Establishment versus population growth in spatiotemporally varying environments

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Abstract

We consider situations where repeated invasion attempts occur from a source population into a receptor population over extended periods of time. The receptor population contains two locations that provide different expected offspring numbers to invaders. There is demographic stochasticity in offspring numbers. In addition, temporal variation causes local invader fitnesses to vary. We show that effects of environmental autocorrelation on establishment success depend on spatial covariance of the receptor subpopulations. In situations with a low spatial covariance this effect is positive, whereas high spatial covariance and/or high migration probabilities between the subpopulations causes the effect to be negative. This result reconciles seemingly contradictory results from the literature concerning effects of temporal variation on population dynamics with demographic stochasticity. We study an example in the context of genetic introgression, where invasions of cultivar plant genes occur through pollen flow from a source population into wild-type receptor populations, but our results have implications in a wider range of contexts, such as the spread of exotic species, metapopulation dynamics, and epidemics.

Keywords

Persistence, Repeated invasions, Environmental autocorrelation, Spatial structure, Inhomogeneous branching process, Introgression

1 Introduction

Invasion dynamics are important in many contexts, such as evolution, epidemics, metapopulation dynamics, and environmental management. Especially in recent years interest in the study of invasions has increased, because human activities such as trade, travel, and agriculture, and processes like climate change increase the spread of exotic species into new habitats, and enhance the risk of genetic introgression (the permanent incorporation of genes of one population or species into the genome of another).

Successful establishment often occurs following repeated invasion attempts. Prior studies by Haccou and Iwasa[1] and Haccou and Vatutin [2] show that, with such invasion patterns, the chances of success are affected by temporal

environmental variation. They argued that this is caused by dependencies between the establishment success of successive invaders due to the interaction between environmental and demographic stochasticity. Their results indicate that the chance of at least one successful invasion in a limited sequence of attempts decreases when temporal environmental autocorrelation increases.

When invasion events are repeated indefinitely, and each invasion has a non-zero probability of success, eventual establishment success is guaranteed. To quantify invasion pressure in such situations, therefore, different measures than the chance of ultimate success should be used. Ghosh and Haccou [3] proposed to use the so-called 'hazard rate' of successful invasion. This is the per-generation chance of a successful invasion given that it has not happened before. Recently, Ghosh et al [4] demonstrated that the hazard rate also decreases with increasing temporal environmental autocorrelation. Thus, the results in [1], [2] and [4] all indicate that temporal autocorrelation negatively affects establishment of repeated invasions.

On the other hand, Gonzalez and Holt [5], and Holt et al. [6] and [7] found a positive effect of temporal autocorrelation on the abundance of populations in a sink habitat with repeated invasions, which appears to contradict the results of [1], [2] and [4].

The results cited above are based on models where invasions occur into spatially homogeneous environments. Spatial variation also affects invasion success, and studies by Claessen et al. [8], Roy et al. [9], Schreiber [10], and Schreiber and Ryan [11] show that it interacts with temporal variation to affect population dynamics. Some of these studies indicate that environmental autocorrelation has a positive (rather than a negative) effect on metapopulation persistence [9] and population growth rate (see e.g. [10], and the review by Schiegg [12]).

Note that these papers focus on different aspects of population dynamics. [1], [2] and [4] look at establishment success. [5] , [6] and [9] focus on population persistence and abundance in sink habitats, and [8], [10] and [11] consider population growth rate. Whereas in temporally constant environments growth rate can be used as a proxy for establishment success (whether invasions are simultaneous or successive) this is no longer true for sequential invasions in an environment which varies in time, because of dependencies between the chances of success of consecutive invasion attempts.

It is currently not clear how the combination of temporal environmental stochasticity, spatial patterns, and demographic stochasticity affects estab-

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lishment success in situations with repeated invasions, since an analysis of this aspect of population dynamics, with a model that incorporates all of these elements is currently lacking. Furthermore, it is not clear how the different characteristics of population dynamics are related, and how the at first sight contradictory effects of temporal autocorrelation on these different aspects can be reconciled.

In this paper we examine these issues, by generalising the model of Gosh et al. [13]. This is a branching process model for genetic introgression between a source population of cultivar plants and a wild-type receptor population. Repeated invasion of cultivar genes is caused by the continued spread of pollen from the source population, leading to the production of hybrids in the recipient population. We consider the fate of an advantageous allele that is linked to a disadvantageous allele in the cultivar plants. Because of this, hybrids have a subcritical fitness. Thus, if the linkage would be complete, the advantageous allele will eventually disappear from the recipient population if pollen flow would stop. However, with incomplete linkage, recombination events during hybridisation and backcrossing with the wild-type lead to a positive chance that the allele will become permanently established in the recipient population. In the presently considered model, the recipient population is spatially structured, which leads to differences between local fitnesses. Furthermore, besides the demographic stochasticity, temporal environmental stochasticity is added, leading to random variation in expected offspring numbers of the different genotypes.

