

How Is Extinction Risk Related to Population-Size Variability over Time? A Family of Models for Species with Repeated Extinction and Immigration

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ABSTRACT: It is well known that for an isolated population, the probability of extinction is positively related to population size variation: more variation is associated with more extinction. What, then, is the relation of extinction to population size variation for a population embedded in a metapopulation and subjected to repeated extinction and recolonization? In this case, the extinction risk can be measured by the extinction rate, the frequency at which local extinction occurs. Using several population dynamics models with immigration, we find, in general, a negative correlation between extinction and variation. More precisely, with increasing length of the time series, an initially negative regression coefficient first becomes more negative, then becomes less negative, and eventually attains positive values before decreasing again to 0. This pattern holds under substantial variation in values of parameters representing species and environmental properties. It is also rather robust to census interval length and the fraction of missed individuals but fails to hold for high thresholds (population size values below which extinction is deemed to occur) when quasi extinction rather than true extinction is represented. The few departures from the initial negative corre-

lation correspond to populations at risk: low growth rate or frequent catastrophes.

Keywords: metapopulation, extinction rate, population variability, immigration rate.

How should variation in population size over time be related to extinction rate? For an isolated population, one might intuitively expect a positive relation between extinction and temporal variability in population numbers: more variable populations should become extinct more frequently (Inchausti and Halley 2003). This intuition is bolstered by theory; stochastic variability in parameters as formulated in some dynamic models (Tuljapurkar 1990; Lande 1993; Foley 1994; Halley and Iwasa 1999; Hakoyama and Iwasa 2000) increases extinction risk. However, in these models, extinction is measured by probability of extinction or time to extinction, and the population is assumed closed.

For a population belonging to a metapopulation, repeated extinction and recolonization occur locally. In this case, extinction risk is estimated by an empirical quantity, the extinction rate, the frequency at which local extinction occurs. When the extinction risk is measured by the extinction rate—computed from the observed population size time series—should we still expect a positive correlation between extinction risk and population size variation? This is a question of conservation interest because temporal variability in population numbers can be measured and can potentially be used to assess the risk of extinction. In fact, the empirical answer to the above question is uncertain. While data on birds support a positive relation (Karr 1982; Pimm et al. 1988; also see Tracy and George 1992; Vucetich et al. 2000), data on mammals (Lima et al. 1996) and spiders (Schoener and Spiller 1992) support a negative relation. Could such taxonomic differences hint at an underlying mechanistic explanation, or is there some axis along which the studies divide that is mainly methodological?

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In the relationship between population size variability and metapopulation dynamics (Hanski and Gilpin 1997; Lecomte et al. 2004), two important parameters have been found in theory to influence deeply metapopulation extinctions: connectivity (or immigration-emigration rate) and pattern of environmental fluctuation (Heino et al. 1997; Ylikarjula et al. 2000; Hanski 2001). Morris and Doak (2002) propose the following classification. For high dispersal rates, individuals mix among sites, and the metapopulation can be considered a single population. For low to medium dispersal rates, the metapopulation viability depends on correlation in population size variation among sites. In the case of low or negative correlation, migrants from populated patches can rescue declining or extinct patches in their vicinity, whereas positive correlation entails the risk of coextinction. It is difficult, however, to test this theory qualitatively (Lecomte et al. 2004) and to compare its predictions quantitatively to actual extinction rates because few species have been studied in a metapopulation framework (Inchausti and Halley 2003). At the local scale, predictions of extinction risk obtained from viability analysis and derived from population size estimates might be flawed because (1) immigration can act as a rescue effect, especially when temporal variability is not spatially correlated (Hanski and Gilpin 1997), and (2) the species life cycle might itself entail population size variation (Schoener et al. 2003) without necessarily contributing much to extinction (Gaillard et al. 2000). Moreover, as Inchausti and Halley (2003) point out, variability in demographic parameters is not the same as variability in population size, the latter being a derived quantity. Finally, those species with large fluctuations in population size might also be those having the largest dispersal rate (Clobert et al. 2004), that is, immigration rate.

In this study, we use several population dynamics models incorporating immigration to generate time series from which both extinction rate and population size variation are computed. The surprising result is that for a local population subjected to repeated extinction and immigration, there is a generic pattern linking variation and extinction along time: a strong negative relation is replaced by a weaker positive one as observation time progresses. Thus, under biologically realistic assumptions on population dynamics and observation conditions, for a local population supplemented by immigration, more variation is generally associated with less extinction. We show that this pattern is usually preserved under a range of variation in (1) intrinsic properties of species (e.g., growth rate, immigration rate, and age structure), (2) environmental parameters (e.g., magnitude of environmental stochasticity and strength and kinds of density dependence), and (3) methodological properties (e.g., frequency of observation

and likelihood of missing various fractions of individuals actually present).

Methods

Measure of Variation in Population Size

Several measures are possible (see Schoener and Spiller 1992). Here we used the coefficient of variation of population size with zeros excluded (CVZ; this measure behaves in a way similar to that of most other proposed measures; see “Results”). In our models, population size along time, $n(t)$, is an integer and is 0 when extinction occurs. We denote by $z(t)$ the number of zeros among $n(t)$, that is, the number of dates $\tau \leq t$ such that $n(\tau) = 0$. The CVZ is computed by taking the series of population sizes up to time t , removing the 0 values of this series (in $z(t)$), and computing the coefficient of variation (CV; standard deviation over mean) of the resulting series.

Measure of Extinction Rate

Let $\varepsilon(t)$ denote the number of extinction events up to time t , that is, the number of dates $\tau \leq t$ such that $n(\tau - 1) > 0$ and $n(\tau) = 0$. The extinction rate at time t is defined as

$$E(t) = \begin{cases} \frac{\varepsilon(t)}{t + 1 - z(t)} & \text{if } n(t) = 0 \\ \frac{\varepsilon(t)}{t - z(t)} & \text{if } n(t) > 0 \end{cases}.$$

For example, suppose the series is 00XXXX0X0 (where X indicates a nonzero population size). There are five chances to observe extinction, and it is observed twice, so the frequency of extinction is 2/5 (first case). Now suppose the series is 00XX0XX0X. There are four chances to observe extinction, and it is observed twice, so the frequency is 2/4 (second case). The measure is identical to that used by Schoener and Spiller (1992).

Measure of Colonization Rate

Let $\iota(t)$ denote the number of colonization events up to time t , that is, the number of dates $\tau \leq t$ such that $n(\tau - 1) = 0$ and $n(\tau) > 0$. The colonization rate at time t is defined as

$$I(t) = \begin{cases} \frac{\iota(t)}{z(t) - 1} & \text{if } n(t) = 0 \\ \frac{\iota(t)}{z(t)} & \text{if } n(t) > 0 \end{cases}.$$

Quasi Extinction

The preceding definitions can be extended to the case of quasi extinction (Inchausti and Halley 2003), in which population size is compared to an extinction threshold H . Quasi extinction occurs when population size $< H$. The function $z(t)$ can be replaced by $z_H(t)$, the number of dates $\tau \leq t$ such that $n(\tau) < H$ (instead of $n(\tau) < 1$). In this case, “zeros excluded” means “populations sizes $< H$ excluded.” Similarly, the function $\varepsilon(t)$ can be replaced by $\varepsilon_H(t)$, the number of dates $\tau \leq t$ such that $n(\tau - 1) \geq H$ and $n(\tau) < H$.

Basic Simulation Assumptions and Procedures

We assume that initial population size is 0 individuals (individuals first enter the population by immigration) and (to remove the initially transient behavior) that the population is observed from some date $t_1 \gg 0$. This assumption corresponds to the natural situation of a population that started with 0 individuals in the past at time 0 and then arose by immigration and was subjected to its own dynamics shaped by the local environment. We now observe this population at time t_1 .

Measures of population variation (V) and extinction rate (E) are computed from time t_1 , when we start observing the population. We use $t_1 = 1,000$. In fact, the value of t_1 has no effect on the results, provided that it is large enough that the initial condition has been forgotten by the dynamical system. Also, because initial population size is 0, some immigration is expected to occur before time t_1 , requiring immigration rate $i > 1/t_1 = 0.001$. We plot E versus V for 1,000 trajectories of the model and compute the regression line (fig. 1). Let $a(\tau)$ be the slope of the regression line (V, E) at observation time τ (i.e., at time $t = t_1 + \tau$). We are interested in the behavior of $a(\tau)$ along time. This kind of plot, the variation/extinction relationship, represented by $a(\tau)$ along time, is hereafter called the VE relation. Most of our results are expressed in this format.

