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Accounting for environmental change in continuous-time stochastic population models

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Abstract

The demographic rates (e.g., birth, death, migration) of many organisms have been shown to respond strongly to short- and long-term environmental change, including variation in temperature and precipitation. While ecologists have long accounted for such nonhomogeneous demography in deterministic population models, nonhomogeneous stochastic population models are largely absent from the literature. This is especially the case for models that use exact stochastic methods, such as Gillespie's stochastic simulation algorithm (SSA), which commonly assumes that demographic rates do not respond to external environmental change (i.e., assumes homogeneous demography). In other words, ecologists are currently accounting for the effects of demographic stochasticity or environmental variability, but not both. In this paper, we describe an extension of Gillespie's SSA (SSA+) that allows for nonhomogeneous demography and examine how its predictions differ from a method that is partly naive to environmental change (SSAn) for two fundamental ecological models (exponential and logistic growth). We find important differences in the predicted population sizes of SSA+ versus SSAn simulations, particularly when demography responds to fluctuating and irregularly changing environments. Further, we outline a computationally inexpensive approach for estimating when and under what circumstances it can be important to fully account for nonhomogeneous demography for any class of model.

Keywords Demographic stochasticity · Environmental change · Stationary · Non-stationary · Homogeneous · Nonhomogeneous · Environment-dependent demography · Stochastic simulation algorithm · Poisson process

Introduction

Ecologists use stochastic population models to account for intrinsic sources of population variability, particularly the variability arising from probabilistic demographic events at the individual level (e.g., random births and deaths), also known as demographic stochasticity. The importance of accounting for demographic stochasticity in populations is well established in the theoretical literature, where it has been shown to increase extinction risk (Shaffer 1981; Lande 1993; Ovaskainen and Meerson 2010), alter coexistence patterns (Orrock and Fletcher 2005; Orrock and Watling 2010; Okuyama 2015; Pedruski et al. 2015; Hart et al. 2016), increase the persistence time of disease (Bartlett 1957), and reduce spatial synchrony in metacommunities (Simonis 2012).

For continuous-time population models, the effects of demographic stochasticity can be approximated by adding white noise terms to differential equations (turning them from deterministic differential equations into stochastic differential equations (SDEs); e.g., Allen 2016) or by embedding such equations into standard probability distributions with an appropriate scaling term for the variance (e.g., the system-size expansion; van Kampen 1992). However, these approximations are generally accurate only for predicting small deviations from the expected value of the stochastic process (e.g., near stable equilibria; van Kampen 1992; Ovaskainen and Meerson 2010; Black and McKane 2012), and can fail to predict large deviations, such as those leading to population extinction (e.g., Wilcox and Possingham 2002; Doering et al. 2005; Kessler and Shnerb 2007). When predicting large deviations is important (e.g., for predicting

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extinction risk or modeling populations not at equilibrium), population models can be reformulated in terms of a set of differential equations that exactly describes the timeevolving probability density of the system (also known as Kolmogorov forward equations (Kolmogoroff 1931), or master equations). In practice, solving Kolmogorov forward equations is often infeasible (even numerically) for ecological systems (Keeling and Ross 2008), particularly those where the state space is large (e.g., systems with many species). A convenient alternative, which effectively samples from the probability density one would obtain by solving the forward equation, is Gillespie's stochastic simulation algorithm [SSA] (Gillespie 1977). Due to its tractability and the relative ease and speed of implementing the algorithm, the SSA is now commonly used in ecology to account for and explore the effects of demographic stochasticity in populations and communities (e.g., Kolpas and Nisbet 2010; Kramer and Drake 2010, 2014; Simonis 2012; Yaari et al. 2012; Gokhale et al. 2013; Huang et al. 2015; Vestergaard and Génois 2015; Nisbet et al. 2016; Palamara et al. 2016).

An important limitation of the SSA as it is currently used in ecology, is that it treats demographic processes, such as birth or death, as time-independent (i.e., as homogeneous [or stationary] Poisson processes). In other words, it assumes that the demographic rates of individuals depend only on internal state variables, such as population size, and otherwise do not change over time. This assumption may be adequate over short-time scales or when environmental conditions are constant (or tightly controlled), but is otherwise unrealistic. In natural systems, individuals often respond to factors that are external to typical population models and which themselves change over time. For example, the demographic traits (e.g., growth rate, birth rate, movement rate, feeding rate) of many species respond to temperature (Parmesan 2006; Deutsch et al. 2008; Angilletta 2009; Dell et al. 2011) and may change frequently within individual lifetimes as a result of short- or long-term temperature variability (e.g., Miquel et al. 1976; Kingsolver et al. 2013, 2015; Paaijmans et al. 2013; Estay et al. 2014; Stroustrup et al. 2016). Similarly, plant growth is strongly associated with precipitation (e.g., Novoplansky and Goldberg 2001; Fay et al. 2003; Angert et al. 2007; Heisler-White et al. 2008), an external factor which, like temperature, may vary considerably over the lifespan of an individual. The strong link between demography and changing environments is why ecologists routinely incorporate directional (e.g., increasing) or regular (e.g., fluctuating as a sine function) environmental change in deterministic models. Numerous studies have also considered the effects of environmental change in continuous-time stochastic models (e.g., Kaplan 1973; Mangel and Tier 1993; Marion et al. 2000; Allen et al. 2005; van den Broek and Heesterbeek 2007;

Varughese and Fatti 2008), but such studies generally use approximations involving moment closure, or use solutions to partial differential equations for probability generating functions (Bartlett 1955), which are known only for a few, simple ecological models (e.g., the linear birth-death process, Kendall (1948)). In comparison, SSA approaches are exact (given a sufficient number of simulations), may be used to simulate complex linear or non-linear processes, and require only the underlying intensity functions (i.e., demographic rates or transition probabilities) to be implemented. To our knowledge, no studies have considered the effects of environmental change and environment-dependent demography in SSA simulations. Thus, ecologists presently lack a tractable, efficient method for forecasting the effects of environmental change in realistic populations and communities.