Note that similar models can be used to study invasion dynamics in other contexts, such as repeated invasions of exotic species in a metapopulation, where mutations may lead to adaptation to sink habitats (as in [7]). In that case, invaders are individuals rather than alleles, the mutation rate is analogous to the recombination rate in our model, and different habitats in the metapopulation correspond to our resident populations. In epidemiological contexts, models like ours may be used to gain insight in the dynamics of novel diseases with adaptive mutations in heterogeneous host populations, such as studied by Gandon et al. [14]. Invaders then correspond to pathogens and the different host types are analogous to our resident populations.

To elucidate the connections between different characteristics of population dynamics, we compare the effects of temporal autocorrelation and spatial characteristics on establishment success of the cultivar gene in the branching process model with the effects of these factors on population growth rate in analogous population projection models that don't include demographic

stochasticity.

The results from the branching process model indicate that environmental autocorrelation can have a positive as well as a negative effect on establishment success, and that this depends crucially on the spatial characteristics of the receptor population. The population projection models, however, show that long term growth rate either increases or stays constant with environmental autocorrelation. Our results indicate that several mechanisms with opposite effects affect establishment success of repeated invasions in environments with spatial structure and temporal variation. The balance of these mechanisms determines the direction of the effect of environmental autocorrelation.

These results highlight the fact that population abundance, persistence, growth rate, and establishment success are different aspects of population dynamics that may be affected in different ways by spatial and temporal environmental characteristics. For a proper understanding of the dynamics of repeated invasions in spatiotemporally varying environments it is therefore imperative to incorporate demographic stochasticity explicitly in models.

2   Model structure

2.1   Genetics and spatial structure

We consider a discrete-generation model with two loci that each have two alternative alleles. The source population has genotype $ABAB$ (i.e. both haplotypes are AB, with A at the first and B at the second locus), and the recipient wild-type population has genotype $abab$. Pollen is transferred from the source population to the receptor population, leading to the formation of hybrids in each generation. It is assumed that this occurs at a constant rate, and that the recipient population is large enough so that all matings occur with wild-type individuals, producing a random number of hybrid offspring ($ABab$) with a constant expected value of m_0.

Hybrids ($ABab$) have a lower fitness (i.e. expected number of offspring) than the wild type ($abab$), but allele A gives a fitness benefit when uncoupled from B through recombination. Thus, type $Abab$ has a superior fitness to the wild type. We are interested in the probability that the A allele becomes established, so the only genotypes we need to keep track of are $ABab$ and $Abab$. The high-fitness genotype $Abab$ can be produced by matings of

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hybrids with the wild type where recombination happens, or by matings of *Abab* with the wild type. Recombination between the two loci occurs with probability ρ. Complete linkage of the two loci corresponds to $\rho = 0$, and $\rho = 0.5$ implies independent assortment of the loci. Note that, for eventually successful invasion, a non-zero recombination rate is required.

We assume a simple spatial structure, where the receptor population is distributed over two separate locations. In each generation the hybrids produced by invading pollen are distributed evenly over the two locations. Migration between the locations occurs after reproduction. The probability that an individual migrates is denoted by λ.

Taking into consideration that there are two locations, there are four types of individuals to keep track of. Individuals with genotype *ABab* are called type 1 when they occur at location 1 and type 3 when they occur at location 2. Individuals with genotype *Abab* occurring at location 1 are type 2 and those at location 2 are type 4.

Note that, since reproduction always occurs with wild-type individuals, the expected number of an individual's offspring that possess the *A* allele is half of its total expected offspring number (i.e. half of its fitness). We will consider situations where types 1 and 3 individuals have on average less than 2 offspring, and therefore their expected number of offspring with the *A* allele is smaller than 1. These types are therefore referred to as being 'subcritical'. Potentially successful lineages may be initiated by the 'supercritical' or 'escape' types 2 and 4, which have an average offspring number greater than 2. Figure 1 shows the model structure.

2.2   Spatiotemporal dynamics

We consider situations where the environment alternates between two states, I and II, according to a two-state Markov chain, with transition probabilities $1 - \eta$ from one state to the other. This implies that each of the environmental states is equally likely to occur when the process is stationary. The one-step temporal environmental autocorrelation equals $2(\eta - 1/2)$ (see supplementary material) and, therefore, increases linearly with η. Values of η smaller than $1/2$ correspond to a negatively autocorrelated environment (meaning the environment is more likely to change in the next generation), and for values of η larger than $1/2$ the environment is positively autocorrelated (meaning the environment is more likely to be the same in the next generation).

