



Scale-dependent portfolio effects explain growth inflation and volatility reduction in landscape demography

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Population demography is central to fundamental ecology and for predicting range shifts, decline of threatened species, and spread of invasive organisms. There is a mismatch between most demographic work, carried out on few populations and at local scales, and the need to predict dynamics at landscape and regional scales. Inspired by concepts from landscape ecology and Markowitz's portfolio theory, we develop a landscape portfolio platform to quantify and predict the behavior of multiple populations, scaling up the expectation and variance of the dynamics of an ensemble of populations. We illustrate this framework using a 35-y time series on gypsy moth populations. We demonstrate the demography accumulation curve in which the collective growth of the ensemble depends on the number of local populations included, highlighting a minimum but adequate number of populations for both regional-scale persistence and cross-scale inference. The attainable set of landscape portfolios further suggests tools for regional population management for both threatened and invasive species.

population demography | scale dependence | growth inflation | volatility reduction | demography accumulation curve

Population demography describes composite features of scaling up from individuals, each with different risks, to populations. It has been studied since Malthus (1). However, it is not straightforward to predict the dynamics of regional ensembles of populations from single populations; scaling up may require a different set of conceptual tools (2). Although most demographic studies of natural populations of plants and animals are conducted at local scales and on few (three or fewer) populations (3), we are often concerned about the behavior of ensembles of populations. When appropriately scaled-up to population ensembles, demography is potentially valuable for understanding many fundamental and applied problems, including risk of regional extinction, biological invasions, pathogen spread, fisheries management, and as the foundation for natural selection. To this end, the concept of landscape demography has been introduced to emphasize the collective behavior of population ensembles across spatial scales (4).

Landscape demography is a generalization of the special case of metapopulation theory and conceptually brings together several approaches and theoretical lines of work. In classic metapopulation theory (5, 6), population persistence at the regional or landscape scale is ensured through the dynamic colonization-extinction balance from recolonization of suitable sites. In scale transition theory (7, 8), with the full knowledge of recruitment and dispersal of all populations over an infinite landscape, the landscape-level multiplicative growth rate can be partitioned into the average growth rate of local populations plus the growth-density covariance (see also ref. 9). The landscape-level persistence can thus be elevated by having positive growth-density covariance. Under similar premises, landscape-level growth rate can be further inflated by affecting the growth-

density covariance from temporal fluctuation and autocorrelation in local population growth rate driven by environmental noise (9–11). Such red noise could further drive intermittent rarity of population dynamics (12) and facilitate invasive establishment (13). Moreover, through connecting local stochastic processes via redistributing individuals, system-level persistence and growth can be achieved (14, 15) through stochastic resonance (16–18). By highlighting the roles of positive growth-density covariance, temporal variability and red noise, redistribution, and spatial heterogeneity these stochastic metapopulation and demographic theories have laid the foundation for connecting local- to landscape-level demography.

Our goal here is to extend this theory by scaling up demography by continuously adding local populations into the landscape ensemble, even when dispersal and the nonlinear population growth function are not explicitly quantified and when some populations are ignored due to limited sampling effort. Economic portfolio theory provides such a framework that can be extended for analyzing the dynamics of ensembles of populations. With this approach dispersal may be incorporated, but the ensemble can be a set of populations without colonization between them, rather than a set of connected subpopulations (as in metapopulation ecology). In this framework, we start with three quantities that are essential for analyzing the

Significance

Population demography is central to many problems in ecology, evolution, and conservation biology, yet there is a gap between the information needed about the demography of population over multiple spatial scales and the available data, which are largely local. Inspired by concepts from landscape ecology and Markowitz's investment portfolio theory, we address this lacuna by developing a method for quantifying and predicting the demography of multiple populations across spatial scales and apply it to gypsy moth populations. We show that population demography is scale-dependent due largely to a tilted portfolio effect from skewed population size distributions and covarying population growth rate; this explains why population ensembles can have growth rates greater than the mean with variance smaller than the mean.