Here, we describe an extension of the SSA that accounts for nonhomogeneous demography and allows demographic trait(s) to respond to nearly any kind of environmental change. Further, we explore how, under a variety of realistic environmental change scenarios, predictions using this method differ from the traditional, homogeneous SSA for models of exponential, and logistic growth (Verhulst 1845; Pearl and Reed 1920). We show that using a homogeneous (or stationary) SSA when demography is nonhomogeneous can lead to biased predictions about the effects of stochasticity on populations. Finally, we also outline a straightforward and computationally inexpensive approach for estimating in advance when ignoring nonhomogeneous demography will bias predictions of population size.

Methods

Nonhomogeneous demography in non-SSA models

Nonhomogeneous demography can be easily incorporated into standard deterministic models, either by converting one or more demographic parameters (e.g., birth rate) into time-dependent functions or, if demography is nonhomogeneous because of some external factor like temperature, by adding that factor as a new state variable and linking it to the relevant parameter(s) with an appropriate parameter or function (also known as a coupling factor; van Kampen 1992). This approach can also be used for stochastic differential equations (SDEs), since they are essentially deterministic equations either embedded in standard distributions or with added white noise terms that are independent of demographic rates or environmental variability. However, as previously discussed, these approximations commonly fail, particularly when there are large deviations from an equilibrium, as might be expected during rapid environmental change. As an exact approach to modeling stochasticity, the SSA has the potential to avoid such failings. However, additional challenges arise when trying to use it when demography is nonhomogeneous.

Gillespie's stochastic simulation algorithm (SSA)

We begin by describing the traditional (homogeneous) SSA (Gillespie 1977), also known as the direct method, and use a simple exponential growth model to illustrate the issue of nonhomogeneous demography. Other implementations of the algorithm have been proposed, such as the tau-leap method (Gillespie 2001), all of which sacrifice accuracy for simulation speed. As a result, we will not address these less accurate implementations here.

The basic SSA can be conceived of as iteratively answering two questions: (1) When does the next demographic process (e.g., birth, death) occur? and (2) Which demographic process occurs? It has four steps (Gillespie 1977):

- Set the rates/intensities of all demographic processes (i.e., the probability the processes occur, per unit time), the effects of those processes (e.g., birth = +1 individual), the starting population size(s), and the end time of the simulation.
- Determine the inter-event time (i.e., waiting time), τ, until the next demographic event by sampling from an exponential distribution with mean equal to the sum of the rates of all demographic processes.
- 3. Determine which demographic event occurs by sampling from the list of possible processes, the probability of each process conditioned on the fact that an event (of any kind) has occurred at $t + \tau$.
- 4. Update the time based on (2) and update population size(s) based on (3) [this may also change future demographic rates if they depend on population size], then return to step 2 until all demographic rates are zero or the end time has been reached.

Implementing the above algorithm is straightforward for most ecological models, the most difficult aspect often being the creation of the rate function(s) in step (1). For example, beginning with an exponential growth model with deterministic equation $\frac{dN}{dt} = rN$, a choice has to be made about whether the parameter r represents only a birth rate (i.e., we are modeling a *pure birth* process) or whether it represents the net effect of a birth rate minus a death rate (i.e., r = b - d). For the purpose of illustrating the SSA, we will keep things simple and model a pure birth process only, in which case r can be interpreted as the expected number of births per unit time. The stochastic formulation for a pure birth model (also known as Yule process; Yule 1925) can be represented as follows:

$$N \xrightarrow{r_N} N + 1 \tag{1}$$

Here, Eq. 1 means that births occur at rate rN and that each birth has the effect of increasing the population by 1. A single iteration through the SSA using this model, beginning at time t and population size N, would proceed in this manner: calculate the birth rate (rN), obtain a sample (τ) from an exponential distribution with mean equal to the birth rate, update the time from t to $t + \tau$, and update the population from N to N + 1.

The decision to sample from an exponential distribution to determine the timing of the next demographic event in the homogeneous SSA is based on assumptions about what it means for a demographic process to be "random." These assumptions are: (a) the process happens at some average rate within a given time interval, although when it happens in the interval is completely random (i.e., the occurrence times within an interval are uniformly distributed); (b) occurrence times of the process are independent of each other. Taken together, these assumptions describe what is known as a Poisson point process, which is used to represent random processes in continuous time across many disciplines (Cox and Isham 1980). One useful feature of these processes in the context of ecological models is that the occurrence time of a set of multiple, independent Poisson processes (e.g., a population experiencing both birth and death) can itself be described by a single Poisson point process with rate, λ , equal to the sum of the rates of the individual processes. For the purpose of modeling the timing of demographic events, it is therefore sufficient to consider only a single Poisson process with rate λ , even though λ may represent a mixture of multiple demographic processes.

When the rate, λ , of a Poisson point process is constant through time, it is called a homogeneous (or stationary) Poisson process and has inter-event times (i.e., times between event occurrences) that follow a cumulative distribution function (CDF), F(t), of the form (Ross 2014):

$$F(t) = 1 - \exp(-\lambda t) \tag{2}$$

Equation 2 is also the CDF of an exponential distribution, so it is possible to generate the inter-event times of a homogeneous Poisson process by sampling from an exponential distribution with rate λ . However, because it is generally faster computationally to sample from a uniform distribution than it is from an exponential distribution, it is common to obtain inter-event times of homogeneous processes by generating sample *U* from a uniform distribution on the interval [0, 1] and then converting it to the appropriate exponential random variable, *X*, using the inverse transform method (Devroye 1986), with equation $X = \frac{-1}{\lambda} \ln(1 - U)$.