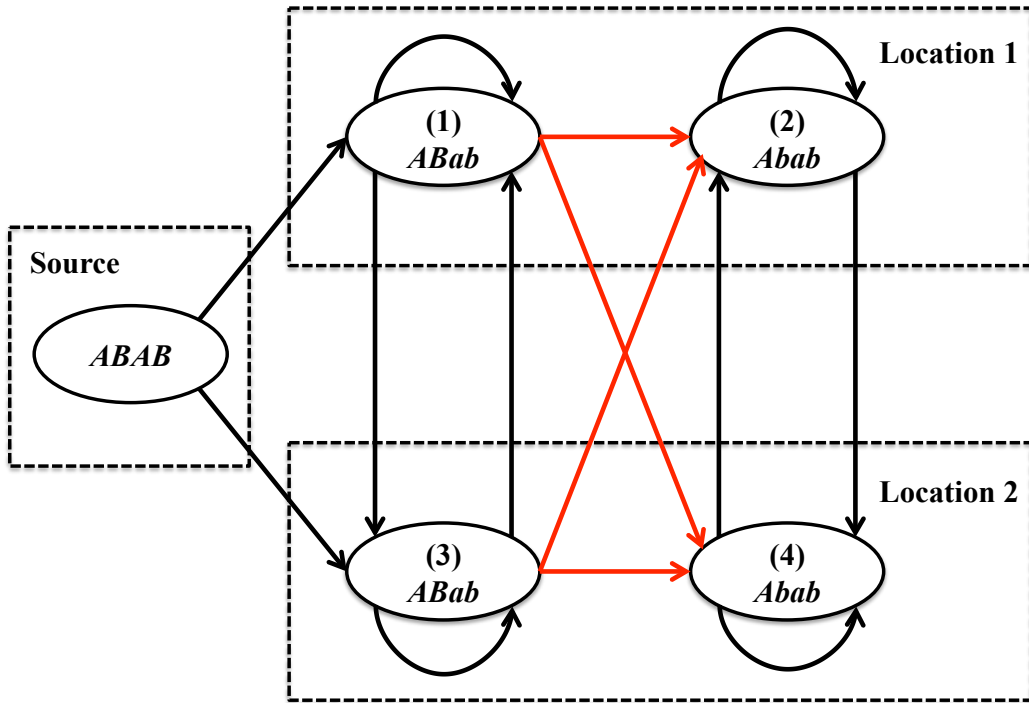There are many possible ways of modelling spatial covariation. Here

Figure 1: Schematic representation of the model structure. Arrows indicate potential offspring production, with recombination events indicated in red.

we consider two different models. In model 1 the environmental state is determined by a single Markov chain that affects both locations, whereas in model 2 two independent and identical Markov chains each affect one location.

In model 1, spatial environmental covariance is determined by how the environmental state affects the fitnesses at the two locations. Positive covariance occurs if the locations are affected similarly by the environmental state, meaning that a change in environmental state either increases or decreases the fitnesses at both locations. Negative covariance occurs if the locations are affected in opposite ways, meaning that an environmental change increases fitness in location I and decreases fitness in location II, or the other way round. If the fitnesses at one of the locations are affected by the environmental state but those at the other location remain constant, the spatial covariance is zero.

To include these different possibilities, we use two parameters, $0 < r < 1$

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and $r \leq \alpha \leq 1$, and assume that the environmental state affects the fitnesses as presented in Fig. 2. Note that for each combination of r and α the geometric mean offspring numbers of the 'subcritical types' (1 and 3) at the two locations are both equal to $\sqrt{r} \cdot m_1$, and those of the 'supercritical' types (2 and 4) are both $\sqrt{r} \cdot m_2$, so for each genotype, the two locations have a similar level of fitness on average.
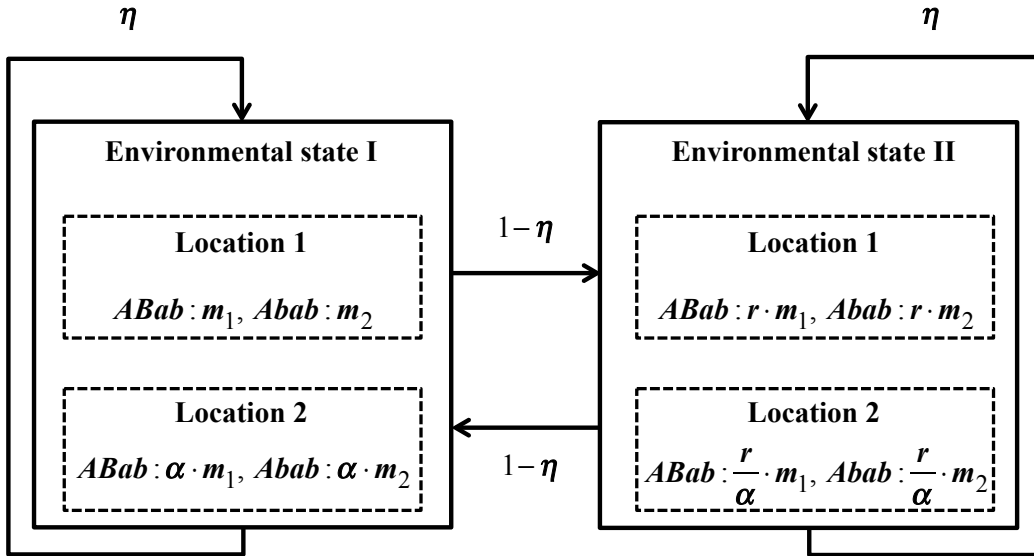