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stochastic demography of population ensembles (19): means, variances, and covariances of local population change rates. Note that the choice of specific metrics of population change rates assume the normality or at least symmetry of measured rate distributions around the mean (discussed below). The first two are indicators of population viability that can be driven by many environmental and ecological factors, such as habitat quality, disturbance, and biotic interactions including density dependence, interspecific competition, and predation. These two quantities have also been highlighted in other demographic theories. The covariance measures synchrony between populations (20) and reflects a range of drivers, including the Moran effect of broad-scale environmental forcing (21–23), cross-trophic or intraspecific biotic interactions (24, 25), distance decay of similarity (26–28), and cross-population migration (29–31). The role of the covariance between local population change rates has not been fully explored in previous demographic theories. Those specific aspects of population demography that have been highlighted in previous theories, such as the growth-density covariance and temporal autocorrelation, are considered later in an expanded formulation of our approach. To transform our understanding of how local demography contributes to the collective behavior of regional ensembles, landscape demography also needs to formulate how these quantities depend on the number of local populations in the ensemble, so that drivers of the demography of the ensemble can be sought and inferences made across relevant scales.

Fortunately, we can borrow from economic theory to address this problem. Models to predict rates of change and minimize volatility for portfolios of assets are well established in economic theory, employing portfolio diversification and constrained optimization to identify financial strategies for ensembles of individual investments (32, 33). The dynamics of both biological populations and investment portfolios typically are characterized by substantial fluctuations of individual units (populations and assets) but smaller fluctuations for ensembles of those units (34, 35). We approach scaling from single populations to an ensemble by borrowing methods for portfolio diversification across populations from these investment models (32, 33). Modern portfolio theory is based on the return, $R = (n_{t+1} - n_t)/n_t$, with n_t the investment size at time t . However, the return for biological population size n is often highly nonnormal, as is the multiplicative growth rate, $\lambda = n_{t+1}/n_t$ (10), making the mean and variance invalid metrics for the centroid and spread of return (see the gypsy moth example below). Instead, the relative growth rate (RGR), $r = \ln(n_{t+1}/n_t)$ is approximately normal. In what follows, we only address the case for positive population size ($n_t > 0$). In the event of a local extinction followed by recolonization, the newly established population is considered to be a new local population in the ensemble.

We propose a platform of landscape demography inspired by modern portfolio theory but using RGR rather than return R or multiplicative growth rate λ . This permits the study of the demography of an ensemble of populations while accounting for the potential interconnections between populations that reflect multiple demographic and environmental factors including not only dispersal but also shared environmental and biotic forcing. We first advance models for this platform, emphasizing the connections that allow scaling up from local dynamics to the collective behavior of many populations at landscape and regional scales. We then demonstrate this platform by scaling up the demography of gypsy moths (*Lymantria dispar*) in the northeastern United States by pooling populations into larger ensembles.

Analytical Results

Let there be z populations in the landscape. The landscape portfolio is the weight vector of populations: $\vec{w} = \{w_1, w_2, \dots, w_z\}$ subject to $w_i \geq 0$ and $\sum_i w_i = 1$, with $w_i = n_i/n_U$, where n_U is the

sum of population sizes. Generally, n_i follows a lognormal distribution (10) and thus the RGR, r_i , a Gaussian, with expectation μ_i , variance σ_i^2 , and $\sigma_{ij} = \text{cov}(r_i, r_j)$. The ensemble RGR is

$$r_U = \ln \left(\sum_i e^{r_i} w_i \right). \quad [1]$$

Following ref. 15, we first present the formulae of landscape demographies for constant weights (called the rebalancing strategy in economic theory) and then extend the formulae later to connect with other stochastic demography theories. Nonetheless, the possible demographies of landscape ensembles are addressed here by exploring the entire feasible range of weights. To find the expectation (μ_U) and variance (σ_U^2) of the ensemble (U) RGR, let $\nabla = \sum_i e^{\mu_i + \sigma_i^2/2} w_i$ and $\Delta^2 = \sum_i \sum_j e^{\mu_i + \sigma_i^2/2} e^{\mu_j + \sigma_j^2/2} (e^{\sigma_{ij}} - 1) w_i w_j$; we then have

$$\begin{aligned} \mu_U &= \ln \left(\nabla^2 / (\nabla^2 + \Delta^2)^{1/2} \right) \\ \sigma_U^2 &= \ln \left((\nabla^2 + \Delta^2) / \nabla^2 \right). \end{aligned} \quad [2]$$

Two landscape ensembles are also synchronized to some extent due to covarying populations (Eqs. S4 and S12).