Changing environments: nonhomogeneous Poisson processes

When the rate of a Poisson point process is not constant over time, for example, when it depends on changing temperatures, it is called a nonhomogeneous (or nonstationary) Poisson process (Cox and Isham 1980). In such cases, the rate of the process is described by a timedependent function, $\lambda(t)$, and the CDF for inter-event time τ , following the last occurrence of the process at time *T*, is (Ross 2014):

$$F(t) = 1 - \exp\left(-\int_0^t \lambda(T+\tau)d\tau\right)$$
(3)

In some cases, analytical solutions to the integral in Eq. 3 are available. For example, if the model can be represented with one nonhomogeneous Poisson process with a rate function of the form $\lambda(t) = \alpha t^{-\beta}$ (i.e., a power law function), Eq. 3 reduces to (Crow 1974; Finkelstein 1976):

$$F(t) = 1 - \exp(-\alpha (T+t)^{\beta} - T^{\beta}),$$
(4)

which is also the CDF of a Weibull distribution. Thus, for extremely simple nonhomogeneous processes, the traditional SSA can be modified to obtain τ via sampling from a Weibull distribution with scale parameter α and shape parameter β . However, many nonhomogeneous demographic processes will not follow a power law function. For example, if the birth rate *r* in the pure birth model (1) were time- or environment-dependent, the model becomes:

$$N \xrightarrow{r(t)N} N + 1 \tag{5}$$

Here, unless the time-dependent rate function $\lambda(t) = r(t)N$ can be expressed as $\alpha t^{-\beta}$, the Weibull method discussed above is not appropriate. Further, even if a particular demographic process could be described by a power law function, most population models will involve many different demographic processes and it is unlikely that the sum of all such processes could be expressed as a power law function.

For most population- or community-level models with any kind of complexity, analytical solutions to the CDF in Eq. 3 are unavailable. Various methods have been proposed to simulate such nonhomogeneous models (e.g., Boguñá et al. 2014; Vestergaard and Génois 2015; Duan and Liu 2015), most of which involve thinning or rejection sampling (Buffon 1774; Von Neumann 1951). We will not describe these methods here, other than to say that while they are often computationally efficient, they require bounded rate functions $\lambda(t)$ and do not perform well for high-dimensional systems (e.g., models of many species) (Ross 2014). In any case, our goal is not to propose the most efficient method for simulating nonhomogeneous biological processes, but rather to explore the conditions in which it is important to fully account for nonhomogeneous demography. Thus, we employ an exact, direct approach to simulating nonhomogeneous stochastic models.

The direct approach, which we will refer to as SSA+, replaces step (2) of Gillespie's SSA by generating τ using the inverse transform method, which can be implemented as follows:

- 1. Generate random number *U* from a uniform distribution on the interval [0, 1].
- 2. Find the value of X which solves F(X) = U, where F is the CDF in Eq. 3.
- 3. Set inter-event time τ to *X*.

Step (2) above is the major difference between homogeneous and nonhomogeneous SSAs, and can be accomplished by searching an interval (generally 0 to the maximum time of a simulation) for the root (zero) of the equation F(X) - U with respect to X. In Appendix B, we provide R code (using the base function *uniroot*) for this step.

Both the direct SSA+ method described here and the rejection-based methods mentioned previously are computationally expensive compared to a homogeneous SSA, and thus many ecologists might be willing to sacrifice some accuracy for a faster approach. One way to do so, which we will call the naive SSA (SSAn), would be to convert a nonhomogeneous process to a homogeneous one for each inter-event period by fixing $\lambda(t)$ to its value at the beginning of the inter-event period. This algorithm would continue to sample inter-event times from an exponential distribution and would be naive to changes in the environment only for the duration of an inter-event period.

Supposing $\lambda(t)$ was an increasing function (i.e., the rates of demographic events increased through time), one would expect the SSAn to, on average, produce inter-event times that were smaller than those produced by the exact SSA+ method. Since inter-event times determine when events occur in the simulations, for an exponential growth model, this method would predict smaller population sizes compared to the SSA+ method. However, for other kinds of models and/or patterns of environmental change, it is difficult to know a *priori* how the SSAn and SSA+ methods might differ. Therefore, to help generate some intuition about when such scenarios might arise, we explore how predictions of the SSAn and SSA+ differ for some common ecological models and a variety of environmental change scenarios.

Stochastic population models

To assess the importance of fully accounting for nonhomogeneous demography, we consider two population models: exponential and logistic growth. The deterministic forms of these models and their stochastic analogs are presented in Table 1.

Each model includes a density-independent birth rate, b(t), which we set as the nonhomogeneous demographic

Table 1 The ecological models considered in the study, specified as deterministic equations with their stochastic analogs

Model	Deterministic equations	Stochastic intensity functions
Exponential growth	$\frac{dN}{dt} = b(t)N - d(t)N$ where $b(t) = b_1 \cdot \text{env}(t)$ $d(t) = d_1$	<i>N</i> birth: $N \xrightarrow{b(t)N} N + 1$ <i>N</i> death: $N \xrightarrow{d(t)N} N - 1$
Logistic growth	$\frac{dN}{dt} = b(t)N - d(t)N$ where $b(t) = b_1 \cdot \text{env}(t)$ $d(t) = d_1 + d_2N$	<i>N</i> birth: $N \xrightarrow{b(t)N} N + 1$ <i>N</i> death: $N \xrightarrow{d(t)N} N - 1$

Parameters b_1 and d_1 are density-independent birth and death rates. Density-dependent growth in species N is incorporated with a densitydependent death rate, d_2 . For the stochastic intensity functions, the functions above the arrows have the same parameter values as their deterministic counterparts. The environment functions, env(t), are defined in Table 2

process in all our simulations. Specifically, we assume a fixed density-independent birth term, b_1 , which is multiplied by a time-dependent environment function, env(t), to produce a birth rate that changes through time. The models also include a homogeneous death rate, so that the probability of any event occurring is the sum of the birth and death rates and corresponds to the $\lambda(t)$ in Eq. 3.