Models

We study the VE relation for several models with increasing realism and complexity.

1. *Patch occupancy model.* We first consider a stochastic patch occupancy model, where we observe a single patch colonized with constant probability i and becoming extinct with constant probability e . The occupancy of the patch along time is

$$o(t + 1) = \begin{cases} \text{Ber}(1 - e) & \text{if } o(t) = 1 \\ \text{Ber}(i) & \text{if } o(t) = 0 \end{cases} \quad (1)$$

where $\text{Ber}(m)$ denotes a sample of the Bernoulli distribution with mean m . For this model only, we use the empirical variance at time t as a measure of variation (the CVZ cannot be used). In this model, there is variation in patch occupancy along time but no variation in population size.

2. *Expanded patch occupancy model.* This model modifies the previous one to allow for minimal population size variation:

$$p(t + 1) = \begin{cases} \text{Ber}(1 - e) + \text{Ber}(i) & \text{if } p(t) \geq 1 \\ \text{Ber}(i) & \text{if } p(t) = 0 \end{cases} \quad (2)$$

Here population size is 0, 1, or 2. The parameter i is the probability of immigration of a single individual (and not the probability of colonization; immigration can occur at any time), and e is the probability of extinction.

3. *Continuous-time population dynamics model.* We use the logistic birth-death process (Lambert 2005) with immigration. This model accounts for demographic stochasticity by construction and incorporates density dependence to avoid population explosion. Population size varies along continuous time according to the rules

$$\begin{aligned} n &\rightarrow n + 1 && \text{with rate } bn + i, \\ n &\rightarrow n - 1 && \text{with rate } dn + cn(n - 1), \end{aligned} \quad (3)$$

where b is the birth rate, d the death rate, and $i > 0$ the probability of immigration. Competition is parameterized by the coefficient $c > 0$ (each of the n individuals compete with $n - 1$ others). The corresponding carrying capacity is $\Omega = 1 + |b - d| / c$. The process is simulated (algorithm of Gillespie [1976]) by drawing the occurrence time Δs of each next event from the exponential distribution with parameter $a(n) = bn + dn + cn(n - 1) + i$. An indicator x is then drawn from the uniform distribution with mean a to determine the type of the event. According to the value of x , the event is birth ($x < bn$), death ($bn < x < bn + dn$), competition entailing death ($bn + dn < x < bn + dn + cn(n - 1)$), or immigration of a single individual ($bn + dn + cn(n - 1) < x$), with this latter event being independent of population size.

We observe the continuous-time process in discrete time t by sampling the continuous trajectories with step Δt . The extinction rate $E(t)$ and measure of variation $V(t)$ are computed from the samples of the continuous trajectories. The immigration probability is constant, but now the extinction probability is not given a priori; it is determined by the population dynamics process, in which immigration occurs continuously.

4. *Discrete-time population dynamics model.* The model has the general form

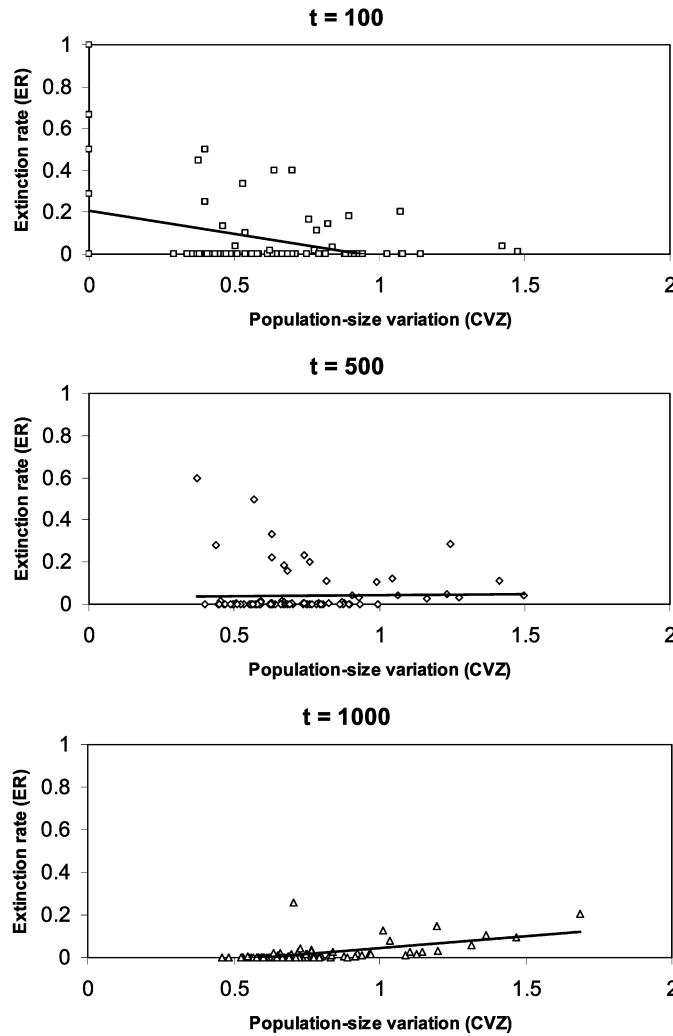


Figure 1: The variation/extinction relation. Regression line of extinction rate (*ER*) on the coefficient of variation of population size with zeros excluded (*CVZ*) at observation time 100 (*squares*), 500 (*diamonds*), and 1,000 (*triangles*), computed for 100 trajectories of the reference model (the discrete-time population dynamics model, with parameters as in table 1). A negative relationship turns into a positive one as time elapses.

$$n(t + 1) = \lambda n(t),$$

where λ is the growth rate. Environmental stochasticity, demographic stochasticity, density dependence, and immigration are incorporated as follows (Schoener et al. 2003).

a) *Environmental stochasticity.* The stochastic growth rate λ_θ is drawn from a normal distribution N with mean the natural growth rate λ and standard deviation θ (the distribution is truncated to ensure nonnegative values):

$$\lambda_\theta \equiv \max(N(\lambda, \theta), 0).$$

b) *Demographic stochasticity.* The number of individuals

at the next time step is computed by summing n samples of the Poisson distribution with mean λ_θ :

$$n(t + 1) = \text{Poisson}(n(t), \lambda_\theta).$$

c) *Density dependence.* The regulated population size n_Ω is computed as

$$n_\Omega(t) = \begin{cases} \frac{\Omega^2}{n(t)} & \text{if } n(t) > \Omega \\ n(t) & \text{if } n(t) \leq \Omega \end{cases}.$$

This means that as soon as population size n goes above

the population ceiling Ω , it is set equal to Ω times the proportional overshoot Ω/n .

d) *Immigration*. At each time step, a single individual can enter the population with probability i .

The basic relation obtained using the above assumptions is

$$n(t + 1) = \text{Poisson}(n_{\theta}(t), \lambda_{\theta}) + \text{Ber}(i), \quad (4)$$

with parameters λ , θ , Ω , and i . We use this final discrete-time approach (model 4) to further explore how variations in the parameters affect the VE relation. More precisely, we consider variations of a reference model where the parameters λ , θ , Ω , and i are assigned biologically realistic values (table 1). The variations can be grouped under three headings: (1) intrinsic species properties, (2) properties with a strong environmental component, and (3) observation properties. To model age structure, we use the life cycle approach of Schoener et al. (2003), expanding model 4 to include five or nine age classes.

Results

Patterns of the VE Relation for the Different Models

For the patch occupancy model (model 1), we find that for $i > e$ (patch more often occupied than empty), the VE relation is positive. For $i < e$ (patch more often empty than occupied), there exists an expected time t^* such that the VE relation is positive for $t < t^*$ and negative for $t > t^*$ (fig. 2A). The value of t^* decreases with e or i increasing and increases with the disparity in e and i . It is small for biologically realistic values of immigration and extinction. This first model shows the possibility of the negative relationship between variation and extinction, and this occurs only when the extinction rate is larger than the colonization rate. However, this model allows for variation only in patch occupancy and not in population size.

