The observed range for temporal mean-variance scaling exponents can be explained by reproductive correlation

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The mean-variance scaling relationship known as Taylor's power law has been well documented empirically over the past four decades but a general theoretical explanation for the phenomenon does not exist. Here we provide an explanation that relates empirical patterns of temporal mean-variance scaling to individual level reproductive behavior. Initially, we review the scaling behavior of population growth models to establish theoretical limits for the scaling exponent b that is in agreement with the empirically observed range ($1 \leq b \leq 2$). We go on to show that the degree of reproductive covariance among individuals determines the scaling exponent b. Independent reproduction results in an exponent of one, while completely correlated reproduction results in the upper limit of two. Intermediate exponents, which are common empirically, can be generated through the decay of reproductive covariance with increasing population size. Finally, we describe how the link between reproductive correlation and the scaling exponent provides a way to infer properties of individual-level reproductive behavior, such as the relative influence of demographic stochasticity, from a macroecological pattern.

Populations fluctuate as a consequence of variability at multiple scales. Determining how different sources of variation affect population dynamics remains a challenge in ecology. Despite our knowledge that intrinsic life-history variation and external environmental variability contribute to population fluctuations (Dixon et al. 1999, Lima et al. 2001, Lande et al. 2003), it is difficult to assess the relative influence of either on empirical populations. This is because the effects of the former occur at the individual level and the latter occur at the population level. Currently, there is no general agreement about how to map individual dynamics onto patterns observed at the level of the population (Maurer and Taper 2002). But once the link is made, a synoptic analysis (Taylor 1986) can illustrate how individual level dynamics are scaled up to population level dynamics. Only then will we be able to understand how variability at different scales contributes to fluctuations in abundance.

Fluctuations in abundance through time and across space are often characterized by plotting the logarithm of variance in abundance as a function of the logarithm of mean abundance. This mean-variance scaling relationship, first described by Taylor (1961) and known since as Taylor's power law, has the form $V = aM^b$, where V is the variance of abundance, the normalization constant, a, is a measure of individual level variability, M is mean abundance, and b is the scaling exponent (the slope of the power law on log-log axes). Taylor's power law is well documented for animal and insect populations (Taylor 1961, Taylor and Woiwod 1980, Taylor et al. 1983, Taylor 1986, Maurer and Taper 2002) and has recently been shown to characterize reproductive output in trees (Kerkhoff and Ballantyne 2003). Although Taylor (1961) initially plotted spatial abundance data, the relationship between temporal mean and variance in abundance is also well characterized by power law scaling (Taylor and Woiwod 1982, Taylor 1986, Maurer and Taper 2002, Kerkhoff and Ballantyne 2003, Ballantyne and Kerkhoff 2005). Empirically, b for temporal data ranges from approximately one to approximately two (Taylor and Woiwod 1980, 1982, Keeling 2000, Maurer and Taper 2002).

The general theoretical framework we present in this paper directly links temporal mean-variance scaling of abundance to the degree of reproductive covariance among individuals in populations. We begin by summarizing mean-variance scaling of well-known population models and then establish a theoretical basis for the empirically observed range of the scaling exponent, b. Next, we show how intermediate slopes may arise from density dependent reproductive covariance. Finally, we discuss how this body of theory for mean-variance scaling relates to the interplay between demographic and environmental stochasticity and how inference about individual behavior can be made from the scaling exponent.

Mean-variance scaling for population models

When describing reproductive behavior in populations, the production and survival of offspring can be independent of population size (density independent) or dependent on population size (density dependent). To formulate models that describe density independent population dynamics, stochastic models, such as birth-death processes, are often the natural choice. In contrast, density dependent population dynamics models are predominantly deterministic. Models that characterize population dynamics as either purely density independent or purely density dependent represent rarified extremes, unlikely to be found in nature and most ecologists would agree that some combination of density independent and density dependent processes interact to cause populations to fluctuate. Theoreticians have addressed the complementary effects of determinism and stochasticity on population fluctuations but conclusions often lack generality because they pertain to specific models only. Despite the fact that describing populations dynamics as either purely density independent or purely density dependent is unrealistic, we briefly summarize the mean-variance scaling properties of population dynamics models that represent these extremes to link density dependence and density independence to the empirical limits of b.