We created time-dependent environment functions, representing six environmental change scenarios: (1) constant, slow increase (increasing 1); (2) constant, fast increase (increasing 2); (3) slow, regular fluctuations around a mean (fluctuating 1); (4) fast, regular fluctuations around a mean (fluctuating 2); (5) slow, irregular fluctuations around a mean (irregular 1); (6) fast, irregular fluctuations around a mean (irregular 2). The two increasing scenarios are analogous to a birth rate that increases as temperature increases, as might occur over a growing season or in an environment, where temperatures are gradually increasing over time. The two fluctuating scenarios are analogous to a birth rate that responds to fluctuating temperatures, as might occur in an environment with strong diurnal or seasonal temperature changes. Finally, the two irregular scenarios are analogous to a birth rate that responds to irregularly varying temperature fluctuations. Figure 1 shows the environment as a function of time for the functions we used (Table 2).

For implementing the SSAn method, we treated demography as homogeneous, but allowed rates to be updated after each step through the algorithm. In particular, we calculated the inter-event time of the next event, τ , by sampling from an exponential distribution with rate $\lambda = \lambda(t)$, where *t* is the current time of the simulation. As mentioned previously, this implementation is naive to changes in the environment for the duration of an inter-event period. In general, if the frequency of inter-event periods in a system far exceeds the rate of environmental change, we would expect SSAn results to closely approximate SSA+ results.

For each model and environment function, we ran 10,000 simulations of both the SSAn and SSA+ methods with a starting population size of N = 100, using the following parameter values: $b_1 = 0.003$ and $d_1 = 0.0027$; and



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 Table 2
 The environment functions or distributions considered in our simulations

Description	Environment function, $env(t)$
Increasing 1 Increasing 2	0.04t + 1 0.08t + 1
Fluctuating 1 Fluctuating 2	$\frac{\frac{\sin(t)+1}{1.5}}{\frac{\sin(2t)+1}{1.5}}$
Irregular 1	env(t) = spline({1, 2,, 100}, {Y ₁ , Y ₂ ,, Y ₁₀₀ }) where $Y_i \sim \mathcal{N}(\mu = 1.5, \sigma^2 = 0.25)$
Irregular 2	env(t) = spline({1, 2,, 100}, {Y ₁ , Y ₂ ,, Y ₁₀₀ }) where $Y_i \sim \mathcal{N}(\mu = 1.5, \sigma^2 = 0.50)$

To create time-dependent equations for the irregular simulations, we first sampled from a normal distribution (n = 100; one for each time step) then used spline interpolation on the samples to create a continuous-time function over which to integrate. Values outside the simulation interval were set as the mean of the distribution (1.5)

for the logistic growth model, $d_2 = 0.000003$ (with this parameterization, carrying capacity $K = \frac{b_1-d_1}{d_2}$). The above values were chosen such that individual demographic processes occurred somewhat slowly in comparison to the rate of environmental change (e.g., in the increasing 1 scenario, the environment changes by 0.04 per unit time, while the density-independent birth rate was 0.003 per individual over the same period). We ran both models to t = 100.

Comparing CDFs of inter-event times

Prior to examining the results of the simulations, we can derive some intuition about which models and environment functions may lead to important differences in the predictions of the SSAn and SSA+. One way to do so is to examine the CDFs of the waiting times for any event, τ , at t = 0 based on both homogeneous and nonhomogeneous treatments. Figure 2 shows these CDFs for each model and environment function. We can see from Fig. 2a, for example, that the CDFs of the SSA+ method are consistently higher than those of the SSAn. This suggests that demographic events will occur earlier in the SSA+ simulations, translating to higher population sizes over time. For fluctuating environment functions, as in Fig. 2b, differences between the CDFs of the SSAn and SSA+ are even more pronounced, as we might expect simply from looking at how quickly the environment changes in Fig. 1b compared to Fig. 1a. In Fig. 2c, the SSA+ CDFs appear to be somewhat lower than those of the SSAn, which we would expect to lead to lower projected population sizes for these early time points. Differences between the inter-event times appear smaller for the logistic growth model (Fig. 2df); thus, we expect to see smaller differences between SSAn and SSA+ results.

Diagnostics and analysis

We performed three independent diagnostic tests of our simulation algorithms. First, we tested our implementation of sampling inter-event times for nonhomogeneous processes. To do so, we simulated a nonhomogeneous process with a rate function of the form $\lambda(t) = \alpha t^{-\beta}$, a power law function. As discussed above, when a nonhomogeneous process has such a rate function, it is possible to obtain interevent times by sampling from a Weibull distribution with parameters α and β . We found nearly identical distributions of waiting times between ours and the Weibull method (Appendix A).

Second, we compared the results of SSAn and SSA+ simulations when the environment function was constant through time. As discussed above, the SSAn method treats demography as being homogeneous by obtaining waiting times from an exponential distribution, whereas the SSA+ method treats demography as nonhomogeneous by using the inverse transform method on the appropriate CDF to obtain waiting times. When the environment is constant, both methods should produce the same distribution of waiting times and, subsequently, the same distribution of population sizes over time. As expected, for both exponential growth and logistic growth with a constant environment function, both the SSAn and SSA+ algorithms produced nearly identical population size distributions (Appendix A).

To analyze the final simulation results (presented below), for each model and environment function, we compared the 95% confidence intervals for the mean across 10,000 replicate simulations of the SSAn and SSA+ methods at each interval time step, obtained using nonparametric bootstraps (percentile method; Davidson and Hinkley 1997). Prior to this, we tested whether 10,000 simulations were enough to accurately characterize the probability density of the stochastic processes. Specifically, we examined how the variation in population projections changed as more simulations were added. For all models and environment functions, there were minimal changes in the mean and standard deviation across simulations for resulting population sizes beyond 1000 simulations (Appendix A). Thus, running 10,000 simulations was more than sufficient to minimize Monte Carlo errors in the estimated means, and confidence intervals were very small.