The expanded patch occupancy model (model 2), though similar to the patch occupancy model, yields a different pattern for the VE relation. Under biologically realistic values of e and i , as given by the bold line with circles in figure 2B, the VE relation along time begins negative, decreases toward more negative values, and then increases toward 0. For large values of e and i in the expanded patch occupancy model, we observe the same alternative as in the patch occupancy model: the VE relation is negative when $e > i$ and positive otherwise.

In the more realistic continuous-time population dynamics model (model 3) and in the discrete-time population dynamics model (model 4), we observe a pattern for the VE relation (fig. 2C, 2D), and this pattern is very similar to that of the case of the expanded patch occupancy model, though there is very little population variation in this model. Except for the patch occupancy model (not a population dynamics model), all models give a generic pattern for the VE relation: population size variation and extinction rate appear negatively correlated on a short timescale, positively correlated on a long timescale, and uncorrelated on a very long timescale.

Deviations from this generic pattern are consistent in the continuous- and the discrete-time population dynamics models. In both models, (1) the VE relation is strictly positive when the immigration rate is very high (also a feature of the first two models), and (2) the VE relation is initially positive when the growth rate is < 1 ($b < d$ in fig. 2C; $\lambda < 1$ in fig. 2D).

Moreover, the VE relation pattern is independent of the measure used for population size variation. Using model 4, the VE relation was compared for the seven measures of population variation considered by Schoener and Spiller (1992) for data on island spiders. Except for the CV, all measures give the decrease/increase/decrease pattern (fig. A1 in the online edition of the *American Naturalist*). When population size is often 0, as is the case in this study, it

Table 1: Parameters of the discrete-time population dynamics model

Parameters		Reference value	Parameter space
Species properties:			
Growth rate	λ	1.1	[.8, 2.0]
Immigration rate	i	.02	[.001, 1.0]
Age structure		No	Five and nine age classes
Environmental properties:			
Standard deviation on environmental stochasticity	θ	.3	[.001, 1.0]
Catastrophe frequency	p_{cata}	0	[0, .5]
Population ceiling	Ω	1,000	[10, 5,000]
Sampling procedure:			
Observation date	t_1	1,000	[0, 5,000]
Initial population size	n_0	0	[0, 100]
Sampling interval	Δ	1	[0, 100]
Proportion of individuals observed	p_{obs}	1	[0, 1]

seems appropriate to exclude zeros, and this has in fact been recommended by McArdle et al. (1990). In particular, the CV (zeros not excluded) does not seem a good measure; indeed, Schoener and Spiller (1992) reported that it is the sole measure giving only positive values of the VE relation (the only two other positive values in their study were for CV1, the only other measure positive for small t). Using model 4, we now explore how the VE relation behaves when demographic, environmental, or sampling characteristics of the process are varied.

Species Properties

Growth rate (λ). The general pattern for the VE relation is conserved for different values of λ (fig. 3A). When $\lambda < 1$, the VE relation is positive on a short timescale and negative at all other timescales. As λ increases, the relation achieves less negative values and flattens out. For large λ , the relation appears entirely flat because as population size never goes to 0, the extinction rate (ER) cannot be computed.

Immigration rate (i). The effect of decreasing immigration rate below the reference ($i = 0.02$) is a shift of the pattern to the right (fig. 3B). The effect of moderately increasing immigration rate ($i = 0.05$) is a shift of the pattern to the left, but when the rate is very high ($i = 0.5$), the VE relation is flat.

Age structure. The models of Schoener et al. (2003) for the orb spiders *Metepeira datona* (five age classes) and *Argiope argentata* (nine age classes) were adapted to this study. For each age-classified model, we build the corresponding model without age structure, with appropriate parameters λ , θ , Ω , and i (fig. A2 in the online edition of the *American Naturalist*). In both cases, the match is quantitatively not very good, but it is qualitatively similar.

Environmental Properties

Environmental stochasticity (standard deviation θ). For large environmental noise (large θ), the VE relation is positive on short timescales (fig. 3C); this is analogous to the case of small λ (fig. 3A) because the realized growth rate is < 1 for large θ . For $\theta = 0$, the VE relation is flat because very little extinction occurs. We checked that the degree of autocorrelation in environmental disturbance had very little effect on the general pattern (fig. A3 in the online edition of the *American Naturalist*).

Catastrophes (p_{cata}). Catastrophes were investigated by superimposing them onto environmental stochasticity. They occur with probability p_{cata} , and when a catastrophe occurs, population size is set to 0. The effect is that the VE relation becomes positive on short timescales, and this

effect increases with increasing catastrophe frequency (fig. 3D). (Note that in the reference model, $p_{\text{cata}} = 0$.)

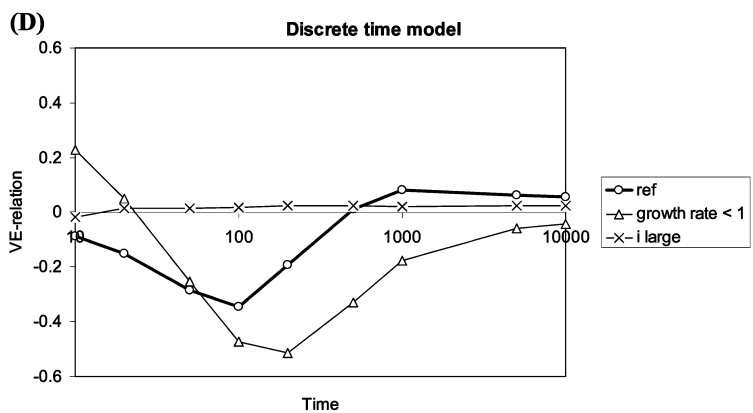
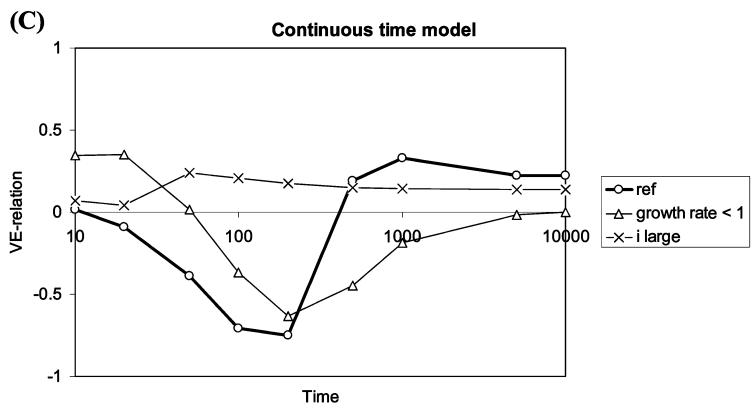
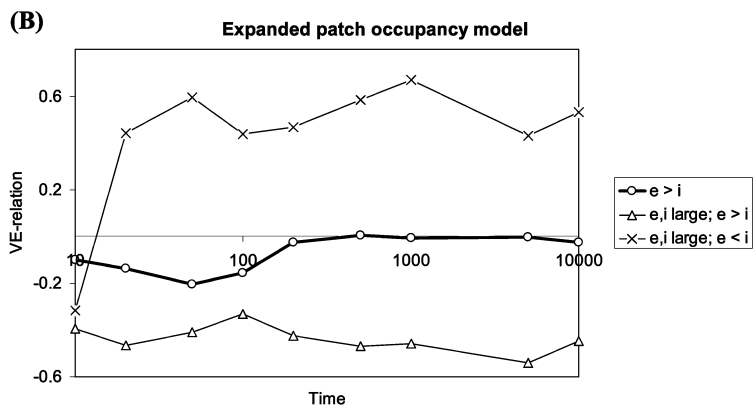
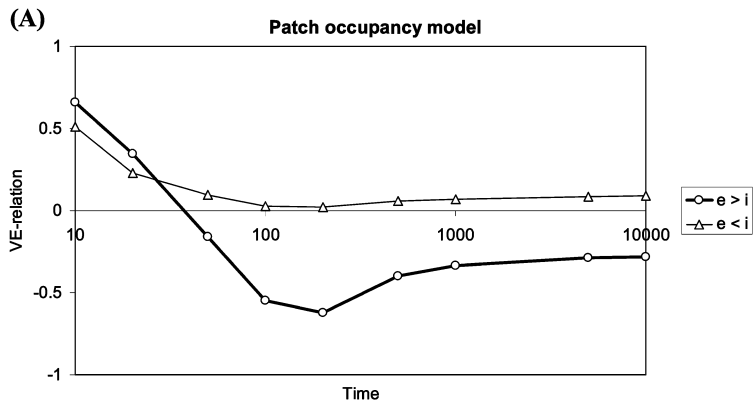
Population ceiling (Ω) and density dependence. For small Ω , we observe an amplification of the VE relation (it is more negative on short timescales and more positive on large timescales; fig. 3E). Furthermore, we checked that changing the functional form of density dependence (under- or overcompensatory) did not influence the general pattern (fig. A4 in the online edition of the *American Naturalist*).