Figure 2: Schematic representation of the spatiotemporal dynamics for model 1. For each possible type of individual the expected offspring numbers are shown. Arrows represent potential transitions between environmental states. Transitions are generated by a two-state Markov chain, with transition probabilities as indicated.

When $r \leq \alpha < \sqrt{r}$ the fitnesses at the two locations are affected by the environmental changes in opposite directions. This is the most extreme when $\alpha = r$: in that case the fitnesses at location 1 and location 2 are switched when the environment changes. When $\alpha = \sqrt{r}$, fitnesses in location 2 stay constant and only fitnesses at location 1 change with the environment. Finally, when $\alpha > \sqrt{r}$ the fitnesses of both locations are affected in similar ways when the environment changes (both increase or both decrease). When $\alpha = 1$ the fitnesses at location 1 and location 2 are equal in each environmental state. This corresponds to a situation without spatial structure.

Thus, increasing α from r to 1 increases the spatial covariance in this

model. This is derived formally in the supplementary material. There it is also shown that for each of the genotypes the correlation between the fitnesses at the two locations equals -1 if $\alpha < \sqrt{r}$, and $+1$ if $\alpha > \sqrt{r}$. When $\alpha = \sqrt{r}$ the correlation is undefined (since in that case the variance in fitness at one of the locations is zero), but the covariance equals zero.

As mentioned above, the situation where $\alpha = \sqrt{r}$ corresponds to an absence of spatial covariation in model 1, but it also implies that the fitnesses in location 2 are constant in time. To examine situations without spatial covariation but with temporal variation at both locations, we considered the additional model 2, in which two independent, but identical, Markov chains each affect a single location. In that model the fitnesses of each of the genotypes is multiplied by a factor r if the corresponding Markov chain is in environmental state II.

3 Quantification of invasion dynamics

In spatiotemporally varying environments such as considered in our models, establishment success of repeated invasions may not be predicted accurately by population growth rate. To compare the effects of spatiotemporal variation on these two characteristics, we determined quantitative measures of the both of them numerically from two different types of models. In this section we briefly explain how this is done.

3.1 Establishment success

When there are infinitely repeated invasion attempts that each have a non-zero probability of succeeding, the chance of eventual establishment equals one. Since, therefore, this chance cannot be used to quantify establishment success, [3] proposed the so-called 'hazard rate of invasions' as an alternative measure. This is the probability that invaders establish a permanent lineage at a certain time, given that this event has not occurred before. It is directly related to other measures of establishment success, such as the probability of successful invasion within a fixed period, the expected time until successful invasion, or the distribution of waiting times until adaptation to a sink environment, as considered by Holt et al. [15] in the context of metapopulation dynamics.

Note that the concept of the hazard rate comes from survival analysis,

where it relates to failure (i.e. mortality). In the current context, however, it relates to success. It is also important to note that the hazard rate represents a *conditional* probability. Thus, whereas the probability of establishment success tends to one in the long run, the hazard rate stabilises at a value smaller than one.

The hazard rate is estimated from branching process models that include demographic as well as environmental stochasticity. In these models it is assumed that, conditional on the environmental state, the numbers of hybrids formed by invasion of genes from the source population as well as the numbers of offspring of the type 1 to 4 individuals in the receptor population are random variables.

In constant environments the hazard rate is an increasing function of time which converges to an asymptotic constant level. Since each sequence of environmental states leads to a different value of the hazard rate, it is a random function when environments change randomly. An efficient computation method for hazard rates in such situations, that avoids having to simulate individual branching processes, is given in [4]. We briefly summarise it here. The first step is to simulate a large number, N, of sequences of length T of environmental states. For each simulated sequence, backward iteration from T to time 1 is used to compute the extinction probabilities of processes started by the escape types at each time. Subsequently, the first n of the environmental sequences and the extinction probabilities are used to compute the hazard rates at each time step up to n. The generated sequences should be long enough to realise a stable distribution of the extinction probabilities of the escape types in this period ($T \gg n$), and n should be large enough to ensure that the average hazard rate has reached its asymptotic level. Details of the computation method for the models considered in this paper are given in the supplementary material.