Since the exponential growth model is linear with respect to population size, the only differences that should arise between the expected (mean) values of deterministic and stochastic versions of the model will be due to lattice effects (Henson et al. 2001), the impacts of which should be minimal at population sizes larger than 100 (as in our case). Thus, in addition to examining the confidence intervals, it is possible to directly compare the results of the SSAn and SSA+ simulations to numerical



Fig. 2 Cumulative probabilities over time (from t = 0) that the next demographic event of any kind will occur, for all models and environment functions. The top row highlights the probabilities for the exponential growth model for the **a** increasing; **b** fluctuating; and **c** irregularly changing environment functions, while the bottom row shows the probabilities for the logistic growth model (**d**–**f**). The solid

solutions of the deterministic equation for exponential growth in Table 1. In the absence of Monte Carlo error or lattice effects, if the SSA+ is properly accounting for nonhomogeneous demography, the mean value of the simulations at particular times should be equal to the solutions of the deterministic equations at those times. Since the logistic growth model is non-linear with respect to population size, both lattice effects and non-linear averaging will lead to differences between the expected values of deterministic and stochastic versions of the model. As such, we compare SSAn and SSA+ results to the deterministic results only for the exponential growth model. For all the simulations and analyses above, we used R, version 3.4.0 (R Core Team 2017), and for solving the deterministic equations, the R package "deSolve" (Soetaert et al. 2010). R code for SSAn and SSA+ simulations is provided in Appendix **B**.

line represents the probabilities for the SSAn method, which assumes that demographic processes occur at constant rates over time (in this case, the rate at t = 0). Dashed and dotted lines represent the probabilities obtained from the SSA+ method, which accurately accounts for nonhomogeneous demographic rates (compare to Fig. 1). At N(0), curves are similar for both models

Results

When the environment was changing, there were often differences in the predicted distributions of population sizes between the SSAn and SSA+ methods (Fig. 3; the [similar] results for the *slower* environment functions are in Appendix C). Generally, the magnitude of these differences corresponded with what could be predicted based on the CDFs in Fig. 2. For example, the distributions of population size predicted by the SSAn and SSA+ algorithms for exponential growth overlapped the least when the environment changed rapidly (Fig. 3b, c), the scenarios that had the largest differences in the CDFs between SSAn and SSA+ (Fig. 2b, c). Similarly, the predictions of SSAn and SSA+ logistic growth were fairly similar (i.e., distributions and expected values were similar) when there was an increasing environment function

Fig. 3 The frequency distribution of population sizes (N) at t = 100 for the exponential growth (a-c) and logistic growth (d-f) models, simulated using either the SSAn (red) or SSA+ (blue) method. Displayed are the population size distributions for environment functions: increasing two (a, d), fluctuating two (**b**, **e**), and irregular two (**c**, **f**). Colors are transparent, so purple indicates overlap between the SSAn and SSA+ methods. Also displayed are the expected values, \bar{N} , for each simulation method (same coloration as above). Note the different scales on both axes for each panel





(Fig. 3d), a function for which there were minimal differences between SSA and SSA+ inter-event times according to Fig. 2d.

Differences between exactly accounting for (SSA+) or not fully accounting for (SSAn) environmental change can also be seen in Fig. 4, which shows the 95% confidence intervals of the expected values over time for the SSAn and SSA+ methods (exponential growth). Furthermore, as expected from theory, the expected values from the SSA+ method closely match that of the deterministic version of the exponential growth model with a changing environment.

Differences in the expected values, \bar{N} , of the SSAn and SSA+ simulations were qualitatively consistent with the CDFs, in that their direction (higher or lower) could be predicted from Fig. 2. For example, for exponential growth the SSA+ CDF curves for increasing and fluctuating environment functions were generally above those of the SSAn curves, suggesting births (the only possible demographic events) would happen more frequently in the SSA+ simulations. Consistent with this, the mean

population size *N* of the SSA+ simulations for increasing and fluctuating conditions were higher at t = 100 than their SSAn equivalents. The CDFs for the irregularly changing environments (Fig. 2c, f) were a notable exception to this: The initial SSA+ CDF curves were below their equivalent SSAn curves at t = 0, but at t = 100, \overline{N} for SSA+ was higher than that of SSAn. This can be attributed to the fact that the irregular environment function gradually declined at early time points (shown in Fig. 2) but ultimately increased at later time points (not shown).

Discussion

Recent uses of SSAs in ecology explore cases where demographic traits (e.g., birth rate, feeding rate, death rate) are constant through time (Kolpas and Nisbet 2010; Kramer and Drake 2010, 2014; Simonis 2012; Yaari et al. 2012; Gokhale et al. 2013; Huang et al. 2015; Nisbet et al. 2016; Palamara et al. 2016), even though by now it is wellknown that such traits can and do respond to changing



Fig. 4 The 95% confidence intervals over time for the expected (mean) population size (N) of the SSAn (red) and SSA+ (blue) simulations of the exponential growth model. Displayed are the expected values (*y*-axis) for increasing 2 (**a**), fluctuating 2 (**b**), and irregular 2 (**c**) environment functions. Also displayed are the numerical solutions to the ordinary differential equation describing the deterministic versions of exponential growth with the same changing environment functions. In general, confidence intervals were tiny and may be hard to distinguish

environments. Here we described one method of extending the standard SSA algorithm to account for the added effects of nonhomogeneous demography (i.e., demography that changes through time) and examined a variety of scenarios and ecological models in which accounting for nonhomogeneous demography can be important. For exponential growth and logistic growth models, we found often large differences in the predicted distributions of population sizes between partly homogeneous (SSAn) versus nonhomogeneous (SSA+) implementations of the algorithm in changing environments. When demography changed rapidly—as in the case of demography responding to significant environmental variability—SSAn and SSA+ simulations differed markedly in their expected values and distributions (Figs. 3, 4). Moreover, these differences could generally be predicted *a priori* based on comparing the CDFs (Fig. 2) associated with the simulation methods.