The attainable set is the set of all possible landscape portfolios. It is useful to describe the attainable set by its projection in the growth-volatility (μ_U, σ_U^2) plane; its boundaries (Fig. 1A) describe demographies for combinations of two or more populations, with single-population portfolios at the ends of each two-population curve. The top-left boundary (Fig. 1A) is of

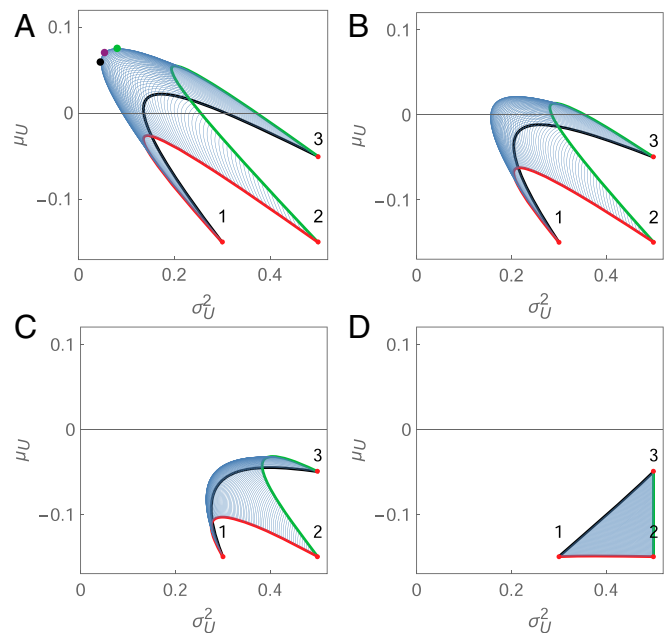


Fig. 1. Expectation and variance of RGR for an ensemble of three populations. Red, green, and black curves: attainable sets for combinations of two populations ($w_i + w_j = 1$). Blue mesh: attainable sets for combinations of three populations ($w_1 + w_2 + w_3 = 1$). Covariances between populations are the same in each plot and are calculated as the correlation (ρ) times the SDs of the two populations ($\sigma_{ij} = \rho \sigma_i \sigma_j$). (A) $\rho = -0.5$; (B) $\rho = 0$ (independent); (C) $\rho = 0.5$; (D) $\rho = 1$ (perfectly synchronized). The efficient frontier is calculated by minimizing $x(\sigma_U^2/2) - (1-x)\mu_U$ for specific x values; $x = 0$ for the maximum growth portfolio (green dot in A), $x = 1$ for the minimum variance portfolio (black dot in A), and $x = 1/2$ for the portfolio on the efficient frontier where the attainable set is stretched the most along the ensemble shifting direction (purple dot in A).

particular interest as it represents portfolios with minimum variance for a given ensemble RGR, or equivalently maximum RGR given a level of volatility. In economics, this represents ideal portfolios of investments, and is thus called the efficient frontier (32, 34). In landscape demography it represents ensembles of populations with minimum collective risk from reduced volatility and maximum potential for regional-scale persistence from growth inflation.

Ensemble portfolios within the attainable set often have reduced volatility and inflated RGR (shifting toward the efficient frontier in Fig. 1). A paradoxical result is that the expected RGR for the ensemble as a whole, μ_U , can be positive even with all negative local RGRs (Fig. 1A and B). More generally, growth inflation occurs when the expected ensemble RGR is greater than the weighted arithmetic mean of local RGRs. Portfolios including many populations generally also have smaller σ_U^2 than those including a few. Covariance between the RGRs of populations, σ_{ij} , is critical in causing volatility reduction and growth inflation; this can be enhanced by negative covariances (compare Fig. 1A with Fig. 1B), but positive covariances can dampen this effect or even exacerbate volatility (Fig. 1C and D); the latter was an important factor that precipitated the Great Recession of 2008 (36).

Volatility reduction and growth inflation in landscape demography result from a tilted portfolio effect. First, due to skewed distributions of n_i , the growth (μ_U) and volatility (σ_U^2) of a landscape ensemble covary with each other (Eq. 2), tilting the efficient frontier from the left corner of the growth-volatility (μ_U, σ_U^2) plane in classic portfolio theory to the top-left corner in a landscape portfolio (Fig. 1), permitting growth inflation. This differs from the classic portfolio theory of investment, where the two quantities are independent and thus the portfolio effect refers only to volatility reduction (32, 33). Second, the covariance of RGRs between local populations determines the degree to which the ensemble demographics are shifting toward the efficient frontier, analogous to classic portfolio theory.