Describing reproduction and survival as density independent has historically lead to stochastic process models. In the prototypical birth-death processes, probabilities of producing offspring, producing no offspring, and dying are all independent of population size. The density independence of vital demographic parameters results in linear mean-variance scaling, $b = 1$ (see Feller 1968, May 1973, Kot 2001 for details). Models of density dependent demographics are virtually always deterministic so all individuals in a population

behave exactly the same with respect to reproduction and survival. All deterministic models that can be linearly rescaled to a dimensionless form, for example logistic growth, result in quadratic mean-variance scaling, $b = 2$ (Ballantyne 2005).

The correspondence between the limits of the mean-variance scaling exponent b determined by population models and the empirical range of b provides more support for the idea that the limiting exponents for Taylor's power law are related to the dependence among individuals in a populations (Keeling and Grenfell 1999, Keeling 2000). The fact that the exponent of Taylor's power law empirically varies between one and two suggests that mean-variance scaling of abundance is constrained by the limits set by totally independent and totally dependent behavior. However, this intuitive relationship between extreme exponents and dependence cannot explain the more frequently observed intermediate slopes (Taylor and Woiwod 1980, Anderson et al. 1982, Keeling 2000, Maurer and Taper 2002) that lie between one and two. Next, we present a general description of a population that allows us to link the entire range of empirically observed exponents for Taylor's power law to the contiuum of reproductive covariance among individuals.

Mean-variance scaling for populations of random individuals

In the study of populations, the dynamics of the entire population are dictated by the aggregated dynamics of the individuals comprising it. The particular combination of life-history and the external environment determines the nature of observed density dependence and observed population fluctuations. Obligate sexual reproducers and aggregates that have highly correlated responses to environmental forcing will exhibit more coherent reproductive behavior than asexual reproducers or organisms that experience a high degree of environmental variability on the scale of an individual. By considering individuals in a population as random variables, we are able to link the exponent of Taylor's power law to the degree of individual reproductive covariance in populations. In this paper we only concern ourselves with populations that, on average, are neither increasing or declining. For such steady-state populations, we are able to show that population variance is a function of mean abundance and to isolate the effect of individual reproductive variation, i.e. demographic stochasticity on overall population fluctuations.

Our description of population dynamics exploits the simple but often overlooked fact that a population is the sum of individuals and therefore population dynamics

are the sum of individual dynamics. All ecologists intuitively know this but since it is key for our development of mean-variance scaling theory and it is fundamental to the definition of a population, we state it explicitly. The theory presented here generalizes the elementary calculation of moments of sums of random variables outlined in Ballantyne and Kerkhoff (2005) for populations with fixed abundance to populations with varying abundance.

Populations as random sums

We consider individual reproductive output $R_i(t)$ for a time interval $(t-1, t]$ a random variable with mean μ and variance σ^2. The reproduction of each individual in a population is characterized by these first two moments, i.e. the R_i are identically distributed. Reproductive output for the entire population $P(t)$ is calculated by summing individual reproductive output,

$$P(t) = \sum_i R_i(t) \qquad (1)$$

If the population size is fixed at a given n, as in Ballantyne and Kerkhoff (2005), the calculation of the mean and variance of reproductive output for the population is straightforward yielding

$$E[P(t)] = E\left[\sum_{i=1}^{N} R_i(t)\right] = \sum_{i=1}^{N} E[R_i(t)] = N\mu \qquad (2)$$

and

$$V[P(t)] = N\sigma^2 + N(N-1)\sigma_{ij}^2$$
$$= N[\sigma^2 - \sigma_{ij}^2] + N^2\sigma_{ij}^2 \qquad (3)$$

respectively. In Eq. 2 and 3, σ_{ij}^2 is the covariance between R_i and R_j and is independent of i and j because all R are identically distributed. If the individuals comprising $P(t)$ are independent with respect to reproduction, $\sigma_{ij}^2 = 0$ which results in linear dependence of both the population mean and variance on population size and an exponent of 1 for Taylor's power law. In complete contrast, if reproductive output of all individuals in the population is completely correlated, $\sigma^2 = \sigma_{ij}^2$ and population variance depends quadratically on population size which in turn results in an exponent of 2 for Taylor's power law. Populations with fixed n are certainly not the general rule in the natural world and only focusing on reproductive output and not survival neglects important demographic and ecological processes. Therefore, we next relax this assumption which permits the number of reproductive adults in a population to vary.

