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Quantifying species extinction risk under temporal environmental variance

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ABSTRACT

Species populations are subjected to fluctuations in their surrounding environment, and the strength of these fluctuations has been hypothesized to be a major determinant of the extinction risk of these populations. Therefore, a key question is: How does temporal environmental variance affect the extinction risk of species populations? Previous theory based on the dynamics of single populations typically predicts an increased risk of extinction from the effects of environmental variance. However, previous studies have focused mainly on the case where environmental effects are temporally uncorrelated (white environmental noise), whereas such effects are typically correlated (colored environmental noise) in nature. Thus, further work on the case of colored environmental noise is required, but this has been hindered by the analytical intractability of corresponding stochastic models. In our study, we address this limitation by developing a new discrete-time Markov chain model of a species population fluctuating under colored environmental noise, with the simplification that the effects of demographic variance are manifested indirectly as an extinction threshold. This simplifying assumption allows us to derive analytical solutions, which show that the expected extinction time of model species declines with the strength of environmental variance under a variety of different scenarios, reflecting greater extinction risk. Our study thus clarifies the situations under which environmental variance tends to increase extinction risk, and provides a novel analytically tractable framework for modeling temporal environmental variance. We also discuss the possible implications of our results for species richness in ecological communities.

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1. Introduction

Ecology aims to develop and test hypotheses about the processes that structure biodiversity in ecosystems across the world. A major driver of ecological dynamics is temporal environmental variance, which affects all ecological communities to some degree. Examples include the effects of forest fires (Ahlgren and Ahlgren, 1960; Turcq et al., 1998), tropical storms impacting coral reef ecosystems (Connell, 1997; Gardner et al., 2005) and human harvesting (Jackson et al., 2001; Ceballos et al., 2015). Temporal environmental variance is likely to increase in the future, especially given future projections of increased variance under continued climate change (Knapp et al., 2008), and this

provides an additional motive for understanding its effects on ecological communities and the populations of species that comprise them. Furthermore, temporal environmental variance has been found to be important for correcting the gross underestimates of temporal changes in biodiversity by neutral models (Nee, 2005; Chisholm and O'Dwyer, 2014; Chisholm et al., 2014; Kalyuzhny et al., 2015; Fung et al., 2016a).

Early population models showed how temporal environmental variance (hereafter, “environmental variance”) can increase the extinction risk of species populations (Leigh, 1981; Lande, 1993; Foley, 1994). These predictions have partial support from empirical data. For example, time-series analyses of 53 temperate lakes in North America and Europe found that larger fluctuations in pH, phosphorus and dissolved organic carbon were associated with fewer species of zooplankton (Shurin et al., 2010). Similar processes may operate over geological timescales: regions with historically stable climates, such as the tropics and the Cape

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Floristic Region of South Africa, tend to have higher present-day floristic diversity and this has been attributed to lower extinction rates (Wallace, 1878; Huntley et al., 2014).

A limitation of the early theoretical results on this topic (Leigh, 1981; Lande, 1993; Foley, 1994) is that they were derived from models that assumed environmental effects are uncorrelated or largely uncorrelated in time, which correspond to the case of white environmental noise. However, environmental variables have often been found to exhibit substantial positive correlations over timescales of days to millennia (Steele, 1985; Inchausti and Halley, 2002), which correspond to colored environmental noise (Halley, 1996). Examination of the case of colored environmental noise has been hampered by a lack of analytical tractability in corresponding stochastic models (Ovaskainen and Meerson, 2010). For colored environmental noise, Kamenev et al., 2008 derived an analytical formula for expected extinction time, but only when the temporal correlation in environmental effects are very large. In contrast, Fung et al. (2016b) analyzed a master-equation model that incorporated colored environmental noise with any degree of temporal correlation, and derived formulae specifying the expected species lifetime. Using these formulae, they found that expected species lifetime increased with the degree of temporal correlation for specific sets of species demographic rates, implying lower extinction risk when environmental noise was colored instead of white (Fung et al., 2016b). But the formulae were complicated and did not provide a clear, general understanding of how extinction risk changed with different regimes of environmental variance.