3.2 Long term population growth

Long term population growth rates are computed from simulations of population projection models. These models disregard demographic stochasticity, and only consider environmental variation as a source of randomness. In the situations considered here, the relation between the numbers of individuals

of different types at times $t, n_{i,t}$ and those at time $t - 1$ is described by:

$$
\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}_t = \mathbf{A_t} \cdot \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix}_{t-1} + \begin{pmatrix} m_0/2 \\ 0 \\ m_0/2 \\ 0 \end{pmatrix} \tag{1}
$$

where $\mathbf{A_t}$ is a matrix of the following form:

$$
\frac{1}{2} \begin{pmatrix} (1-\lambda)(1-\rho) c_1 m_1 & 0 & \lambda(1-\rho) c_2 m_1 & 0 \\ (1-\lambda) \rho \cdot c_1 m_1 & (1-\lambda) c_1 m_2 & \lambda \cdot \rho \cdot c_2 m_1 & \lambda \cdot c_2 m_2 \\ \lambda(1-\rho) c_1 m_1 & 0 & (1-\lambda)(1-\rho) c_2 m_1 & 0 \\ \lambda \cdot \rho \cdot c_1 m_1 & \lambda \cdot c_1 m_2 & (1-\lambda) \rho \cdot c_2 m_1 & (1-\lambda) c_2 m_2 \end{pmatrix},
\tag{2}
$$

(Remember that m_0 is the expected number of hybrids produced in each generation, and λ the migration probability). The $c_i (i = 1, 2)$ are constants determined by the model and the environmental state. For model 1 there are two different forms of $\mathbf{A_t}$. If the environmental state is I, $c_1 = 1$, $c_2 = \alpha$ and if it is II, $c_1 = r$, $c_2 = r/\alpha$. For model 2 there are four different forms, depending on the combination of environmental states that determine the fitnesses at the two locations. If the environmental process affecting location 1 is in state I, $c_1 = 1$, and if it is in state II, $c_1 = r$. Similarly, $c_2 = 1$ or r, depending on the state of the environmental process that affects location 2.

Note that the matrices $\mathbf{A_t}$ are reducible, since individuals of types 2 and 4 do not produce offspring of types 1 or 3. Population models with reducible projection matrices are not necessarily ergodic, meaning that their growth rates may be affected by initial conditions (see e.g. Caswell [16]). Using the methods of Stott et al. [17] it can be shown, however, that for both models all the possible $\mathbf{A_t}$ are ergodic. Since, furthermore, in all environmental states type 2 and 4 individuals have the largest expected offspring numbers, the ergodicity continues to hold in the situation with environmental stochasticity. This implies that for each specific situation the long term growth rate can be estimated from a simulation of a single, long sequence of population vectors.

To estimate growth rates, long sequences of population vectors are simulated according to Eq. (1). The log-growth rate at each time step is then estimated as the logarithm of the ratio of total population size in the current generation divided by the total population size in the previous generation. The estimated log-growth rate equals the average of these numbers over a long sequence of generations (see e.g. [16]).

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4 Results

We here present results for the parameter values $r = 0.7$, $\rho = 0.1$, $m_0 = 1$, $m_1 = 1.8$, $m_2 = 2.4$. Remember that only half of the offspring of each type carry the A-allele, so with these parameters, the expected numbers of offspring of the two genotypes carrying this allele are 0.9 and 1.2. Furthermore, note that the recombination rate, ρ is the rate at which the superior genotype is produced in hybrid mating events. Thus, the probability of establishment is zero if ρ equals zero, and increases with higher recombination rates.

We examined effects of several values of the environmental transition probability η between 0.1 and 0.9, and several migration probabilities λ between 0 and 0.5. Note that a migration probability of 0.5 corresponds to complete mixing of the two subpopulations. For model 1, we considered three possible situations: $\alpha = 0.7$ ($= r$, oppositely varying locations), $\alpha = \sqrt{0.7}$ ($= \sqrt{r}$, location 2 constant), and $\alpha = 0.9$ (≈ 1, locations are nearly identical).

4.1 Establishment success

In the branching process models we assumed that the numbers of hybrids produced per time step have a Poisson distribution, with expectation m_0 and that the offspring numbers of individuals of each type are also Poisson distributed, with expectation equal to the type's fitness given the environmental state. Hazard rate computations were based on $N = 5000$ simulated environmental sequences, with a maximum time of $T = 5000$. Graphical inspection showed that in all examined situations the distribution of extinction probabilities Q_k stabilised within 4000 time steps and that by time $n = 100$ the expected hazard rate was sufficiently stable to provide an accurate estimate of the expected asymptotic hazard rate. Because the distribution of estimated hazard rates was (in some cases extremely) skewed, the median hazard rates rather than the averages were used as a measure of central tendency of the distribution. The maximum standard error of the mean hazard rate at time $n = 100$ was less than $3 \cdot 10^{-4}$.