Sampling Properties

Observation time (t_1). Figure 4A shows the VE relation from different dates of first observation, t_1 , with initial population size 0 (note that the reference model has $t_1 = 1,000$). We see that the general pattern exhibited by the VE relation is not affected much by the date t_1 , even when $t_1 = 0$. Figure 4B shows that irrespective of initial population size ($n(0) = 0$ or $n(0) = 100$), the VE relation is similar when the population is observed from time $t_1 = 1,000$ and $t_1 = 5,000$. In contrast, if the population is observed from time $t_1 = 0$, a small change in initial condition ($n(0) = 1$ instead of $n(0) = 0$) has a large impact on the VE relation.

Sampling interval (Δ). Natural populations are often censused at time intervals that are larger than the time step one would use in modeling. For example, orb spider censuses in the Bahamas were conducted on a yearly basis, while the chosen time step for modeling the species was 14 days (Schoener et al. 2003). In this case, the sampling interval was $\Delta = 26$ ($14 \times 26 \approx 365$). The effect of increasing Δ (poorer sampling than the reference model) is to flatten out the general pattern on short timescales and to amplify it on large timescales (fig. 4C). The curves of the VE relation cross the X-axis at a single point (at $t \approx 500$). For comparison, figure 4D gives the effect of the sampling interval on the VE relation for the continuous-time population dynamics model (model 3). In this case, the effect of increasing the observation interval Δ is a shift of the curves to the left. When changing the sampling interval for the continuous process, time is like an elastic band that stretches as the sampling interval decreases. Thus, sampling does not bear the same meaning in discrete time as in continuous time; in the former, the time unit is determined by the life cycle, and in the later, the time unit must be specified.

Proportion of individuals observed (p_{obs}). In natural populations, not all individuals may be observed; this can lead to a false designation of extinction, among other things. If p_{obs} is the probability of observing an individual, the number $n_{\text{obs}}(t)$ of individuals observed at time t is drawn from $n(t)$ according to the binomial distribution with pa-



parameter p_{obs} . This bias (poor sampling) amplifies the VE relation (fig. 4E).

Discussion

We find a general pattern for the slope of the regression of extinction rate against temporal population variability (the VE relation). As the length of the time series increases, the slope first decreases, then increases, and then decreases again. It typically begins negative, eventually becoming (relatively weakly) positive as time increases. The VE relation is an observed relation. In this study, models were used to generate population trajectories, and the quantities leading to the VE relation—extinction rate and measure of population variation—were computed from these simulated trajectories. We infer that on a realistic timescale, the relationship of population size variation to extinction computed from observed time series should generally be negative.

Previous and Present Explanations for a Negative VE Relation

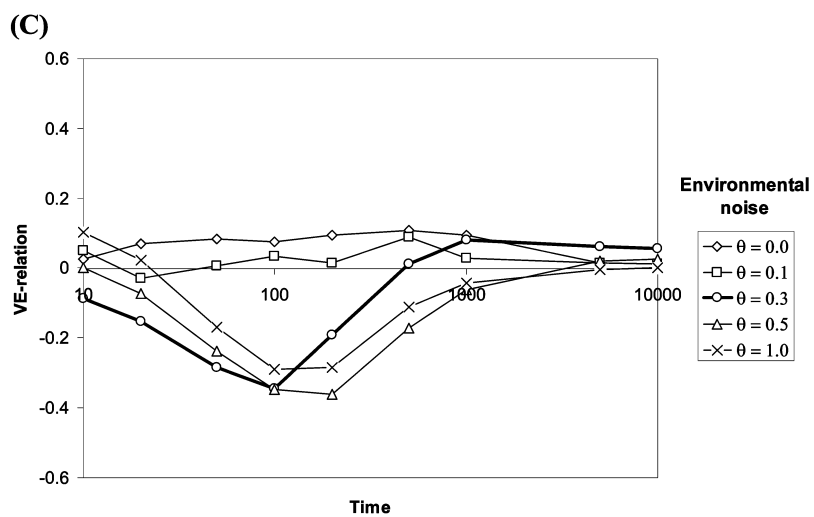
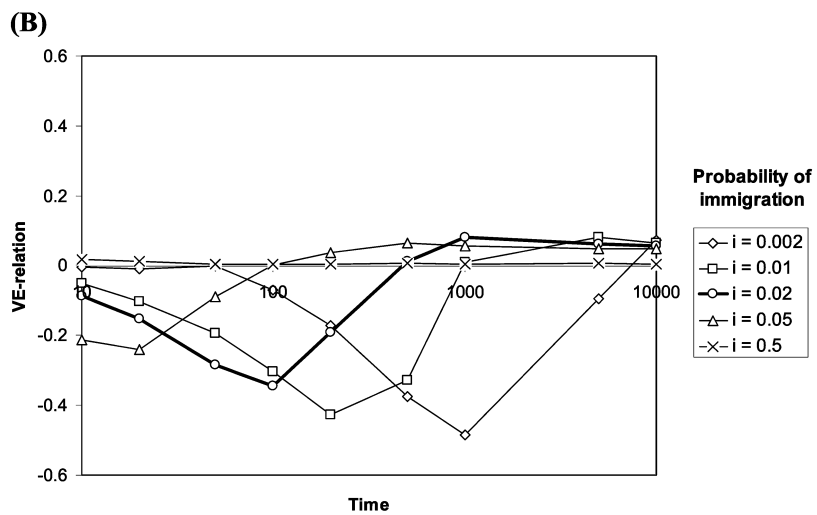
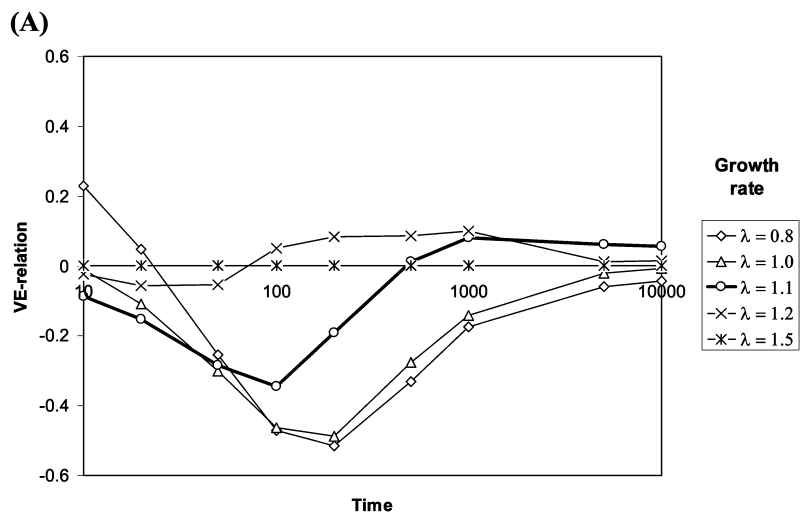
As reviewed by Inchausti and Halley (2003), the negative relation between extinction rate and temporal variability in population size is, at first glance, counterintuitive. Although some dismiss the negative empirical result as largely a statistical artifact (Vucetich et al. 2000), others take it at face value and relate it to reduced variability of small populations (Schoener and Spiller 1992; Pimm 1993) or to short time series (Inchausti and Halley 2003). Pimm (1993, p. 46) further argues that “high extinction rate restricts variability and progressively so at lower densities.” Pimm (1993) correctly points out that there are mathematical limits on the maximum variability that populations with a given mean can attain. However, our models neither (1) show a progressive restriction of variability with population size nor (2) predict that high extinction rate restricts variability to the extent that it has much effect on the VE relation. With respect to point 1, in addition to the small effect of the population ceiling (fig. 3E), plots of population size variability give unimodal relations (fig.