To incorporate fluctuations in the number of reproductive adults in a population and to derive limits for Taylor's power law for population size, we define n,

the size of the population, to be a random variable with mean N and variance η^2, both independent of R_i, and compute the mean and variance of the now random sum $P(t)$. By allowing n to vary, we implicitly incorporate the fact the abundance of reproductive adults fluctuates around a carrying capacity N. We also change the definition of R_i to include survival. For the following random sums, R_i is the number of surviving adults the following time step produced by one adult, not just reproductive output. Consequently, the sum $P(t)$ now describes the number of individuals in the population. The detailed calculation is left to the appendix but the resulting mean and variance of the now random sum $P(t)$ are

$$E[P(t)] = N\mu \qquad (4)$$

and

$$V[P(t)] = \mu^2\eta^2 + \sigma_{ij}^2\eta^2 + N(\sigma^2 - \sigma_{ij}^2) + N^2\sigma_{ij}^2 \qquad (5)$$

respectively. First it is important to notice that $\mu = 1$ meaning that on average each adult only replaces itself in the population. Again we see that both the mean (Eq. 4) and the variance (Eq. 5) of the random sum are linear functions of N, the mean number of reproductive adults in the population, if $\sigma_{ij}^2 = 0$. Similarly, the mean variance scaling exponent is one if n and R are independent. As was the case for reproductive output, if $\sigma_{ij}^2 = \sigma^2$, the linear term in N in Eq. 5 vanishes and variance in the number of reproductive adults scales quadratically with mean population size. When covariance equals variance, all individuals exhibit the same per capita dynamics. This gives rise to the familiar result that for a scalar N, $V(NR) = N^2V(R)$ which is consistent with the fact that rescaling many population dynamics models in a similar manner results in an exponent of two for Taylor's power law (Ballantyne 2005).

The upper and lower limits for the exponent of Taylor's power law characterizing reproductive output and abundance of reproductive adults are equal and directly related to the correlation of individual dynamics. However, empirically observed exponents often assume intermediate values as opposed to the theoretical limits of 1 and 2. Below we describe two potential scenarios that could give rise to intermediate values for the exponent of Taylor's power law.

Constant moments and scaling breaks

Under the assumption of second order stationarity, σ^2 and σ_{ij}^2 are constant and the intermediate values of b often observed for empirical data can result from a transition from a range of population sizes for which individual level variance, σ^2, dominates reproductive covariance among individuals, σ_{ij}^2, to a range of

population sizes for which the inverse is true. If we do have reason to believe the assumption of second order stationarity, we are able to calculate the population size at which a scaling break occurs. For example, in Eq. 3 and 5, we see that if $\sigma^2 > \sigma_{ij}^2$, the scaling of aggregate variance will be predominantly linear for populations smaller than σ^2/σ_{ij}^2, and predominantly quadratic for those larger. Thus, the ratio of variance to covariance determines the population size at which behavior of individuals appears correlated. The transition from linear to quadratic scaling is plotted in Fig. 1 using a variance to covariance ratio of 100:1, which is the critical population size described by Lande et al. (2003). The models of Keeling (2000) and Anderson et al. (1982) exhibit this type of scaling. It is certainly likely that empirical data span this threshold because estimates of environmental stochasticity, which influence σ_{ij}^2, are often an order of magnitude smaller than estimates of demographic stochasticity (Lande et al. 2003), which influences σ^2. A range of population sizes that spans the critical threshold given by the variance to covariance ratio, and sampling error could be responsible for an intermediate slope. Although this explanation seems unlikely because of the high degree of correlation and the homoscadistic variance observed for empirical Taylor's power law, evaluating the presence or absence of such scaling breaks in limited data remains a significant statistical challenge.
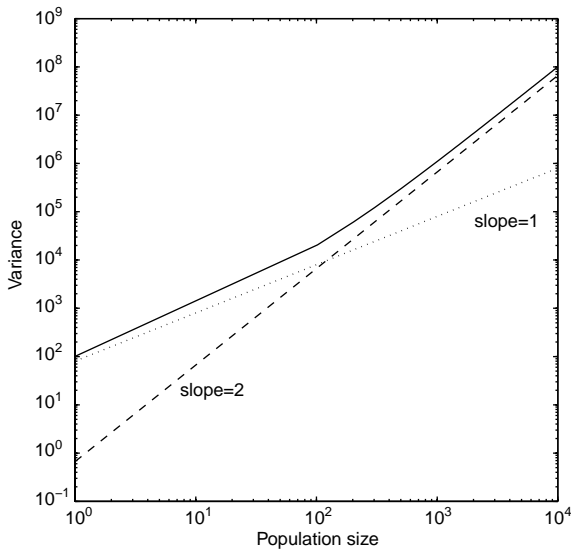