We do not intend for this paper to be a criticism of homogeneous SSAs as there are numerous circumstances in which it is appropriate to treat demographic parameters as constant through time. Rather, because of the moderate computational cost of fully nonhomogeneous SSAs, one of our goals is to highlight the circumstances in which partly homogeneous SSAs and fully nonhomogeneous SSAs would differ substantially. Based on our findings, which compare a naive SSA that updates demographic rates only after each event (SSAn) to an SSA that fully accounts for continuously changing demographic rates (SSA+), these circumstances are (1) strong coupling between demographic traits and the environment (in our simulations, this coupling was always 1 to 1, with no lag); and (2) large environmental variability.

Research on thermal ecology and thermal performance over several decades suggests strong coupling between demography and environmental conditions, particularly for ectotherms and temperature (e.g., Davidson and Andrewartha 1948; Huey and Stevenson 1979; Huey and Kingsolver 1989; Adolph and Porter 1993; Deutsch et al. 2008; Angilletta 2009; Dell et al. 2011; Estay et al. 2011; Meisner et al. 2014). It is therefore already wellestablished that condition (1) is often satisfied in the natural world, particularly with respect to temperature. Regarding condition (2), environmental variability is also common in many systems and is likely to increase in the future. For example, inter-annual temperature variability has increased markedly in some regions in the past 50 years (Donat and Alexander 2012; Huntingford et al. 2013; Hartmann et al. 2013) and will probably continue to increase in the future (Collins et al. 2013). Similarly, rainfall is also highly variable over time (e.g., Loik et al. 2004) and can strongly influence demography, particularly in arid or semi-arid areas (Knapp and Smith 2001; Huxman et al. 2004). Thus, many natural systems satisfy the two conditions which favor the use of nonhomogeneous SSAs.

Understanding the interaction of environmental stochasticity and nonhomogeneous demography could be particularly important. In our work, the irregularly changing environment functions (irregular 1 and 2) followed specific (randomly generated) trajectories that did not differ between simulations. This approach effectively compared SSAn and SSA+ models for a single realization of a random environment, but did not compare them for randomly changing environments more generally. To fully assess how SSAn and SSA+ models might differ for randomly changing environments, one could employ stochastic differential equations for the environment functions, for example, modeling them as Ornstein-Uhlenbeck processes (Uhlenbeck and Ornstein 1930). Alternatively, one could run many SSA+ simulations for a set of realized stochastic environments, or generate different realizations of a random environment for each simulation. More broadly, if demographic traits respond to a randomly changing environment, the sum of all demographic rates (i.e., the rate that any demographic event occurs) may be treated as a doubly stochastic Poisson process, or Cox process (Cox 1955). While stationary Cox processes are relatively well-studied (e.g., Grandell 1976; Cox and Isham 1980), considerably less attention has been given to non-stationary Cox processes, especially in ecology.

As mentioned previously, various authors have suggested alternatives to the exact approach we used to sample inter-event times of nonhomogeneous Poisson processes, most of which use a variation of thinning or rejection sampling (Boguñá et al. 2014; Vestergaard and Génois 2015; Ross 2014; Duan and Liu 2015). However, we were not concerned with finding the most computationally efficient method for simulating nonhomogeneous SSAs. Indeed, our simulations would have been many times faster if they had been written in a lower-level language, such as C or FORTRAN rather than R. Rather, since both our exact approach (SSA+) and current rejectionbased methods are costly computationally (though not that costly: all our SSA+ simulations took less than a day to run on a single 12-core server), we were more interested in knowing when it was worth considering any nonhomogeneous simulation approaches. In doing so for some simple ecological models and environment functions, we also found a fairly general, computationally inexpensive approach-involving the comparison of easily calculated homogeneous and nonhomogeneous CDFsfor predicting when large differences between SSAn and SSA+ might arise. We suggest comparing such CDFs prior to deciding whether to implement any of the resourceintensive nonhomogeneous methods.

Some caution is necessary when deciding between homogeneous and nonhomogeneous approaches based on CDFs for particular time intervals. We examined initial CDFs (i.e., those beginning at t = 0) to gain some intuition about overlap between the SSAn and SSA+ methods, and while that intuition was correct for most models and environments considered, it failed for the irregular environment. This was because the irregular environment trended down at t = 0 but trended upwards near the end of the simulations. In Appendix D, we highlight the sensitivity of different starting points for the CDFs, showing that they largely match what one would expect from inspecting the trajectories of the environment functions at those different times (e.g., SSA+ CDFs are generally below SSAn CDFs during periods where the environment function is decreasing, and vice versa). However, it is straightforward to conceive of other cases, involving both highly variable environment functions or models with complicated state space, where examining one or a small number of CDFs would provide incomplete information about differences between SSAn and SSA+ methods; for instance, chaotic systems, systems that cycle (e.g., predator-prey models), and community-level models where individual species can go extinct. One way around this issue would be to compare CDFs across a broad range of time intervals and initial conditions.

We compared the predictions of homogeneous and nonhomogeneous implementations of Gillespie's stochastic simulation algorithm (SSA) when demography was nonhomogeneous, for two simple ecological models and six different environmental change scenarios. For our simulations, we allowed only a single model parameter (b_1) to be affected by a changing environment. We nevertheless found an important effect of nonhomogeneous demography for these simple, low-dimensional models. In real systems, multiple demographic traits have the potential to respond to the environment in different ways and such systems are also typically high-dimensional (i.e., contain many populations), non-linear, and have complicated dynamics. Our study should therefore be considered a fairly conservative test of the importance of fully accounting for nonhomogeneous demography in stochastic population models.

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Appendix A: Diagnostic tests of SSA+ method

To ensure we were generating appropriate inter-event times, τ , using our implementation of the SSA+ method, we performed two diagnostic tests:

1. We simulated a non-stationary exponential growth model using our SSA+ implementation with a rate function of $F(t) = \alpha t^{-\beta}$ (a power law function) and compared our results to taking samples from a Weibull distribution with parameters α and β , as discussed in the main text. These results should align nearly exactly if our implementation is correct, which appears to be the case (Fig. 5).