5A, 5B). Point 2, that high extinction rate restricts variability in general, is also highly suspect. In figure 5A, CVZ versus MZ (mean with zeros excluded) is plotted for three values of the immigration rate at time 1,000: $i = 0.2$ (ER = 0.0023), $i = 0.02$ (reference model; ER = 0.0193), and $i = 0.002$ (ER = 0.2636). Very different ER values lead to similar variability, and the smallest ER value ($i = 0.2$; fig. 5A, *black triangle*) is associated with smaller, not larger, variability. Again, the peak variability is for quite intermediate means. These results show that previous explanations of the negative relation of extinction rate to population size variability are largely incorrect.

What, then, is the explanation? It can be proved (appendix in the online edition of the *American Naturalist*) that as time t becomes large, the extinction rate $E(t)$, the colonization rate $I(t)$, and the empirical variance in population size approach respective constants, and so does the CVZ (fig. 6A; when catastrophes are present, convergence is very slow; see fig. 6B). This explains why the VE relation eventually goes to 0. Indeed, the covariance $\text{Cov}(\text{CVZ}(t), \text{ER}(t))$ has the same sign as the VE relation. As $t \rightarrow \infty$, $\text{CVZ}(t) \rightarrow v$, $\text{ER}(t) \rightarrow e$, the covariance converges to 0, and the regression line goes through a single point and therefore has slope 0. The behavior of the VE relation before time becomes large is less transparent, and we provide here only a heuristic explanation.

In this explanation, we consider the whole set of population trajectories and use the empirical mean with zeros excluded at time t , $\text{MZ}(t)$. First, note that the ER is negatively related to the MZ at any time t and that populations with a small MZ have a high ER, while populations with an intermediate or a large MZ have a low ER (fig. A5 in the online edition of the *American Naturalist*). When we start observing the process (at time t_1), CVZs are rather low because the population has not had much time to range over the full variability possible. Next, observe that the relation of MZ to the population size variability CVZ has a single maximum (fig. 5A, 5B). It can be proven that for a process $x(t)$ with values in $\{0, 1\}$, the relation of the empirical mean $M(t)$ to the empirical variance $V(t)$ is $V \approx M(1 - M)$, a parabola with a maximum at $M = 1/2$.

Figure 2: The variation/extinction (VE) relation along time (log scale) for different models (1,000 trajectories in each case). A, Patch occupancy model. The VE relation is always positive when the colonization probability i is larger than the extinction probability e , $i > e$ (triangles; $i = 0.02$, $e = 0.01$). The VE relation is positive up to some specific time and then negative when $i < e$ (bold line; $i = 0.02$, $e = 0.05$). B, Expanded patch occupancy model. The VE relation is negative in general (bold line; $i = 0.02$, $e = 0.05$; triangles; $i = 0.2$, $e = 0.5$) but positive for large extinction probability e and large immigration probability $i > e$ (crosses; $i = 0.5$, $e = 0.1$). C, Continuous-time population dynamics model (bold line; birth rate $b = 0.105$, death rate $d = 0.10$, population ceiling $\Omega = 100$, immigration probability $i = 0.002$; growth rate $\lambda < 1$; $b = 0.10$, $d = 0.11$; large immigration probability: $i = 0.02$). D, Discrete-time population dynamics model. The bold line corresponds to the reference model (table 1). The reference case (circles) and the cases of growth rate $\lambda < 1$ (triangles; $\lambda = 0.8$) and large immigration probability (crosses; $i = 0.2$) are similar in the discrete- and continuous-time models.



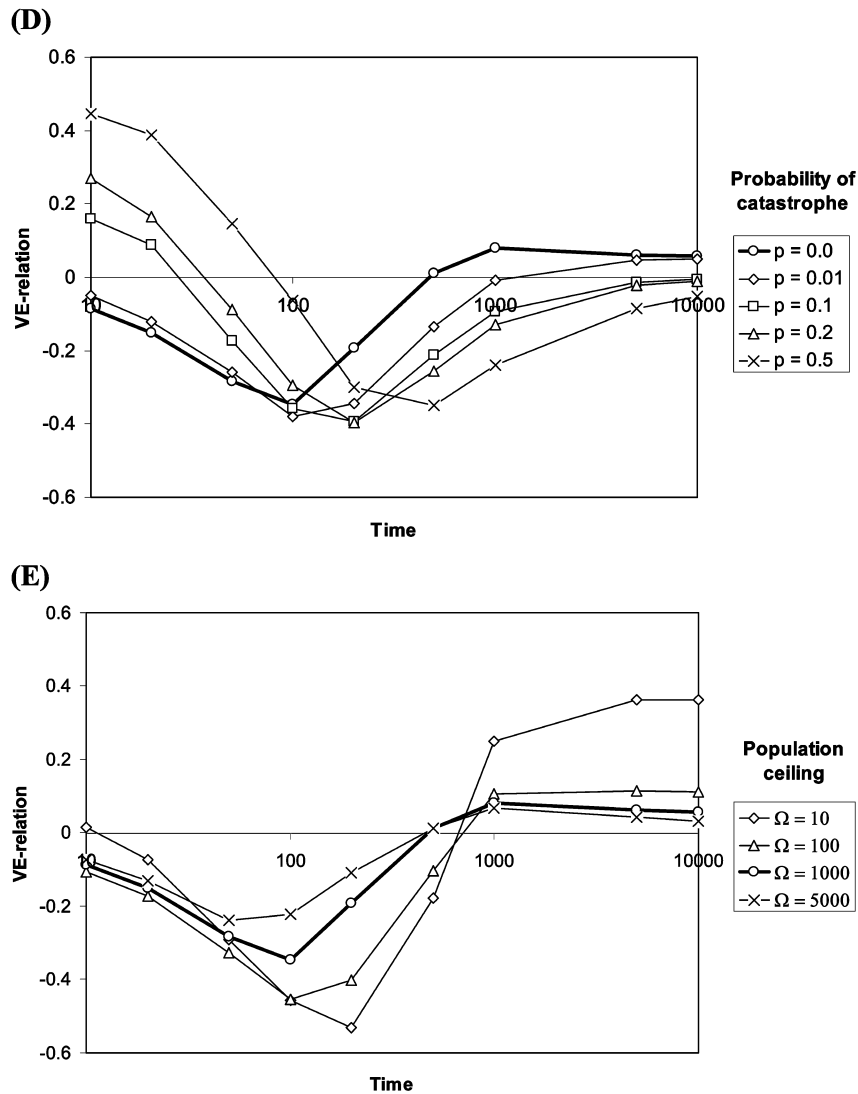
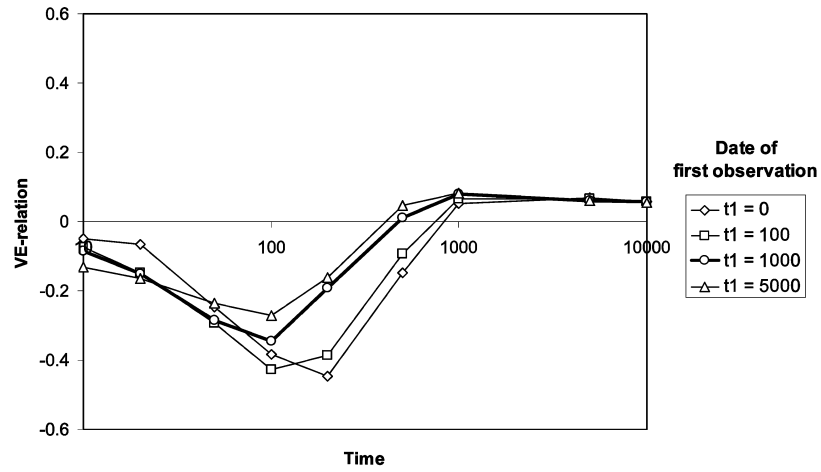


Figure 3: The variation/extinction (VE) relation along time (1,000 trajectories of the reference model). Effects of species and environmental properties. *A*, Varying the growth rate λ . *B*, Varying the immigration rate i . *C*, Varying the standard deviation of environmental stochasticity θ . *D*, Catastrophes added with frequency p_{cata} . *E*, Varying the population ceiling Ω .