Figure 3 shows that the effects of migration probability and temporal autocorrelation on the median asymptotic hazard rates are non-monotonic. When environmental fluctuations affect the two locations in nearly the same way (model 1, $\alpha = 0.9$), temporal autocorrelation decreases the probability of invasion success. When the two locations are affected in opposite ways (model

1, $\alpha = 0.7$), however, this is reversed, and temporal autocorrelation increases the probability of success. The situation where location 2 is unaffected by temporal fluctuations (model 1, $\alpha = \sqrt{0.7}$) shows a mixture of these two trends: at low migration probabilities temporal autocorrelation has a positive effect on invasion success, whereas at high migration probabilities the effect is negative.
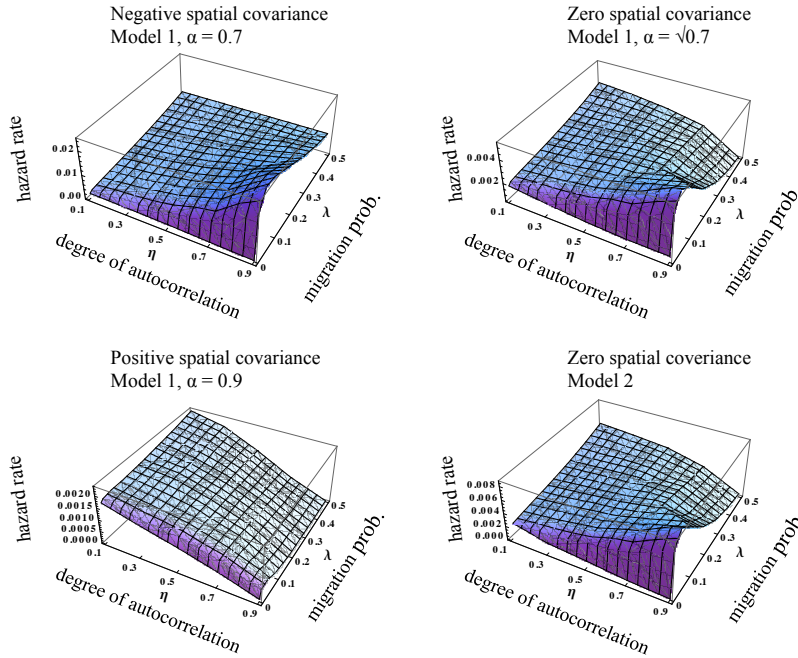

Figure 3: Effects of environmental autocorrelation η and migration probability λ on the median asymptotic hazard rate, for different types of spatio-temporal variation.

When the two locations vary independently in time (model 2) the effect of environmental autocorrelation also depends on migration: for low migration probabilities η increases success rate, and at migration probabilities close to 0.5 autocorrelation initially slightly increases, and then decreases invasion success. The result for this model and that of model 1 with $\alpha = \sqrt{0.7}$ are very similar. In both of these models, the spatial covariance is zero, since the two environments react differently to changes in environmental states.

When $\alpha = 0.9$, the fitnesses at the two locations are nearly equal for each of the environmental states (see Fig. 2). Since, furthermore, in this case the two locations are similarly affected by the environmental states, migration is not expected to have a large effect in this situation. This is indeed confirmed by the results. In the other cases it appears that for small values of η invasion success increases with migration probability, whereas for high temporal autocorrelation there is a maximum at a moderate value of λ.

For model 2, migration has only a slight effect at small values of η. At higher values of η there appears to be a maximum invasion success at intermediate migration probabiltities.

The effect of the spatial covariation parameter α in model 1 is monotonic. Regardless the migration probability λ or temporal autocorrelation (determined by η) the hazard rate decreases as spatial covariation increases. Results are shown in the supplementary material, but the effect can also be seen by comparing the subfigures for model 1 in Fig. 3. It appears that the highest invasion success rate is achieved at negative spatial covariation, high temporal autocorrelation and a moderate migration probability.

4.2 Long term population growth

Average logarithmic growth rates were estimated from simulations of population projection models (Eq. (1)), using sequences of $400,000$ time steps. For the case $\alpha = 0.9$ in model 1 the sequence lengths were increased to $800,000$ time steps, to achieve greater accuracy. The standard deviation of the estimated log-growth rates was estimated according to the method described in [16]. Its maximum value was less than $3 \cdot 10^{-4}$.