Fig. 5 The probability density of 1,000,000 arrival times, obtained by sampling from a Weibull distribution with scale parameter α and shape parameter β (black), or using our SSA+ method for a non-stationary stochastic process with rate function $F(t) = \alpha t^{-\beta}$ (blue). In both cases, $\alpha = 1$ and $\beta = 1.5$

Population size (N)

Fig. 6 The frequency distribution of population sizes at t = 100 for 50,000 simulations of exponential growth (**a**) and logistic growth (**b**), simulated using the SSA (red) or SSA+ (blue) methods with a constant environment. Colors are transparent, so the color purple indicates overlap between the SSA and SSA+ methods. Also displayed are the (overlapping) expected values, \overline{N} (rounded) for each simulation method

Fig. 7 The expected population sizes at t = 100 of the SSA+ method (exponential growth) for different numbers of simulations (x-axis). Displayed are the population sizes for the increasing (**a**), fluctuating (**b**), and irregularly changing (**c**) environment functions. Points represent the mean population size (across simulations), while bars are the standard deviations of the simulations

2. We set the environment function to a constant value (i.e., demography was stationary) and compared the results of 50,000 simulations of the SSA+ method to an independent SSA implementation (since demography is stationary in this case, we refer to it simply as the SSA rather than the SSAn, though both use the same methods). With a constant environment, the SSA+ method should match the SSA method, which appears to be the case (Fig. 6).

Finally, we also examined the extent to which 10,000 simulations was sufficient to capture the ensemble mean and variance of the stochastic simulations. To do so, we examined how the means and variances of the exponential growth models were affected by the number of simulations used. We found only very small differences in the means and variances from 1000 to 10,000 simulations used (see Fig. 7 for this comparison).

Appendix B: R code for SSA+ method

This section contains sample code for simulating 1 run of the Gillespie algorithm (SSA or SSAn in the main



```
## Function gillespie: SSA function (grid version)
2
   ## Performs one run of the homogenous SSA, outputting population sizes at different times.
3
   ## We refer to this as a 'grid' version because it does not record all events, rather it
   ## records the state of the system across a vector of monotonically increasing time points.
   ## The vector must begin with 0, but can otherwise be any size and need not be regular.
   ## The grid of times does not affect the accuracy of the simulation and can be easier to
   ## work with than a function that records all events.
8
9
  ##
  ## Function 'gillespie ' requires the following arguments:
10
  ##
     'init '= Array containing initial conditions (e.g. initial population size)
  ## 'times'=Vector of times over which to record the system state
   ##
       param '= Array containing all parameters and functions required for calculating intensities
      'inten '= Function which returns intensities of point process(es) given 'param'
   ##
14
   ##
       pproc '= Array containing state changes caused by point process(es) [same order as 'inten ']]
   ## 'hpp'=Function for sampling inter-event times
16
   ##
   gillespie <- function(init, times, param, inten, pproc, hpp){
18
      if(length(times) == 0)
19
         stop ("No time points provided in 'times '")
20
      else if (times [1] != 0)
        stop ("First time point is not 0")
      } else {
         tottime <- times [1]
24
         tinc <- length(times)
25
         N <- init
26
         results <- matrix (nrow = tinc, ncol = length (init))
         results [1, ] <- N
28
         for(i in 2:tinc){
29
              results[i,] <- results[i - 1,]
30
31
              while(tottime <= times[i]){</pre>
                  intentemp <- inten(tottime, N, param)
32
                  if (all(intentemp == 0)){
                     results [i:tinc, ] <- N
34
                     i <- tinc
35
                     warning ("Exiting with all intensities equal to 0")
36
                     break
                 } else if (\min(\operatorname{intentemp}) < 0) {
38
                     results [i:tinc, ] <- NA
39
40
                     i <- tinc
                     warning ("Exiting with intensity less than 0")
41
                     break
42
                 } else {
43
                     tau <- hpp(intentemp)
44
45
                     tottime <- tottime + tau
46
                     which.pproc <- sample(1:nrow(pproc),
47
                                             size = 1
                                             prob = intentemp)
48
                     if (tottime > times[i])
49
                         results [i, ] <- N
50
                         N <- N + pproc [ which . pproc , ]
51
52
                         break
                     } else {
53
                         N \ll N + pproc[which.pproc, ]
54
55
                 }
56
57
            if (i == tinc) break
58
59
        cbind(times, results)
60
     }
61
  }
62
63
  ## Function hpp: inter-event time sampling function (homogenous Poisson process)
64
65
  ## Argument 'intentemp' is the output of the intensity function at a given time
```

```
66 ##
   hpp <- function (intentemp) {
67
    -(1 / (sum(intentemp))) * log(1 - runif(1))
68
69
   }
70
   ## Function nhpp: inter-event time sampling function (nonhomogenous Poisson process)
71
   ## Generates inter-event times for a continuous nonhomogenous process using inverse transform
   ##
   ## Function 'nhpp' requires the following arguments (provided by 'gillespie_plus' below):
74
   ## 'tottime '= Current time of simulation
75
   ## 'N'=Current system state
76
   ## 'param'=Array containing parameters and functions required for calculating intensities
   ##
       'inten '= Function which returns intensities of point process(es) given 'param'
78
   ##
       'timeleft '= Time left in the simulation
79
80
   ## Subdivisions and tolerances (in integrate) may be altered to increase speed or precision.
   nhpp <- function(tottime, N, param, inten, timeleft){
81
     tryCatch(uniroot(function(X, Y) {
82
         1 - exp(-integrate (Vectorize (function (X) {
83
             sum(inten(tottime + X, N, param)), 0, X, subdivisions = 200, subdivision - Y,
84
                      lower = 0, upper = timeleft, tol = 1e-5, Y = runif(1))$root,
85
86
              error = function(c) timeleft + 1)
   }
87
   ##
88
   ## Function gillespie_plus: SSA+ function (grid version)
89
   ## Performs a run of the nonhomogenous SSA, outputting population sizes at different times.
90
   ## The only major difference between this and 'gillespie' is the use of 'nhpp' over 'hpp'.
91
92
   ##
   gillespie_plus <- function (init, times, param, inten, pproc, nhpp) {
93
    if(length(times) == 0){
94
95
         stop ("No time points provided in 'times '")
    else if (times [1] != 0) 
96
         stop ("First time point is not 0")
97
98
    } else {
         tottime <- times [1]
99
         tinc <- length(times)
100
        N <- init
101
         results <- matrix (nrow = tinc, ncol = length(init))
102
         results [1, ] <- N
103
104
         for(i in 2:tinc){
             results [i, ] <- results [i - 1, ]
105
             while(tottime <= times[i]){</pre>
106
                 intentemp <- inten(tottime, N, param)
107
                 if (all(intentemp == 0)){
108
                      results [i:tinc, ] <- N
109
                     i <- tinc
                     warning ("Exiting with all intensities equal to 0")
                     break
                 } else if (min(intentemp) < 0) {
                      results [i:tinc, ] <- NA
114
                      i <- tinc
                     warning ("Exiting with intensity less than 0")
116
117
                      break
                  } else {
118
                       tau <- nhpp(tottime, N, param, inten, (times[tinc] - tottime))
119
                       tottime <- tottime + tau
120
                       intentemp <- inten(tottime, N, param) # recalculate for new tottime
                       which.pproc <- sample(1:nrow(pproc),
                                          size = 1,
                                          prob = intentemp)
124
                       if (tottime > times[i]) {
                           results [i, ] <- N
126
                           N <- N + pproc [which.pproc, ]
128
                           break
                       } else {
```

```
N <- N + pproc[which.pproc, ]
130
                       }
                   }
              if (i == tinc) break
134
135
          cbind(times, results)
136
       }
138
   }
139
   ####### Example application of 'gillespie ' and 'gillespie_plus' [exponential growth]
140
   ## Initial population size
141
   init <- 100
142
   ## Times
143
   times <- seq(0, 10, 1)
144
   ## Terms for 'param' list
145
   ### Environment function (constant)
146
147
   constant <- function(t) 1
   ### Demographic functions
148
   exponentialfun <- list (
149
150
     births = function(b, envres) b * envres,
      deaths = function(d, envres) d
151
152
   )
153
   ### Combine parameters and demographic functions into list
   param <- list (b = .03, d = .027, exponential fun, env = constant)
154
   param <- unlist(param) # collapse to one-dimensional list
155
   ## Intensity functions which use the demographic functions (above)
156
   inten <- function(t, X, param){
157
    with (as.list(c(param)), {
158
         bint <- X * births(b, env(t))</pre>
         dint <- X * deaths(d, env(t))
160
         c(bint, dint)})
161
162
   ## State changes caused by the point processes (birth = N + 1, death = N - 1)
163
   pproc \ll matrix(c(1,-1), nrow = 2)
164
   ## Run 1 simulation of gillespie and gillespie_plus
165
   set.seed(20170915)
166
   gillespie(init, times, param, inten, pproc, hpp)
167
168
   set.seed(20170915)
  gillespie_plus(init, times, param, inten, pproc, nhpp)
```

