the spatial distribution of resources. Strikingly, by letting sexual and parthenogenetic species compete, the model produced the typical pattern of geographic parthenogenesis with sexual lineages dominating at the centre and partheno-genetic lineages at the boundary of the species' range. However, due to the high-dimensional and binary genotype description (eight biallelic features/loci, corresponding to an eight-dimensional resource space), the dynamics of resource use of the sexual population is difficult to resolve and to represent graphically in the framework of this model. Therefore, in the present paper, we again adopt the quantitative genetic approach of Scheu and Drossel (2007), investigating the mechanisms responsible for the prevalence of sexual reproduction for a broad range of parameters and illustrate the spatial and temporal dynamics in resource use. To simultaneously explore different extents of resource exploitation, we use a spatial set-up that ranges from low to high mortality, or from diverse to few resources. We show that the advantage of sexual reproduction is largest when the benefit of switching to unused resources is high and when mortality is low, suggesting that in structured resource space low mortality supports genotype diversity, the most pertinently acknowledged advantage of sexual reproduction.
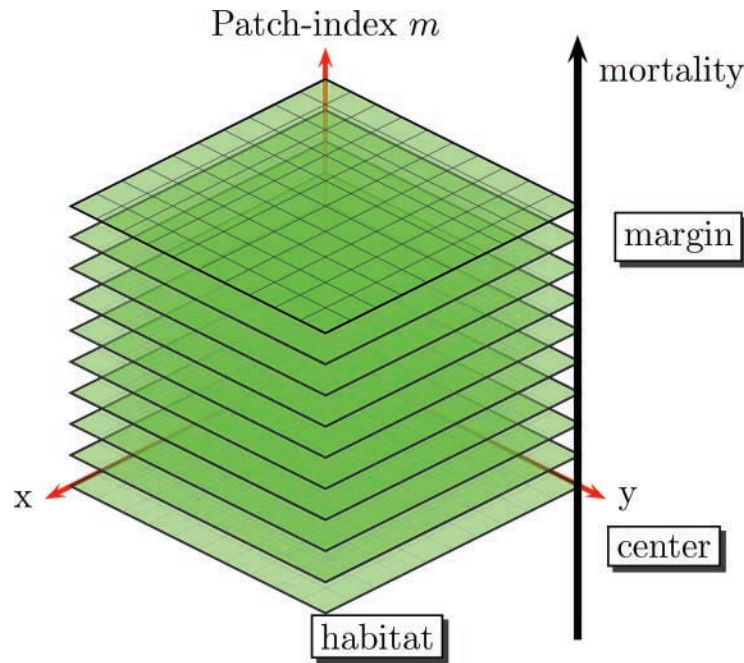
Fig. 1. The arrangement of patches and niches in the model.

MODEL

Twenty resource patches are arranged along a one-dimensional chain, as illustrated in Fig. 1. This chain of patches represents a one-dimensional cut through the two-dimensional range of a species. The cut starts at the centre and continues to the boundary of this range. At the centre, the environment is favourable for the consumer, and becomes harsher towards the boundary. A gradient of up to three patch features (specified below) reflects this change in habitat properties from the centre to the boundary. In each patch, resources are arranged in a two-dimensional array with $L \times L$ 'niches', which are labelled with 'trait values' (j_x, j_y, j_z), with $(j_x, j_y) \in [1, L]^2$ being the (integer) coordinates of the niche, and $j_z \in [1, 20]$ the index of patch m, increasing from the centre ($m = 1$) to the boundary ($m = 20$) of the species' range. We assume that a property of each resource changes as one moves from the centre to the boundary of a species' range. For example, as climate becomes dryer and/or cooler, the leaves of plants – the food of herbivores – become harder. Consumers are characterized by their mode of reproduction and by their genotype, which for simplicity is denoted by the same trait values (niche coordinates and patch index) as the niches. The consumer genotype has therefore three coordinates and is thus identical with the niche the consumer is best adapted to.