Volatility reduction and growth inflation can be severely damped or even reversed if there are large discrepancies in σ_i^2 (compare Fig. 1B with Fig. 2). In a two-population ensemble (Fig. S1), the effect of growth inflation and volatility reduction reverse when $d \equiv \sigma_2^2 - \sigma_1^2 > d^*$ for some threshold d^* . The existence of this threshold confines the portfolio effect of volatility reduction and growth inflation. This is because (with increasing d) the denominator of the function for μ_U (Eq. 2) grows faster than its numerator, while the denominator of the function for σ_U^2 grows more slowly than its numerator, eventually reversing the portfolio effect. Covariance also plays a role, with highly synchronized

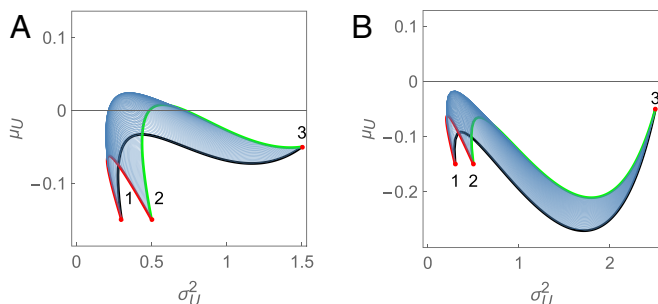


Fig. 2. Expectation and variance of RGR for the ensemble with increasing discrepancy among variances. Plots A and B are the same as Fig. 1B (three populations are independent from each other, $\rho = 0$), but with increasing variance for population 3. Others are the same as in Fig. 1. See Fig. S1 for more explicit effect of variance discrepancy on ensemble demography.

dynamics having small d^* and weak effects on volatility reduction and growth inflation (Fig. S1).

Connecting Demographic Theories

This framework of landscape demography can be connected to stochastic demography theories. After relaxing the assumption of constant weights and allowing temporal autocorrelation of r_i , we have the expected regional RGR of the ensemble (*Supporting Information*):

$$\mu_U = \ln \left(\alpha \cdot \sum_i \left(\text{cov}(\lambda_i, w_i) + \bar{w}_i \cdot \exp \left(\mu_i + \frac{1 + \beta_i}{1 - \beta_i} \frac{\sigma_i^2}{2} \right) \right) \right). \quad [3]$$

This expected ensemble RGR can explain the growth inflation from existing demographic theories. First, α represents intertwined μ_U and σ_U^2 , as well as the temporal autocorrelation of r_U , reflecting the tilted portfolio effect (*Supporting Information*). Second, a positive covariance between multiplicative growth rate and population weight, $\text{cov}(\lambda_i, w_i) > 0$, can add to ensemble growth as highlighted in scale transition theory (7, 8). Third, connecting multiple random variables (\bar{w}_i and σ_i^2) can lead to elevated growth of the combined variable through both the tilted portfolio effect and stochastic resonance (16, 17), with the extreme case of a Parrondo game. Finally, positive temporal autocorrelation ($0 < \beta_i < 1$) in stochastic growth rate can further enhance regional growth via the inflation effect of red environmental noise (9, 10, 13). All these quantities are interconnected in Eq. 3 to enhance the persistence and growth of landscape ensembles. This expanded framework of landscape demography could contribute to the eventual design of a unified platform for multisite population viability analysis and regional inference (19, 37, 38).

Demography Accumulation Curve

We define the demography accumulation curve (DAC) as the parametric forms of r_U and σ_U^2 with an increasing number of local populations in the ensemble (z); see *Supporting Information* for an example (Fig. S2). In practice, the DAC can be estimated as the rarefaction curve of ensemble demographics for a given number of randomly selected nonoverlapping local populations. The DAC serves two purposes. First, it can serve to examine the adequacy of a regional survey; that is, whether a sufficient number of local populations have been included in the sampled ensemble so that the DAC starts to approach its asymptote, if one exists. Regional inference (e.g., whether the species is expanding or contracting at regional scales) and cross-region comparison can be made on asymptotes of landscape demographics or rarefied values under equal survey coverage. Second, the DAC implies changes in behavior of a landscape ensemble at different ensemble sizes. Persistence and survival at regional scales require a minimum number of local populations, and this minimum threshold of ensemble size is related to multiple demographic quantities (Eq. 3): Negative covariance of growth ($\sigma_{ij} < 0$), positive growth-density covariance ($\text{cov}(\lambda_i, w_i) > 0$), red environmental noise ($0 < \beta_i < 1$), and large fluctuations (large σ_i^2 ; Fig. S2) can reduce this threshold of regional persistence. Management could target these quantities to ensure that the ensemble size for threatened (invasive) species is above (below) the threshold.