Fig. 1. Mean-variance scaling with constant individual moments. The variance to covariance ratio of 100:1 determines where the change in scaling region occurs. Below population sizes of 100 mean variance scaling is approximately linear and above 100 it is approximately quadratic. The solid line is the actual scaling relationship and power laws with slope = 1 (dotted line) and slope = 2 (dashed line) are plotted for comparison.

Non-constant moments and intermediate exponents for Taylor's power law

If we choose to relax the assumption of second order stationarity, we not only have a more realistic description of population dynamics but we can also more easily reproduce the apparently constant intermediate exponents for Taylor's power law by explicitly allowing the mean, the variance, and/or the covariance of individual reproductive output to be functionally related to population size. The expressions for the moments of whole population reproductive output now become

$$E[P(t)] = Nf_M(N) \qquad (6)$$

and

$$V[P(t)] \alpha N[f_V(N) - f_C(N)] + N^2 f_C(N) \qquad (7)$$

in the most general sense. The functions f_M, f_V, and f_C respectively characterize the dependence of the mean, the variance, and the covariance of reproductive output on aggregate population size. Although individual reproductive variability may be a function of population size in some populations (Lande et al. 2003), to our knowledge it is not a general phenomenon so, for simplicity, we assume no relationship between population size and individual reproductive variability (f_V constant, independent of N). Again, for steady state populations, $f_M \equiv 1$.

The above assumptions allow us to infer how reproductive covariance changes with population size from the exponent of Taylor's power law. Given an exponent b for Taylor's power law, it is straightforward to show from Eq. 7 that covariance, or $f_C(N)$ is proportional to N^{b-2}. Thus, for a given exponent $1 \leq b \leq 2$, reproductive covariance decreases as a function of aggregate population size. The decrease in correlation (rescaled covariance) with population size is plotted in Fig. 2, for different values of the scaling exponent b. Initially the correlation coefficient decreases quite steeply as population size increases, but then remains relatively constant. Eventually the correlation among individuals will asymptote to zero but at a constantly decreasing rate. The relative constancy of the correlation coefficient across a wide range of aggregate population sizes suggests that the exponent of Taylor's power law could be predicted by measurements of correlation in the field. In this paper, we are quite restrictive about the functions f_M, f_V, and f_C, but in certain situations, it may also be necessary to allow both f_M and f_V to change with aggregate population size.

Discussion

Regardless of its underlying causes, Taylor's power law is a useful characterization of population fluctuations.
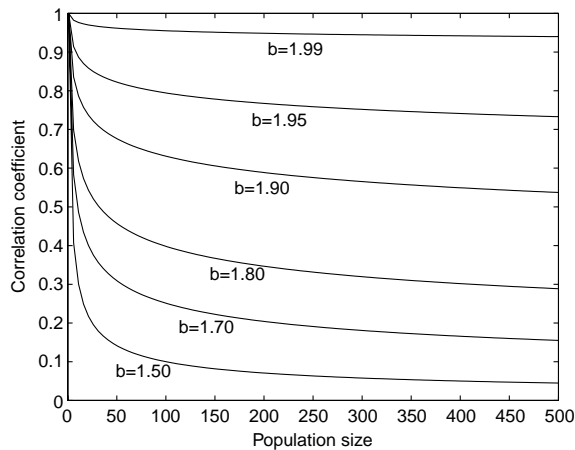
Fig. 2. Correlation coefficient for individuals in a population as a function of population size and b, the slope of Taylor's power law.