The model is initiated with a maximum resource biomass $R_j = R_{max} = 100$ in each niche, and with some niches being occupied by sexual or asexual individuals with a matching genotype. The life cycle of the consumers is tailored to that of species with intermittent mixes such as *Daphnia* (Bell, 1982; Hebert *et al.*, 1988). We take the body mass of an individual as the unit for biomass. Thus, the biomass P_i of consumer i increases from the initial value $P_i = 1$ by asexual reproduction during the growing season according to the equation

$$\dot{P}_i = \lambda \sum_{j_y=1}^{L} \sum_{j_x=1}^{L} \alpha_{ij} P_i R_j - d P_i, \tag{1}$$

while the resource biomass decreases according to

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

where the sum is taken over all consumers in the same patch. We assume that stochastic effects are not important during the growing season, because the populations multiply fast. The parameters are $\lambda = 0.2$ (Stephens and Krebs, 1986) and $\alpha_{ij} = 1/e^S$, where S is the squared distance between genotypes i and j. When the distance in any of the three directions is larger than 2, or when a resource j is not present in a patch, we set α_{ij} to zero. A consumer can feed efficiently only on those resources that are sufficiently close to its own genotype in resource space. The death rate d and the resource array size L can vary between patches. Variation in L is implemented such that from patch m to patch $m + 1$, resources in the last row and the last column in resource space are deleted.

   Population dynamics (1) is applied for each consumer until $\dot{P}_i$ becomes zero. If a consumer continued to eat beyond this moment in time, it would obtain less energy from the resources than it needs for metabolism. Consumers that cannot multiply any more, lay eggs and die.

   Next, the starting configuration for the next season is calculated: Resources re-grow partially according to the equation

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

With our choice of $R_{\max} = 100$, G represents the re-growth percentage of resources. Equation (3) implies that G percent of the exploited resources, R_j^{consumed}, are recovered between the growing seasons. The number of consumer individuals in each patch at the beginning of a new season is chosen from a Poisson distribution with a mean value $n = 20$, which reflects the situation that only few of the many eggs laid at the end of the previous season give rise to surviving individuals at the beginning of the next season. Due to the twofold cost of sexual reproduction, each initial individual is sexual with probability

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

and parthenogenetic with probability $1 - p_s$, with the P_i being the biomasses at the end of the previous season. The genotype of a parthenogenetic individual is randomly chosen among the genotypes of parthenogens present in the previous season, with weights proportional to their final biomass. The genotype of a sexual individual is determined by randomly choosing two parent genotypes with probabilities proportional to their biomass at the end of the previous season, and by assigning to the offspring a genotype chosen from a Gaussian distribution around the mid-parent value in each of the two or three dimensions of genotype space, rounded to the nearest integer that still lies within the allowed range $[1, L]$. Unless indicated otherwise, the variance of the Gaussian distribution is $V_g = 2.5^2$ in

the x- and y-direction (i.e. the within-patch genetic variance), and $V_{gz} = 1$ in the z-direction (the between-patch genetic variance). This means that the offspring of sexuals can obtain a genotype that makes it better adapted to a neighbouring patch than to the patch in which it resides. This rule implements the fact that sexual reproduction can destroy adaptation as well as generate it. When the z component of the genotype i of an offspring differs from the patch in which it resides, it can feed less efficiently on the resources, since α_{ij} is smaller than 1 for all resources j in that patch.

Finally, with a small probability $u = 0.001$, the offspring of sexual individuals become parthenogenetic, implementing the 'frozen niche variation hypothesis' of Vrijenhoek (1979), which is based on the fact that parthenogenetic lineages can arise in sexual populations.

Before the onset of resource consumption, each individual is allowed to migrate to each neighbouring patch with a migration probability η. While there is only one neighbouring patch to the first and last patch, all other patches have two neighbours. Then, we apply again equations (1) and (2), starting with an initial consumer biomass P_i in each niche i that is equal to the number of individuals in this niche.

We iterated this process for 1000 seasons before evaluating the resulting pattern of sexual and asexual reproduction, the genetic variance of the sexual population, and the temporal change in resource use.