Figure 4 shows the effects of environmental autocorrelation and migration on long term population growth. Comparison with Fig. 3 shows that, whereas long term growth rate is a good predictor of establishment success in many situations, there are some striking differences. While in all situations the growth rates either increase or stay constant with increasing values of η, establishment success may decrease. This happens when environments are nearly identical (model 1, $\alpha = 0.9$), or when environmental covariation is close to zero and migration probabilities are high (model 1, $\alpha = \sqrt{0.7}$, and model 2). When $\lambda = 0$, too, establishment success decreases with η.

Thus, under circumstances that resemble a situation without spatial structure, i.e. with high spatial covariance, high migration probability, or complete absence of migration, long term growth rate appears to be affected by η in
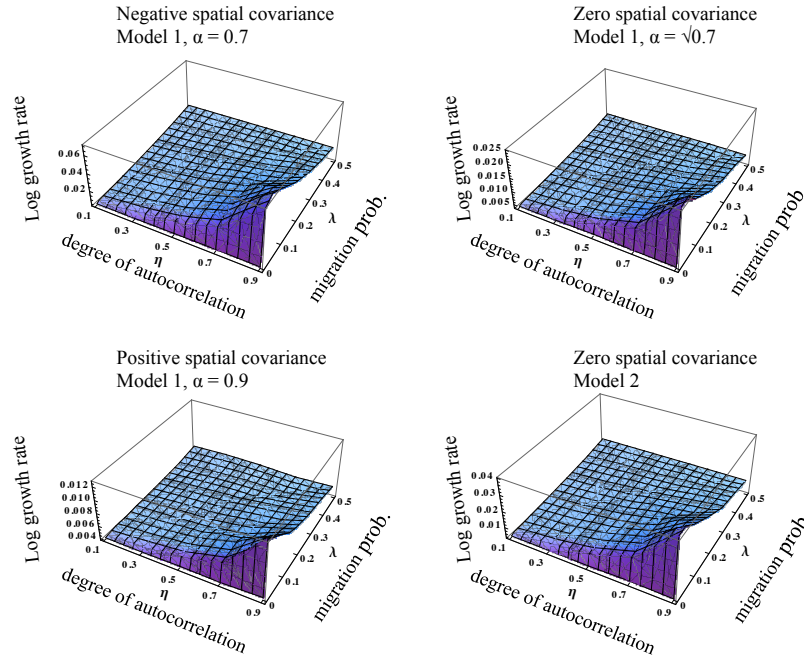
Figure 4: Effects of environmental autocorrelation η and migration probability λ on long term average logarithmic growth rates, for different types of spatio-temporal variation.

an opposite way to establishment success.

Effects of the spatial covariance parameter α in model 1 on long term growth rate are similar to those on establishment success (see figure in the supplementary material).

5 Discussion

We have combined three sources of stochasticity: demographic, temporal, and spatial variation, to examine establishment success of repeated invasions. Our results reconcile at first sight opposite findings on the effects of temporal autocorrelation on population dynamicss: the negative effect on establishment success of sequential invasions, found by [1], [2] and [4], and the positive effects on population persistence and abundance ([5], [6], [9]),

and population growth rate (e.g. [8] , [10], [11], and [12]). As we have shown, both effects can occur, and which one is prevalent depends crucially on the spatial structure of the receptor population. We will now discuss the mechanisms behind these effects.

The mechanism underlying the negative effect on establishment succces in spatially homogeneous, time-varying environments can be understood by considering that the expected chance of success of n successive invasions from time t onwards equals one minus the expected product of $q_t, q_{t+1}, \ldots, q_{t+n}$, where q_t is the probability that an invasion in time period t fails, conditional on the future environmental sequence (see [1]). Even in temporally independent environments, the q_t values are positively autocorrelated, because the progeny of successive invaders experience nearly the same environmental sequence ([1], [2]). Positive environmental autocorrelation is likely to enhance the covariance between subsequent q_t values. In the supplementary material it is shown that this increases the expectation of their product, and therefore decreases the establishment chance.

It was demonstrated in [4] that in a single-location version of our model the hazard rate of establishment is affected in a similar way, which is to be expected. However, [5], [6], and [7] found a positive effect of environmental autocorrelation on the abundance of populations established by repeated invasions into a sink habitat. Their explanation is that repeated immigration maintains the population, which can then capitalise on runs of good luck.

Note that there are essential differences between the models. Since [5] and [6] study invasions into a sink habitat without evolution of the invaders, populations will go extinct unless recurrent immigration occurs. In our models, however, whenever supercritical types are formed by recombination, extinction is not a certainty anymore, i.e. the habitat changes from a sink to a source (as in the metapopulation model of [7], which does include adaptive mutations). As long as no supercritical types have been produced, however, the situations are similar. Furthermore, factors that promote population abundance in sink habitats will also promote population growth in source habitats.