The exponent of Taylor's power law indicates how the magnitude of relative fluctuations in abundance changes with population size. An exponent of two means that population dynamics are invariant with respect to population size. An exponent of less than two means that the coefficient of variation of fluctuations in abundance is a decreasing function of population size and that larger populations experience smaller relative fluctuations. The smaller the exponent, the greater the damping effect of population size on the relative magnitude of fluctuations in abundance. The fact that most empirical data are characterized by exponents less than two indicates that larger populations are less susceptible to large relative fluctuations than smaller populations. Therefore, at the most superficial level, the exponent of Taylor's power law can be used to assess the stability of populations. Even in the absence of a mechanistic understanding of the underlying causes of Taylor's power law, exponents have been related to community level stability properties (Doak et al. 1998, Tilman 1999, Cottingham et al. 2001). The utility of b as a metric for population viability analysis should be further investigated in detail.

The results presented here suggest that some individual-scale variability might be a hallmark of stable systems in general because it reduces system-scale variability. Individual-scale variability decouples individual behavior and prevents all individuals in a population from responding the same way in response to sytem-wide perturbations. When individuals exhibit some degree of independence in their behavior, a population has greater potential to respond differentially to environmental variability. If individuals are completely correlated, a population is only capable of one response to a particular environmental change. Theoretical studies of meta-populations have shown

that highly connected subpopulations fluctuate more synchronously than those that are isolated (Czaran 1998, Hanski 1999) and therefore experience large relative fluctuations in abundance (Foley 1994). As a result, some degree of isolation can stabilize metapopulations (Hassell et al. 1994, Czaran 1998, Hanski 1999). The fact that decorrelation can exert a stabilizing influence on both single species populations and on meta-populations suggests that Taylor's power law exponents may be linked to meta-population processes. We see this as an exciting avenue for future research.

Traditionally, two major sources of variation in abundance have been thought to be demographic and environmental stochasticity (Lande et al. 2003). Demographic stochasticity is associated with life-history and variability at the scale of the individual and environmental stochasticity is variability that affects all members of a population similarly. Taylor's power law suggests that increasing demographic stochasticity increases individual reproductive variance while increasing environmental stochasticity increases reproductive covariance. Thus, a high degree of demographic stochasticity may tend to stabilize populations as long as they are large, whereas environmental stochasticity can destabilize populations by correlating reproductive behavior. However, the absolute magnitude of both demographic and environmental stochasticity obviously plays a crucial role in determining population fluctuations. As can be seen in Eq. 3 and 5, individual level variability (σ^2) resulting from demographic stochasticity as well as covariance (σ_{ij}^2), often the result of environmental stochasticity, both influence the normalization constant of the power law. Particular combinations of demographic stochasticity and environmental stochasticity can mask the importance of one or the other except at extreme population sizes (Lande et al. 2003).

The scale of stochasticity affecting populations can potentially be inferred from the exponent of Taylor's power law. Populations for which demographic stochasticity is greater than the magnitude of environmental stochasticity should generate exponents closer to one than to two. In contrast, populations subject to large relative environmental stochasticity should be characterized by exponents closer to two. Therefore, an empirically calculated exponent near one may imply that demographic stochasticity has a larger relative effect on population fluctuations than environmental stochasticity. The exponent, b, also allows one to compare the relative influence of demographic and environmental stochasticity on different populations. It is a scale-free parameter because it reflects the relative influence of these two types of stochasticity.

The greatest potential utility of the explanation we suggest for Taylor's power law is that it allows us to ascertain information about individual-scale behavior from a macro-scale pattern. Traditionally, individual

behavior is scaled up to population dynamics (Sutherland, 1996), but using the results presented here, it is possible to relate population dynamics to individual reproductive behavior. From b, which is a macro-scale or synoptic description, we are able to recover the degree of correlation of individual reproductive behavior in ecological populations. In the past, population biologists have relied on detailed life table data to understand reproductive behavior at the level of the individual, but b can potentially allow inference concerning the functional correlation among interacting individuals based only on the macroscopic dynamics of large populations. By looking at a large-scale pattern, we can potentially infer the scale of influential variability for populations.