The present model differs from the original model (Scheu and Drossel, 2007) by including a spatial dimension, and from Ament *et al.* (2008) by making the patches different from each other. Recently, we also investigated a version of the model that is genetically explicit, with several loci with two alleles at each locus, and with free recombination during production of sexual offspring (Song *et al.*, 2011). The two ways of implementing the genetics represent two limiting cases: Here, we implement two features, j_x and j_y, each of which can assume 20 different values. In the other model, there are more features (6–8), each of which can assume only two values. Both types of model give the same general results concerning the conditions under which sexual reproduction prevails, thus indicating that these results are generic and do not depend on the details of the implementation.

RESULTS

Figure 2 shows the average proportion of sexuals in each patch obtained after a sufficiently long time, when an equilibrium had been reached, averaged over 1000 runs of the simulation. In Fig. 2A, the death rate d was increased with increasing patch index, varying overall by a factor of ~2; in Fig. 2B, the number of different resources, L^2, was decreased from 20^2 to 1 with increasing patch index. In each case, the proportion of sexuals decreases from (almost) 100% to (almost) 0% with increasing patch index (i.e. with increasing harshness of the environment). Compared with the simpler situation where all patches contain an identical set of resources (dashed lines), the percentage of sexuals decreases faster in the model version chosen for the present study (solid lines), due to the fact that sexual offspring may be better adapted to a neighbouring patch than to its own patch, while asexual offspring retain the (well-adapted) genotype of the parent.

These results are independent of the initial distribution of genotypes and modes of reproduction, and they remain approximately the same when a decrease in G is super-imposed to the increase in d or the decrease in L. The pattern of geographic parthenogenesis is robust against changes in other ecological factors. Figure 3 shows the influence of the migration rate η (Fig. 3A) and of the genetic variance V_g of the sexuals (Fig. 3B). The
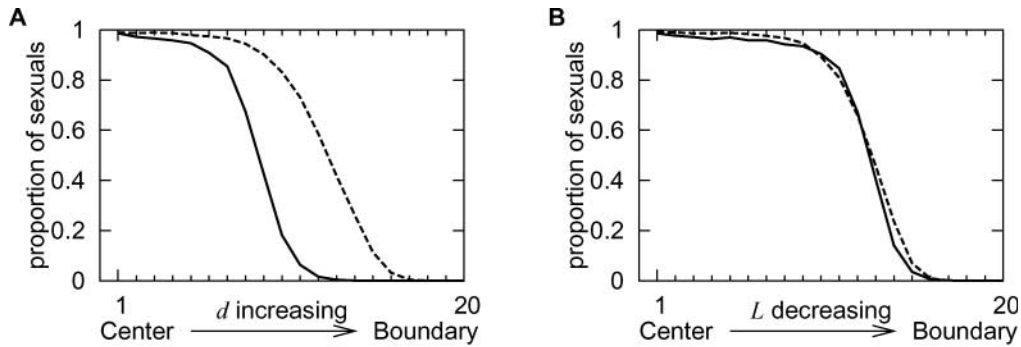
Fig. 2. Average equilibrium proportion of sexuals in the 20 patches, with the index increasing from the centre (1) to the boundary (20). The parameters that vary between patches are (A) the death rate d increasing in constant steps from 25 (in patch 1) to 53.5 (in patch 20), and (B) the resource array size L decreasing in contant steps from 20 (in patch 1) to 1 (in patch 20). The parameters that are not varied between patches are $d = 25$ and $L = 20$. The remaining parameters are: re-growth percentage of resources $G = 20$ (i.e. 20% of the exploited resource biomass is recovered between the seasons); average number of initial individuals per patch $n = 20$; sexual-to-asexual mutation rate $u = 0.001$; migration rate $\eta = 0.01$; within-patch genetic variance of consumers $V_g = 2.5^2$; between-patch genetic variance $V_{gz} = 1$. For comparison, the dashed lines show the curves obtained when the resources are identical in all patches (in which case we set $V_{gz} = 0$).
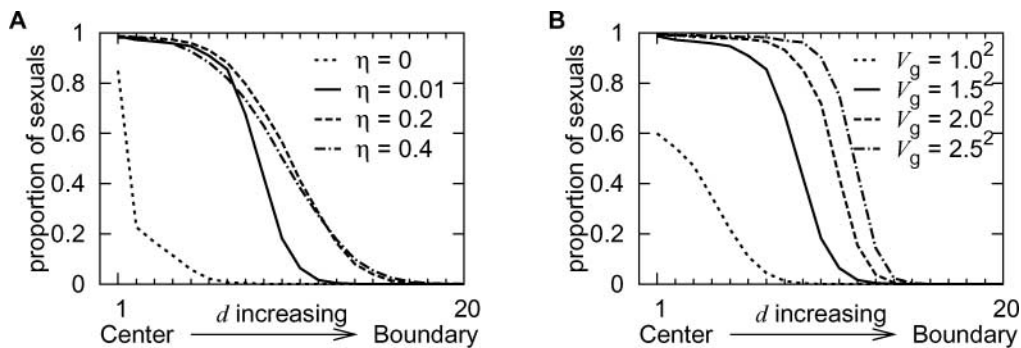