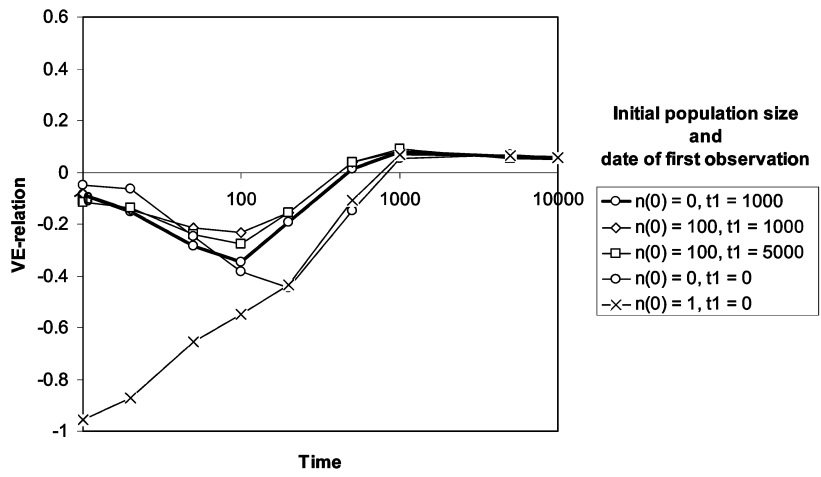
For a process with values in $\{0, 1, \dots, K\}$, there is still a single maximum. As time elapses, this gives three kinds of populations across trajectories: (1) intermediate MZ, high CVZ; (2) large MZ, small CVZ; and (3) small MZ, small CVZ. When these populations are arranged on a plot of ER versus CVZ, a triangular relation and a tendency toward a negative slope are obtained (fig. 5C). As time further progresses, populations tend to average larger; in particular, category 3 dwindles away. This gives a weakly positive slope in figure 5C. In this explanation, it is necessary to distinguish the current (instantaneous) state of a trajectory from its history since time t_1 ; the empirical

quantities MZ, CVZ, and ER computed from time t_1 present transient behavior before stabilizing to their respective constants. It can be shown that as time increases, the fraction of trajectories currently with 0 individuals becomes roughly constant. But to keep the fraction of 0 populations constant, populations must become extinct at a definite rate. However, when a formerly large population becomes extinct, it still has large MZ because MZ is computed over the entire trajectory that has elapsed since t_1 . The large values that such a population had in the past prevent it from being a population with a small MZ, and therefore, the fraction of populations with a small MZ declines.

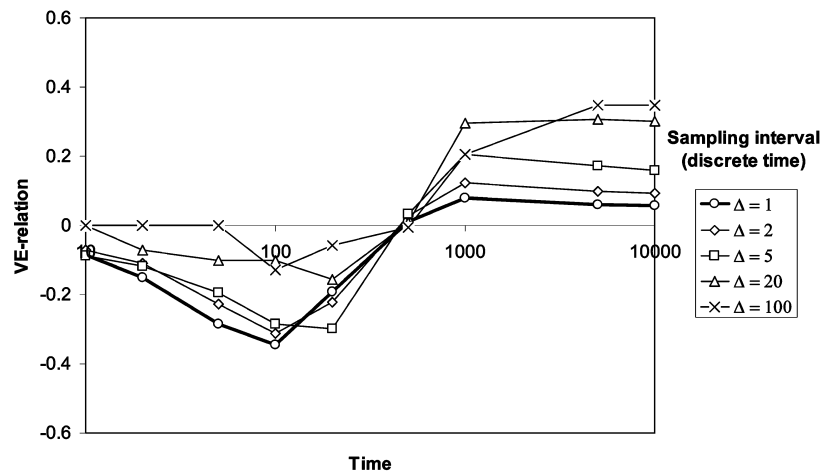
(A)



(B)



(C)



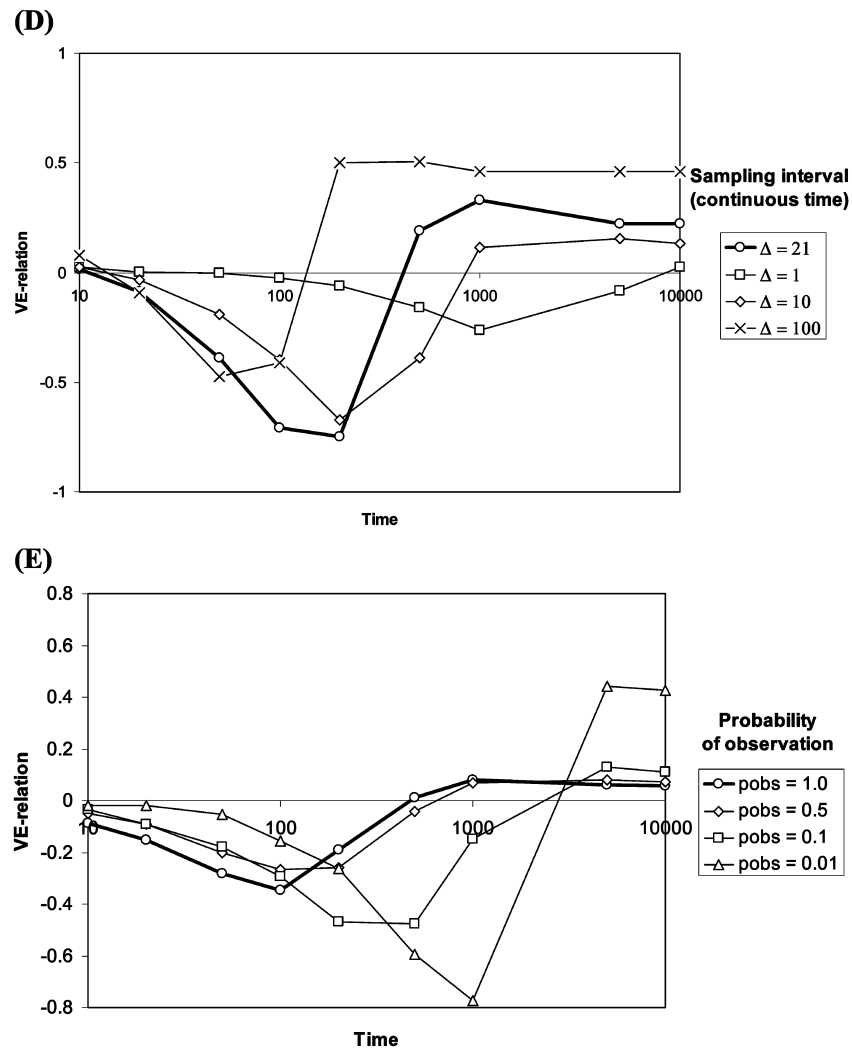


Figure 4: The variation/extinction (VE) relation (1,000 trajectories of the reference model). Effects of sampling properties. *A*, The population is observed from time $t_1 = 0, 100, 1,000$ (reference model), and 5,000. The general pattern is not affected much by the date t_1 at which the population is observed. *B*, The cases $n(0) = 0$ and $n(0) = 1$, observed from time $t_1 = 0$, show the substantial impact of population size on the VE relation when the first observation date t_1 is small. In contrast, the initial condition makes little difference when the first observation date t_1 is large ($n(0) = 100, t_1 = 1,000, 5,000$). *C*, Sampling interval Δ using the discrete-time population dynamics model. *D*, Sampling interval Δ using the continuous-time population dynamics model (parameters as in fig. 2C). *E*, Probability p_{obs} of observing an individual.

Change in Population Size Variability with Increasing Time

Inchausti and Halley (2001, 2002) conclude from their review of earlier studies and analysis of the global population dynamics database (GPDD) that temporal variability in population size increases over time. The GPDD has more than 4,500 data sets longer than 10 years (or generations), of which Inchausti and Halley (2001) used 544 data sets that were annually censused or otherwise counted for more than 30 years (median 46.5 years; maximum 157 years). In 96.9% of cases, the increase decelerates with time

series length, but in most cases, “variance fails to exhibit an overall tendency to converge to any limit” (Inchausti and Halley 2001, p. 656).