To summarize, the empirical range for the exponent of Taylor's power law (approx. $1 \le b \le 2$) suggests that observed population fluctuations are the result of competing processes that correlate and de-correlate individual reproductive behavior. We have shown that completely uncorrelated reproduction produces the lower limit of one for the exponent of Taylor's power law, that completely correlated individuals produces the upper limit of two and that intermediate exponents can be the result of a functional dependence of reproductive covariance on population size. Our proposed explanation provides a general context that subsumes previously proposed causes for mean-variance scaling (Gillis et al. 1986, Sugihara et al. 1990, Keeling and Grenfell 1999, Keeling 2000, Kilpatrick and Ives 2003). Furthermore, it allows us to relate variability at different scales to variability at the population level. Most generally, processes that are variable at the scale of the individual lead to exponents closer to one which reflect independence among individuals and processes that are variable at the scale of the population result in exponents closer to two which reflect dependence among individuals. For ecological populations, total independence prevents individuals from capitalizing on constant properties of their environment but total dependence increases the likelihood of precipitous declines and reduces the capacity for response to environmental change. Organisms must therefore strike a balance between correlated and independent reproductive behavior in order for populations to persist.

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Appendix 1.

The calculation of the mean of a random sum $P(t) = \sum_{i=1}^{n} R_i(t)$ in which $E[R_i(t)] = \mu$, $V[R_i(t)] = \sigma^2$, $E[n] = N$, and $V[n] = \eta^2$.

For the mean:

$$E[P(t)] = \sum_{i=1}^{\infty} E[P(t)|n = i]p_n(i) \tag{8}$$

$$= \sum_{i=1}^{\infty} E[R_1(t) + R_2(t) + \cdots + R_i(t)|n = i]p_n(i) \tag{9}$$

$$= \mu \sum_{i=1}^{\infty} ip_n(i) = \mu E(n) = \mu N \tag{10}$$

For the variance:

$$V[P(t)] = E[(P(t) - \mu N)^2] = E[(P(t) - n\mu)^2] + E[\mu^2(n - N)^2] + 2E[\mu(P(t) - n\mu)(n - N)] \tag{11}$$

First notice that

$$E[\mu^2(n - N)^2] = \mu^2 E[(n - N)^2] = \mu^2 \eta^2 \tag{12}$$

Next,

$$E[\mu(P(t) - n\mu)(n - N)]$$

$$= \mu \sum_{i=1}^{\infty} E[(P(t) - i\mu)(i - N)|n = i]p_n(i) \tag{13}$$

Since $(i - N)$ are numbers, they can be removed from the expectation operation to yield

$$E[\mu(P(t) - n\mu)(n - N)]$$

$$= \mu \sum_{i=1}^{\infty} (i - N)E[(P(t) - i\mu)|n = i]p_n(i) \tag{14}$$

and because $P(t) = R_1(t) + R_2(t) + \cdots + R_i(t)$, $E[(P(t) - i\mu)] = 0 \forall i$. Therefore Eq. 14 is equal to zero. Finally

$$E[\mu(P(t) - n\mu)^2]$$

$$= \sum_{i=1}^{\infty} E[(P(t) - n\mu)^2|n = i]p_n(i) \tag{15}$$

and again remembering that $P(t) = R_1(t) + R_2(t) + \cdots + R_i(t)$, the above sum can be separated into two parts,

$$E[(P(t) - n\mu)^2] = \sum_{i=1}^{\infty} E[(R_1(t) - \mu)^2 + (R_2(t) - \mu)^2 + \cdots + (R_i(t) - \mu)^2|n = i]p_n(i) \tag{16}$$

$$+ \sum_{i=1}^{\infty} \sum_{j=1}^{\infty} \sum_{k=1}^{\infty} E[(R_j(t) - \mu) \times (R_k(t) - \mu)|n = i]p_n(i) \tag{17}$$

for $j \neq k$ The first summation corresponds to variance and the second summation corresponds to covariance and can be rewritten as

$$E[(P(t) - n\mu)^2] = \sigma^2 \sum_{i=1}^{\infty} ip_n(i) + \sigma_{ij}^2 \sum_{i=1}^{\infty} i(i - 1)p_n(i) \tag{18}$$

$$= \sigma^2 N + \sigma_{ij}^2 \eta^2 + N^2 \sigma_{ij}^2 - N\sigma_{ij}^2 \tag{19}$$

$$= \sigma_{ij}^2 \eta^2 + N(\sigma^2 - \sigma_{ij}^2) + N^2 \sigma_{ij}^2 \tag{20}$$

Adding Eq. 12 and 20 gives the variance of the sum $P(t)$

$$V[P(t)] = \mu^2 \eta^2 + \sigma_{ij}^2 \eta^2 + N(\sigma^2 - \sigma_{ij}^2) + N^2 \sigma_{ij}^2 \tag{21}$$