Therefore, their results indicate that environmental autocorrelation promotes the abundance of invaders. This enhances the chances that supercritical types are produced, and increases the growth rate of supercritical types. Thus it increases the chances of success of single invasions (it decreases the expected value of q_t). Our results and those of [4] show, however, that (at least under the conditions that we have examined), this effect is not strong

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enough to compensate for the detrimental effect of enhanced covariance between the establishment chances of successive invasions.

In spatially heterogeneous, temporally varying environments, migration can increase population growth rate (Wiener and Tuljapurkar [18]). An intuitive explanation for this is that migration allows a certain amount of bet hedging, allowing effects of bad conditions at some locations to be compensated by those of good conditions at other locations. Thus, at moderate migration probabilities, populations can grow and exploit runs of good luck, which becomes more profitable as environmental autocorrelation increases. However, this effect diminishes when migration probabilities become too large ([9], [10], and [11], and Fig.4). The reason for this is that locations that experience good environmental conditions will produce larger populations than those experiencing bad environmental conditions, which implies that larger numbers of migrants will go from good locations to bad ones than vice versa, especially in environments with low spatial covariation and high temporal autocorrelation.

Thus, moderate dispersal rates increase the positive effect of environmental autocorrelation on establishment success. Furthermore, in spatially heterogeneous environments with migration the autocorrelation between establishment success chances of successive invaders can be expected to be lower than in more homogeneous environments. Consequently, the strength of the mechanism with negative impact decreases.

As shown in Fig.3, the net outcome of these mechanisms depends on the spatiotemporal variation of the subpopulations. Temporal autocorrelation has a negative effect on establishment when spatial variation is low, migration probabilities are high, and/or different locations are affected by time-varying factors in a similar way (high spatial covariation). These are all aspects that make the receptor population more spatially homogeneous. When the receptor population is more spatially diverse, i.e. when locations vary differently in time, and migration probabilities have low to moderate values, however, temporal autocorrelation enhances establishment.

Whereas the effect of temporal stochasticity varies, we found that spatial heterogeneity facilitates establishment (Fig. 3 and supplementary material). This agrees with the results of [9], [10], and Melbourne et al. [19]. One of the factors contributing to this effect is that in environments with weakly negative to positive autocorrelation spreading invasions over different locations increases their probability of success [1] and [2].

Note that in random environments, each parameter combination leads to

a distribution of asymptotic hazard rates rather than a single value. Because the distributions are highly skewed, we represent their central tendencies by medians rather than means. The skewness is especially prevalent at values of α and η close to one, in combination with large migration probabilities. For instance, when $\alpha = 0.9$, skewness ranges from 3.2 to 4.5 (with the maximum attained at $\eta = 0.9, \lambda = 0.5$), and the ratio of the mean to the median ranges from 3 to 370. Using the means of the distributions would give a totally different picture. In fact, the results would then be similar to those of the asymptotic growth rate. This illustrates that the effect of demographic stochasticity on establishment success may be overlooked when using the wrong measures.

The extreme skewness of hazard rate distributions implies that, even though the vast majority of environmental sequences result in low hazard rates, rare sequences may bring about extremely large ones. This finding has consequences for risk management in the context of invasions. For instance, monitoring environmental changes might be a good strategy in such settings.

One of our main conclusions is that, when there are repeated invasions, establishment, persistence, and growth rate are three different aspects of population dynamics, that may be affected in different ways by spatial structure and temporal variation of the environment. This implies that including demographic stochasticity in models is crucial. Numerical analysis of such models may require excessive amounts of computer resources. Our method is very efficient, because it avoids simulation of individual branching processes, by using recursive relations between probability generating functions. This method assumes that density- or frequency dependence is either absent (i.e. 'hard selection', Wallace [20]), or negligible. In the context of introgression, frequency dependence does occur, because the chances of producing different genotypes are affected by the proportion of hybrids in a population. [13] showed, however, that, with parameters of a similar order of magnitude as we consider here, receptor population sizes of 100 individuals are already sufficiently large to be able to ignore the effects of frequency dependence on the hazard rate.

In practice, temporal autocorrelations in biotic as well as abiotic factors are likely to be positive (see e.g. Steele [21], Pimm and Redfearn [22], Wigley et al. [23], Cuddington and Yodzis [24], and Inchausi and Halley [25]). Our results indicate that with such temporal patterns, environments with high spatial diversity and moderate migration probabilities are most vulnerable to repeated invasions (see Figs. 3 and 4).

Insight in the way in which general environmental factors affect invasions may be useful to design mitigation strategies against introgression of genes from crops into wild resident populations, based on managing the spatiotemporal structure of nearby receptor populations. The importance of such characteristics of receptor populations for introgression of transgenes was pointed out previously by Meirmans et al. [26]. Our results also have implications in other contexts, such as invasions of exotic species in spatiotemporally varying metapopulations (as in [9]), or novel pathogens in heterogeneous host populations (e.g. [14]).

Funding

Acknowledgements

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