Our simulations for the reference model (fig. 6A) have CVZ increasing up to $t \approx 1,000$, after which it plateaus at a somewhat lower value. The CVZ plateaus very late when catastrophes are added (fig. 6B).

Two interpretations of our models can explain the tendency for population size variability to increase with time series length, as shown by Inchausti and Halley (2001). The first interpretation is that all series examined by In-

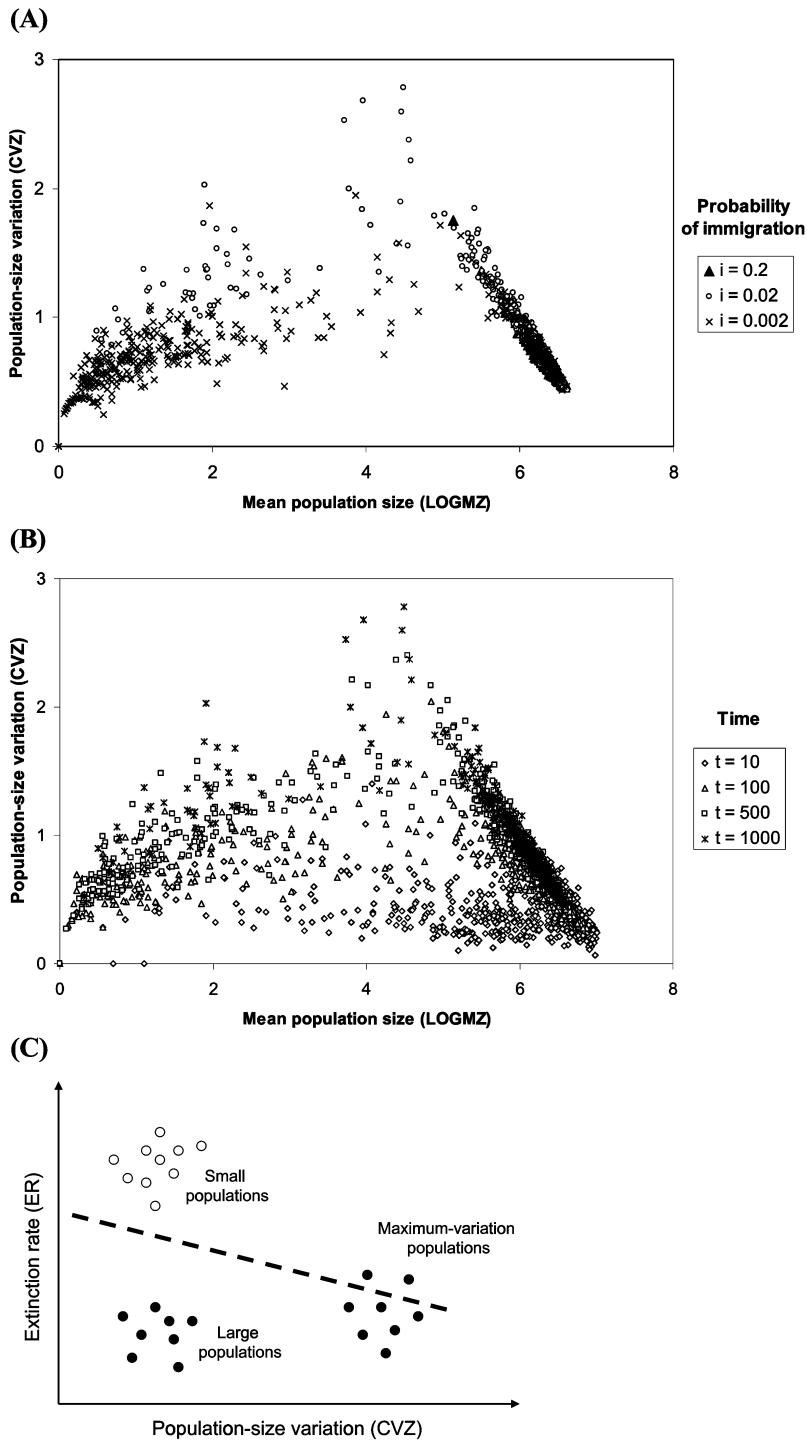


Figure 5: A, The relation of mean population size with zeros excluded (MZ; log scale assuming $\log(0) = 0$) to population variation with zeros excluded (CVZ) for three values of the immigration rate: $i = 0.2$ (filled triangles), $i = 0.02$ (circles), and $i = 0.002$ (crosses), using the reference model at time 1,000 (1,000 trajectories; each point corresponds to a trajectory). B, As in A, 1,000 trajectories of the reference model at times 10, 100, 500, and 1,000. C, Schematic representation of the CVZ-ER correlation for short to moderate time series; a negative slope is observed. As the length of the time series increases, the number of populations in the top left portion of the plot decreases, giving a mildly positive slope.

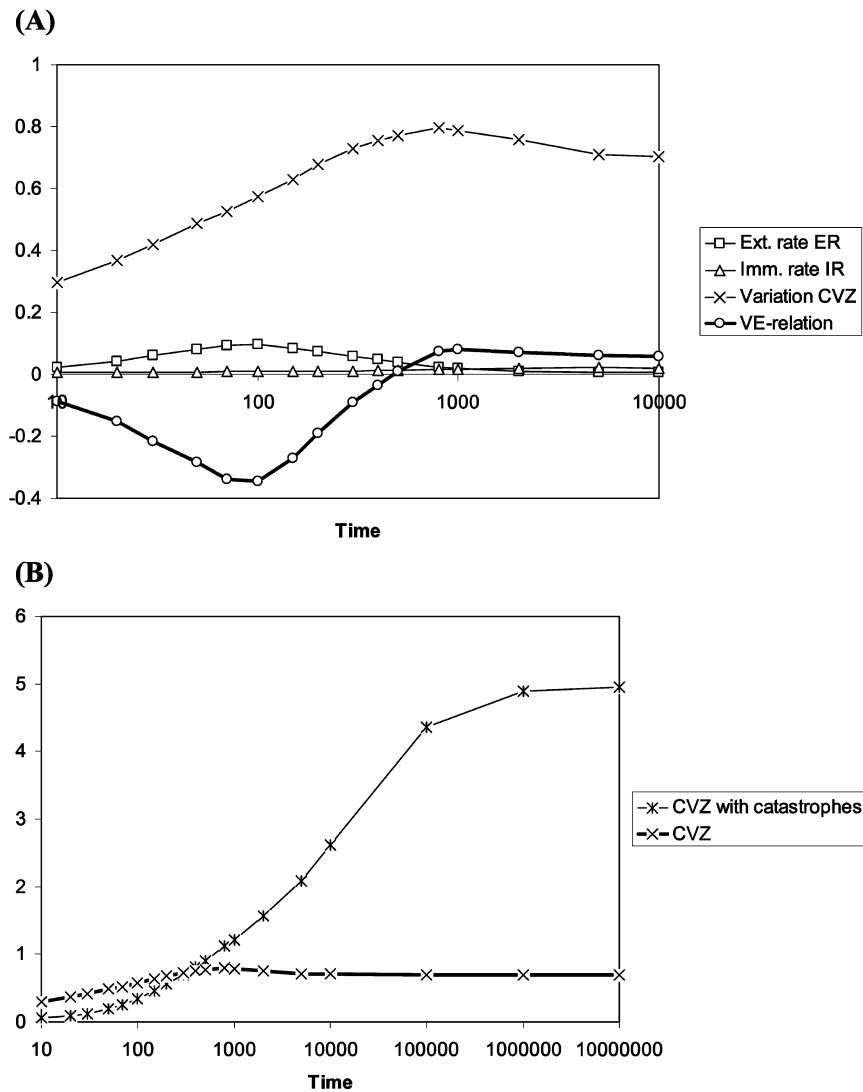


Figure 6: A, The variation/extinction (VE) relation, the extinction rate (ER), the immigration rate (IR), and population size variation with zeros excluded (CVZ) along time (average over 1,000 trajectories of the reference model). Roughly, the VE relation is negative when $ER > IR$ and positive otherwise. B, The CVZ along time for the reference model with catastrophes added (probability $p_{cata} = 0.1$) compared to the usual reference model (average over 1,000 trajectories for each).

chausti and Halley (2001) are shorter than our value ($t = 1,000$) at which the CVZ begins to decline. Assuming that the units of the GPDD time series used by Inchausti and Halley (2001) correspond to the units of our model, this would be so. However, if there were numerous generations per year, it would not be so. Indeed, in our study of extinction in spiders (Schoener et al. 2003), there are 26 time units (about two generations) per year, so $t = 1,000$ corresponds to about 40 years, well within the range of the GPDD data. In that case, the second interpretation is necessary: catastrophes (fig. 6B) must be invoked to explain a persistent increase in population variability as

time series length continues to increase. Infrequent catastrophes may, in any event, occur in natural systems and generally contribute to a population's increase in variability over time, but they are, in fact, not necessary to give this increase for shorter time series in our models.