Fig. 3. Influence of (A) the migration rate η and (B) the within-patch genetic variance $V_g = \sigma^2$ on the equilibrium proportion of sexuals in the 20 patches from the centre (1) to the boundary (20). In both graphs, the solid curve is the same as that in Fig. 2A, since all parameters are identical.

advantage of sexuals increases at first with increasing migration rate, because some sexual migrating offspring can be adapted to the new patch, while asexual clones are never adapted to neighbouring patches; furthermore, sexual migrants can counteract the local loss of genetic variance. When the migration rate becomes even larger, the curve becomes more flat, but a source–sink effect (Dias, 1996) prevents the proportion of sexuals from becoming constant. The advantage of sexuals is larger when the genetic variance is larger, because sexual offspring can more easily exploit niches that have not been depleted in previous seasons, and the competition between sexual siblings (and the resource conflict with parent generation) can thus be more efficiently reduced. We also investigated the case where
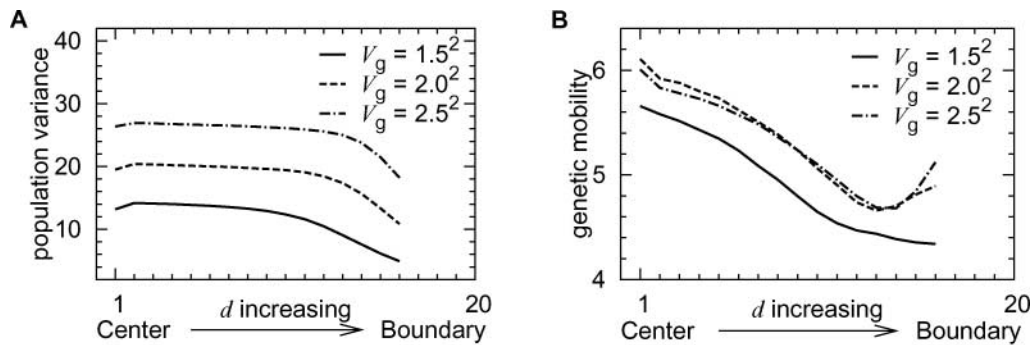
Fig. 4. Genetic variance of the sexual population (A) and the average distance over which the barycentre of the sexual population moves during five seasons (B), in the first 16 patches (where the sexuals exist most of the time). In both graphs, the solid curve is produced with the same parameters as that in Fig. 2A, while the other curves are produced with different $V_g = \sigma^2$ values.

migration happens before selecting which offspring survive (which can be interpreted as egg dispersal). The curves changed only little with this modification.