The DAC of Gypsy Moth

The level of defoliation from the forest pest *L. dispar*, used as a proxy of population size, has been intensively surveyed in northeastern United States since 1975 (39–41). We analyzed annual time series (1975–2010) for 84 64×64 -km quadrats based on the USDA Forest Service dataset, covering ca. 350,000 km² (Fig. S3). Evidence that the RGR is an unbiased metric of

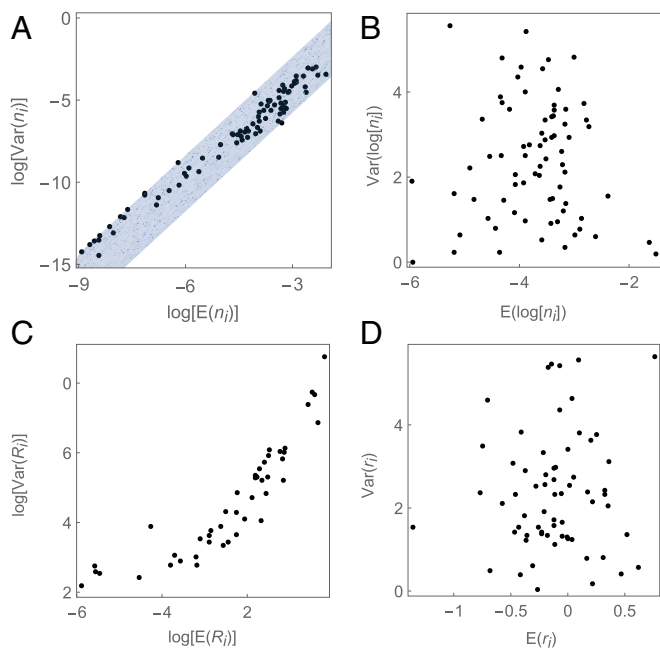


Fig. 3. Features of the population size and demography of the gypsy moth in the northeast United States. (A) The log-transformed relationship between the temporal expectation and variance of population size, with each point representing a local population, all located within a thin belt around a power law. (B) The relationship between the temporal expectation and variance of log population size, showing the power law in A to be artificial due to the skewed distribution of population size. (C) The log-transformed relationship between expectation and variance of the return, showing the distribution within a narrow belt. (D) The relationship between the expectation and variance of the RGR, justifying its use as an unbiased metric of population demography.

population demography for *L. dispar* is provided in Fig. 3, with the notable statistical artifact of Taylor's power law from a skewed size distribution (42). We were able to calculate means and (co)variances of local population RGRs (Dataset S1) for 38 quadrats (Figs. S4 and S5). The DAC of μ_U demonstrated a clear upward trend with an increasing number of included populations, shifting from negative to positive at $z = 30$ (Fig. 4A), indicating growth inflation. The DAC of σ_U^2 eventually declined when $z > 15$ (Fig. 4B), indicating volatility reduction through portfolio diversification. The annual ensemble RGRs (blue lines in Fig. 4C) fluctuated strongly within a belt perpendicular to the efficient frontier, showing that the annual ensemble RGR and its variance are negatively correlated (as expected in a system prone to massive outbreaks). The DACs of gypsy moths point to a minimum of 30 local populations to be monitored for meaningful, qualitatively correct, regional inference.

Conclusions

The theory developed here provides tools for estimating ensemble mean RGRs and their variances, which may change nonlinearly across scales (i.e., the DAC). Useful extensions of this theory may include the role of nonstationarity, density dependence, and spatial autocorrelation in time series. The gypsy moth example suggests a strategic approach for invasive species: If we can drive ensembles below the sizes at which growth inflation and/or volatility reduction operate, we may be able to achieve regional control; for threatened species, there can be a critical threshold for the number of populations below which regional extinction is likely. These results point to mechanisms of regional persistence that do not follow from local demographic results and are not possible under classic metapopulation models,