Given the variety of predictions from models with environmental variance, a current research priority is to establish quantitative criteria for predicting the conditions under which environmental variance increases or decreases extinction risk, particularly in the case of colored environmental noise. To address this need, we develop here a new analytically tractable model describing the non-linear dynamics of a population exposed to fluctuating environmental disturbances, which may exhibit weak to strong correlations in time. Afterwards, we analyze the model to show how extinction risk in the model typically increases with the strength of environmental variance, conceptualized as the degree to which environmental factors change the population growth rates of species over time. We conclude by relating our results to those of previous models and discussing general implications for the role of environmental variance in shaping the persistence of species populations and hence biodiversity.

2. Methods

2.1. Model description: biological perspective

We begin by constructing a population model that describes how the abundance of a species fluctuates under random changes in the environment. We choose to represent the dynamics using a discrete-time Markov chain process because this allows temporally correlated environmental effects on species abundance to be represented simply as transition probabilities, integrating the correlated effects over a discrete time-step. At the end of each time-step, the environmental regime randomly changes, such that environmental effects are uncorrelated between time-steps. In addition, representation of our model using a discrete-time Markov chain allows us to take advantage of mathematical theory available for computing the expected extinction time of a model species (Brémaud, 1999). The model represents the abundance of a species on a log-scale to allow simpler representation of the transition probabilities. Technically, the log-abundance of a species extends to negative infinity and never reaches a value corresponding to an abundance of zero; therefore, it is necessary to impose a

log-abundance extinction threshold below which the effects of demographic variance are implicitly assumed to cause extinction. Following classic population models with environmental variance (Leigh, 1981; Lande, 1993; Foley, 1994), we set a log-abundance of zero as the extinction threshold, which corresponds to an abundance of one on a linear scale. Furthermore, again following classic population models (Leigh, 1981; Lande, 1993; Foley, 1994), a carrying capacity is imposed on each species population. This implicitly represents negative density-dependence caused by processes such as resource limitation, intraspecific competition and density-dependent predation (e.g., Janzen, 1970; Connell, 1971; Harms et al., 2000; Webb et al., 2006; Comita et al., 2010; Bagchi et al., 2014).

In the first version of our model, the log-abundance of the model species is assumed to fluctuate according to a truncated symmetric Laplace distribution (SLD) (also referred to as a symmetric double-exponential distribution), where the truncation is from above, with the maximum value representing the species carrying capacity. In the second version of the model, the log-abundance is assumed to fluctuate according to a truncated asymmetric Laplace distribution (ALD), which allows greater flexibility over how environmental variance affects species abundance. The ALD includes the SLD as a specific instance, when the asymmetry is zero. Our choice of an ALD is based on the reasonably good fits that it provides to changes in tree species abundances in 12 temperate and tropical forest communities around the world (Chisholm et al., 2014).

Fig. 1 shows a schematic diagram of our model, highlighting the key biological processes modeled.

2.2. Model description: mathematical perspective

In the first version of the model, during one time-step, the probability of the model species transitioning from log-abundance y given that it has log-abundance x is defined by the probability distribution function (pdf)

$$f_1(y|x) = B_1 \exp(-\gamma|x - y|), \quad (1)$$

where the parameter γ measures the rate of decay of the probability density either side of x and $-\infty < x, y \leq A$. Here, A is the maximum abundance on a log-scale with base a , so that $K = a^A$ is the maximum abundance on a linear scale, i.e. the species' carrying capacity. Also, the parameter B_1 is a normalization constant given by

$$B_1 = \frac{\gamma}{2 - e^{\gamma(A-x)}}. \quad (2)$$

Eq. (1) is the pdf of a truncated SLD (Fig. 2). It can be shown that the smaller the value of γ , i.e. the greater the value of $1/\gamma$, the greater the expected absolute change in log-abundance over one time-step (Appendix A in Supplementary material). Furthermore, it can be shown that the greater the value of $1/\gamma$, the greater the expected deviation of the instantaneous population growth rate from zero in one time-step (Appendix A in Supplementary material) – this growth rate reflects the net balance of the rate at which new individuals are recruited and the rate at which existing individuals die, and changes randomly across time-steps (Appendix A in Supplementary material). Together, these results imply that $1/\gamma$ is a measure of the strength of environmental variance on changes in species abundance, as mediated by changes in key demographic rates.

To permit application of Markov chain theory for discrete-time processes with discrete states, we sample the continuous log-abundance scale at equidistant points (later, after derivation of formulae for extinction times, we move back onto the continuous log-abundance scale by taking the limit as the distance between

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