Having established the winning mode of reproduction under a variety of conditions, we next evaluated the genetic variance of the sexual population in each patch, and the rate at which the barycentre of the sexual population moves within the patch. Figure 4A shows the genetic variance of the sexual population for the first 16 patches (where the sexuals are present most of the time), for different values of V_g. The variance of the population is larger than twice V_g, which is the value expected for a population with random mating and without selection. The selective advantage of exploiting unused resources thus manifests itself in the increased genetic variance of the population. The variance of the population decreases towards the value $2V_g$ only in the last patches, where the advantage of exploiting unused resources is small. In all patches, the sexual population covers only part of the niches.

Figure 4B shows the average distance over which the barycentre of the sexual population moves in five seasons. This distance is greatest where selection pressure is largest, and it is less when V_g is smaller. This means that the selection pressure towards using unexploited resources causes the sexual population to change continuously (the increase of part of the curves in the last two patches is due to the sexuals vanishing from the patch and immigrating anew). Figure 5 shows this motion of the sexual population for one simulation run, for three neighbouring patches, and for both the x- and the y-coordinate of the barycentre in genotype space. The graphs document that the motion in neighbouring patches is partially coupled, which is due to migration. The population moves back and forth in both coordinates and thus visits all niches over a greater period of time. For smaller V_g (not shown), the maximum and minimum x- and y-values are closer to the boundary, due to the smaller genetic variance of the population, which would otherwise never extend to the boundary niches.

DISCUSSION

We have investigated advantages and disadvantages of sexual reproduction and the temporal change of resource use in a model that takes explicitly into account feedback
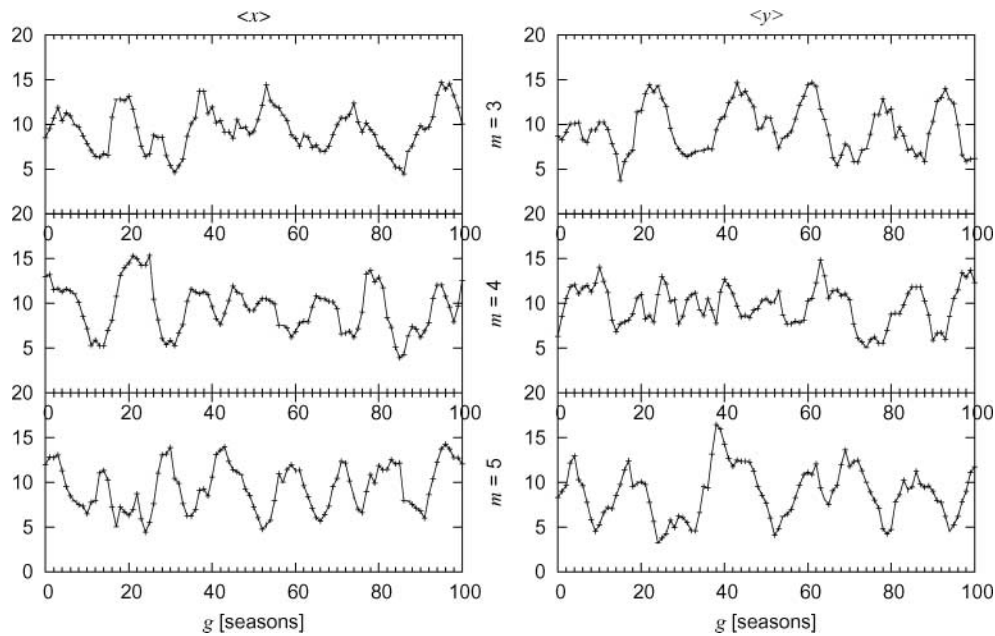
Fig. 5. Motion of the barycentre of the sexual population, represented by the two coordinates ⟨*x*⟩ and ⟨*y*⟩, in the third, fourth, and fifth patch for a time window of 100 seasons at equilibrium. The curves are produced with the same parameters as the dashed line in Fig. 2A.