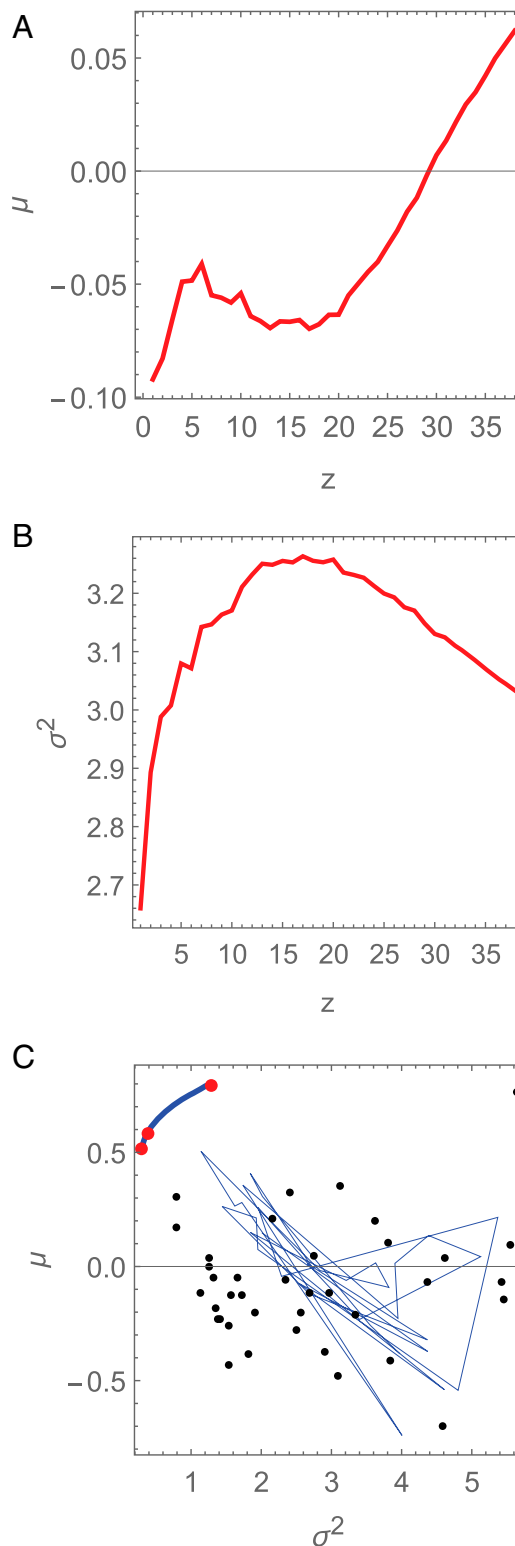


Fig. 4. Landscape demography and DACs of 38 gypsy moth populations. Accumulation curves for expectation (A) and variance (B) of ensemble RGRs as a function of the number of included local populations (z). Red lines: averages of 1,000 rarefaction curves. (C) Black dots: expectation and variance of the RGR for specific populations (Fig. 3 and Dataset S1). Blue lines: demographic trajectory for the ensemble. Blue curve: efficient frontier for the ensemble, calculated as in Fig. 1 (Dataset S2).

where regional persistence results from a dynamic colonization–extinction balance. Persistence in a landscape portfolio can be enhanced through inflated growth and reduced volatility largely due to the tilted portfolio effect for covarying populations with comparable magnitudes of variability, which is distinct from existing stochastic demography theories that focus on the roles of growth–density covariance, temporal autocorrelation, and stochastic resonance. Finally, the attainable set of landscape portfolios and the DAC of ensemble mean and variance suggest tools for regional population management for both threatened and invasive species through changing the relative weights and other demographic quantities of, as well as the covariance between, target populations and pinpointing the minimum number of populations for reliable regional-scale decision making.

Materials and Methods

We used population time series to calculate annual RGRs of local populations and their means, variances, and covariances; expected ensemble

RGR and its variance are found from these using properties of the log-normal distribution. Plotting the expected ensemble RGR and its variance, for all possible relative weights of local populations, permits visualization of the possible ensemble growth rate and its variance and identification of the maximum RGR given a level of volatility. We derive a general expression for the expected ensemble RGR, permitting connections to other theories of stochastic demography. We introduce the DAC, the expectation and variance of ensemble RGR as a function of the number of local populations. The DAC, as estimated with rarefaction curves from gypsy moth populations, permits inference on the action of growth inflation and volatility reduction.

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