text) and 1 run of the extended, nonhomogeneous (i.e., non-stationary) version of the algorithm (SSA+) for an exponential growth model. The code is specifically designed to allow for environment- or time-dependent demography, but in this example the environment is constant. Additional code and more detailed examples are available at https://github.com/legault/SSAplus.

Appendix C: Comparison of SSAn and SSA+ for slower environment functions

In Fig. 8, we compare SSAn and SSA+ predictions for the slower environment functions, specifically "increasing 1", "fluctuating 1", and "irregular 1". The qualitative results are

169



Fig.8 The frequency distribution of population sizes at t = 100 for the exponential growth (**a**–**c**) and logistic growth (**d**–**f**) models, simulated using either the SSAn (red) or SSA+ (blue) method. Displayed are the population size distributions for environment functions: increasing 1 (**a**, **d**), fluctuating 1 (**b**, **e**), and irregular 1 (**c**, **f**). Colors are transparent,

so purple indicates overlap between the SSAn and SSA+ methods. Also displayed are the expected values, \bar{N} (rounded to nearest integer), for each simulation method (same coloration as above). Note the different scales on both axes for each panel

similar to those in Fig. 3 (in main text), albeit with more overlap between the distributions.

Appendix D: CDFs beginning at different time points

In Fig. 9, we compare the CDFs for the exponential growth model assuming the simulations began at t = 3 (Fig. 9a–

c) or t = 5 (Fig. 9d–f), with respect to the environment functions. For the fluctuating and irregular environments, these CDFs differ from those displayed in Fig. 2 of the main text. For example, at t = 3 environment function "fluctuating 1" is decreasing rapidly thereby lowering the birth rate and consequently the CDF in Fig. 9b. In contrast, the function "fluctuating 2" is increasing rapidly at t = 3and the resulting CDF is elevated compared to the SSAn CDF. Fig. 9 Cumulative probabilities over time (starting at t = 3 for $(\mathbf{a}-\mathbf{c})$; at t = 5 for $(\mathbf{d}-\mathbf{f})$ that the next demographic event will occur for the exponential growth model under increasing (a, d), fluctuating (**b**, **e**), and irregular (c, f) environments. The solid lines represent the probabilities for the SSAn method, which assumes that demographic processes occur at constant rates over time (in this case, the rate at t = 3 or t = 5). Dashed and dotted lines represent the probabilities obtained from the SSA+ method, which accurately accounts for nonhomogeneous demographic rates (compare to Fig. 1). As in Fig. 2, the CDFs assume an "initial" (i.e., beginning at t = 3or t = 5) population size of 100

1.0

0.8

0.6

0.4

0.2

0.0

1.0

0.8

0.6

0.4

0.2

0.0

Probability event has occurred

Probability event has occurred

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6 7 8

8

10

9



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