between resource use of the parental generation and the fitness of offspring. The model is guided by the assumption that resources are the most important factor determining the mode of reproduction (Ghiselin, 1974; Williams, 1975; Bell, 1982, 1988). Building on the previous models of Scheu and Drossel (2007) and Song *et al.* (2011), we intended to explore the spatial and temporal dynamics in resource use and illustrate the results graphically. As in the model by Song *et al.* (2011), which adopted an explicit genetic approach, our model produced patterns of sexual and parthenogenetic reproduction that resembled that of geographic parthenogenesis, i.e. with sexual lineages dominating in the centre and parthenogenetic lineages at the boundary of a species' range (Vandel, 1928; Kearney, 2006). This was achieved by simply varying mortality and resource number along a spatial gradient. Graphics on the dynamics of resource use illustrated that the genetic variance in sexual population was strengthened substantially in 'favourable' environments in the framework of this model. The genetic variance of the sexual population and the rate at which resource use changed with generations were largest when the advantage of the sexual mode of reproduction was largest and it completely dominated the local population.

In contrast to the model of Song *et al.* (2011), the current model uses quantitative genetics, with offspring of sexual individuals having a Gaussian distribution around the mid-parent value in genotype space allowing the illustration of resource use. The underlying assumption is that there is enough genetic variance present in the population that adaptation is not limited by genetic constraints. Our local population sizes are small (around 20 individuals per patch at the beginning of a season, with 20 patches in total), but one has to keep in mind that our chain of patches represents a one-dimensional cut through a two-dimensional space that has a large extension and provides in total enough genetic

variation to permit the continuous production of new genetic combinations. As Song *et al.* (2011) showed that a genetically explicit model produces similar results, the type of genetics used is therefore of minor importance as long as the basal ingredients of the model remain the same, i.e. slow re-growth of resources, stochastic effects due to restrictions on the number of locally co-existing genotypes, combined with geographical gradients in density independent mortality and/or in resource diversity. Similarly, a simpler version of the quantitative genetic model that uses a one-dimensional resource space and in which resources do not change along the geographic gradient, also produces the effect of geographic parthenogenesis (I. Ament, unpublished data).

Sexual reproduction has the advantage that offspring can exploit resources that have not been used for a long time and are therefore abundant. It has the disadvantage that adaptation can be destroyed, because the offspring genotype may become that of a recently heavily exploited resource, or one that fits better into a neighbouring patch than into the patch where the individual resides. In addition, there is always the twofold cost of sex (Maynard Smith, 1978), which in our model is incurred once per season. Due to this combination of advantages and disadvantages, it depends on the values of the parameters whether sexual or asexual reproduction wins. Thus each of the two modes of reproduction can be the equilibrium mode at a different location in space, and since asexual reproduction is favoured under 'harsh' conditions, it tends to prevail at the boundaries of a species' range, which in our model was represented by patches with high mortality or small number of resources.

In contrast to conventional tangled-bank models (Bell, 1982), a larger population size does not increase the advantage of sexual reproduction in our model. The reason is that n asexual clones together may cover a wider range of resources than n sexual individuals, because random mating keeps the variance of the sexual population within certain limits (cf. Gorelick and Heng, 2010). When n becomes too large, the unused resources are not sufficient for the sexual population to adapt to, and the advantage of sexual reproduction vanishes. The rule that locally only a few genotypes can co-exist is thus a vital ingredient of our model. Furthermore, compared with conventional resource use models (Case and Taper, 1986), our model introduces a temporal component: the sexual population wins due to the fact that it can adapt to the continually changing pattern of resource abundance. This finding resembles Red Queen processes, although they are turned upside down. Red Queen models are based on parasite–host interactions (Jaenike, 1978; Hamilton, 1980; Hamilton *et al.*, 1990), whereas the changes of population composition in space and time in our model are due to feedback mechanisms of resource use (i.e. they are based on bottom-up forces). Notably, resources in our model can be of any kind, abiotic (such as nutrients) or biotic (such as living or dead organic matter), and therefore the model is not necessarily based on co-evolutionary arms races as Red Queen processes. Furthermore, as shown by comparison of the present results with those of Song *et al.* (2011), the outcomes of our model are basically the same irrespective of the type of genetics used. Therefore, we believe the results of the model to be robust and to apply to a wide range of organisms.

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