Related to temporal variability in population size is spectral reddening, a tendency for low (or high) abundances to be temporally autocorrelated. The larger the spectral exponent, the faster the increase of population variability with the length of the time series (Inchausti and Halley 2001, 2002). The spectral exponent ν (computed as minus the regression slope of log spectral density against

log frequency) has a mean value of 1.022 (SD = 0.025) and ranges from about -0.3 to 2.5 in the GPDD data analyzed by Inchausti and Halley (2003). In our study, the reference model has $\nu \approx 1.1$. The reference model with catastrophes added ($p_{\text{cata}} = 0.1$) has $\nu \approx 1.3$, and the age-structured models for the spiders *Metepeira* and *Argiope* have $\nu \approx 1.3$ also. Thus, our models are well within the amounts of spectral reddening observed in natural populations (Inchausti and Halley 2002, 2003) as well as in other models (Akçakaya et al. 2003). Our model also shows the expected increase in the spectral exponent with autocorrelation of stochastic noise in the growth parameter λ . For mild autocorrelation, $\nu = 1.3$, and for strong autocorrelation, $\nu = 1.5$. This is expected if the autocorrelation in λ is positively related to the autocorrelation in population size (see also Vucetich et al. 2000).

VE Sensitivity to Model Structure and Parameter Values

Exceptions to the negative slope for short timescales occur when the population is at relatively great risk, including growth rate <1 (fig. 3A), low immigration rate (fig. 3B), large environmental noise (fig. 3C), and high frequency of catastrophes (fig. 3D). The slope can also be positive at all timescales, including short ones, when ER is very low, immigration rate is very high, or environmental noise is very high.

Our simulations show that on short timescales, the pattern in the VE relation is most sensitive to varying immigration rate (fig. 3B), growth rate (fig. 3A), and catastrophes (fig. 3D). On long timescales, the pattern is most sensitive again to immigration rate (fig. 3B) and also to sampling frequency (fig. 4C) and population ceiling (fig. 3E). Overall, the pattern seems most sensitive to immigration rate. This is not surprising in light of studies of metapopulation persistence, which show the key role of this very important quantity (Hanski and Gilpin 1997). However, the relationship between the immigration rate and the VE relation is not simple (fig. 3B). For large immigration rates, the VE relation is almost 0 and insensitive to timescale. In such a case, it is likely that population size variation at the local scale is not an appropriate indicator, the pertinent demographic entity being the metapopulation (Morris and Doak 2002). As immigration rate decreases (and as local dynamics play an increasing role compared to global dynamics), the curves appear to shift to the right (fig. 3B). The likely explanation is that a decrease in immigration rate sharply increases the extinction risk and dampens population fluctuations.

Elsewhere (Schoener et al. 2003), we compared the adequacy of models with and without age structure to fit spider data on extinction as a function of time observed. For both species tested, models without age structure gave

good fits to data on large but not small initial population sizes. We concluded that life cycle characteristics interact with the various sources of stochasticity and so have to be taken into account for a precise description of the extinction process. In this article, the overall form of the VE relation (decrease, increase, decrease to an asymptote) is fairly well preserved, but the curves are rather different quantitatively (fig. A2). This is especially true for *Argiope*, for which the model with age structure reaches more negative slopes and retains negative values for nearly the entire time span examined. Because the real data give quite negative slopes, especially in *Argiope* (Schoener and Spiller 1992), the age-structured model seems a more precise representation for purposes of this article as well. Two reasons can be suggested. First, when a perturbation arises, age structure increases the convergence time to the asymptotic state, usually by inducing dampening oscillations. This causes spurious (not environmentally induced) autocorrelation in time, that is, an increase in spectral reddening; if not taken into account, this effect can lead to overestimating the role of temporal autocorrelation. Second, environmental variations may act on vital rates that cause large fluctuations in total population size but have little effect on population extinction rates (Gaillard et al. 2000).

Quasi Extinction versus Extinction

Building on their previous work, Inchausti and Halley (2003) argue that in the GPDD data, extinction risk increases with population variability (computed as $CV(n)$ or $SD(\ln(n))$). However, extinct versus extant is here measured by the time to quasi extinction, defined as the time required to observe a 90% decline in population abundance. In part, quasi extinction is used because the GPDD series frequently do not contain any zeros—true extinction does not occur. Our measure of extinction requires that the population falls to 0 from time to time (where indeed it can remain for a while when immigration is low). Accordingly, in our model, extinction rate cannot be computed when growth rate is large (fig. 3A), immigration rate is large (fig. 3B), or environmental noise is small (fig. 3C). When the population does not go to 0 in our model, could ER be replaced by a quasi-extinction rate (qER), where going below 1 is replaced by going below a threshold value $H > 1$? The answer is that qER does indeed produce a similar decrease-increase pattern in the VE relation for the reference model, provided that the threshold H is not too high (fig. A6 in the online edition of the *American Naturalist*). The decrease-increase pattern cannot be recovered when using qER as the growth rate λ becomes large or the environmental noise low (not shown). Thus, the use of qER when there is no true extinction is not, in general, an alternative to the use of ER. A major difference between

the two is that when population size goes to 0, the population can restart only by immigration, whereas it can still climb away from 0 through its own internal dynamics when falling below the threshold H .

Conclusion: Relevance to Conservation

What are the implications of our results for conservation? First, note that our models represent a system whose populations have a reasonably high rate of extinction, as in a metapopulation whose subpopulations wink in and out, empty sites at which extinction occurred, eventually being regenerated by immigration. As discussed, many data on extinction deal with quasi extinction, and there are differences between our results on true extinction and our initial attempts to simulate a kind of quasi extinction. This issue deserves substantially more exploration, and conservation managers will have to choose from among the various approaches, according to which is the most appropriate match for their system. Second, we emphasize that sensitivity of the VE relation shown at small timescales to small differences in immigration has important consequences. Indeed, metapopulation theory tells us that when environmental stochasticity is not spatially correlated, immigration-emigration processes are acting as a rescue effect at the local scale (Hanski and Gilpin 1997; Lecomte et al. 2004). Because most time series are collected on populations open to immigration, measuring and incorporating immigration into these studies is obligatory whenever the focus is on local population protection. This also means that monitoring of populations should be accompanied by immigration rate measurement (Doligez et al. 2004). Indeed, the different conclusions of studies finding positive versus negative slopes of extinction rate on temporal variability in population size might be caused by differences in immigration rate between their subjects: spiders, mammals, and birds. The slope attains maximally more negative values the lower the immigration rate (fig. 3B). Third, although no simple general pattern seems likely to work for all species (as in many viability analyses), a number of general statements can be made. The VE relation is not very sensitive to local population growth rate (fig. 3A), which means that sink populations experience no stronger impact of population variation than do source populations. Beyond a certain threshold, the strength of environmental stochasticity has little impact on the relationship between extinction probability and fluctuations in population size (fig. 3C). This is not the case for catastrophes (fig. 3D), implying that local population protection should deal much more with unexpected events than with year-to-year climatic variation. Fortunately, frequency of observation (fig. 4C) has little effect on the VE relation for the reference model. Similarly, population size

has only a minor effect on the way temporal fluctuations and extinction probabilities are correlated at the local scale (fig. 3E). As emphasized above, only immigration does. Contrary to theoretical expectations, even small rates of immigration are enough to render population viability analysis projection based on single populations misleading (Morris and Doak 2002). However, a more detailed analysis, including examination of the pattern of spatial autocorrelation in population growth and immigration-emigration processes, will be needed to describe more fully the conditions under which a single-population approach would be sufficient compared to a metapopulation approach.

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