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Reproductive correlation and mean–variance scaling of reproductive output for a forest model

Ford Ballantyne IV[a,*], Andrew J. Kerkhoff[b]

[a]Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA
[b]University of Arizona, Department of Ecology and Evolutionary Biology, Tucson, AZ 85721, USA

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Abstract

We analyse the mean–variance scaling of reproductive output for a previously published forest model. The model relates individual reproductive effort and pollen limitation to the degree of synchrony in reproduction throughout a forest. We show that the exponent of Taylor's power law reflects the degree of synchrony of reproduction because it indicates the covariance of reproductive behavior. Further, we are able to relate the three components of masting, individual variability, population variability and synchrony in reproductive output, using Taylor's power law. Therefore Taylor's power law can be used as a synoptic index of masting.

Keywords: Scaling; Power law; Masting; Reproductive variability

1. Introduction

Reproduction in plants ranges from asexual selfing to obligate sexual fertilization with many species lying somewhere in the middle of an apparent contiuum. The particular reproductive life-history strategy of a plant species can have profound influence on population level reproductive variability (Satake and Iwasa, 2000, 2002; Kerkhoff and Ballantyne, 2003). Many tree species exhibit the synchronous and intermittent reproduction of trees in a stand, known as masting (Janzen, 1971; Hererra, 1998; Koenig and Knops, 2000), which results in more variable population level reproductive output than constant annual reproduction. Various explanations have been proposed for why masting occurs, the most widely being that synchronized intermittent seed production oversatiates seed predators and allows seeds to germinate, but that is not our concern here. In this paper we are more interested in how the three components of masting, individual reproductive variability (CV_{ind}), population reproductive variability (CV_{pop}), and synchrony can be linked through a macroecological (Brown, 1995) pattern, Taylor's power law.

Taylor's power law (Taylor, 1961) is a mean–variance scaling relationship that characterizes reproductive output for a wide taxonomic range of tree species and is produced by a mechanistic model of masting (Kerkhoff and Ballantyne, 2003). The general functional from of Taylor's power law is $V = aM^b$ where V is variance in abundance, a is a normalization constant, M is mean abundance and b is the scaling exponent, or the slope of the power law.

Here, we extend previous work relating the Satake and Iwasa (2000) forest model to Taylor's power law by presenting a detailed analysis of the mean–variance scaling patterns generated by the model. In particular, we analyse mean–variance scaling for individual trees

*Corresponding author. Present address: Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA. Tel.: +1 858 534 4150.
E-mail address: fballantyne@ucsd.edu (F. Ballantyne IV).

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and for entire forests in the absence of pollen limitation, neither of which have been previously analysed. We then use the results of these analyses of the forest model to confirm predictions from random variable theory about the relationship between reproductive synchrony and Taylor's power law. Finally, we describe how the heretofore unrelated components of masting can be explicitly linked through Taylor's power law.

2. Models and theory

2.1. A model of reproduction for trees in a forest

The Satake and Iwasa model is based on the energy budget of an individual tree. If the energy reserve of a tree is above a critical threshold for a given year, the tree reproduces. A tree reproduces with the same effort each time its energy reserve surpasses the critical threshold, regardless of past reproductive history or the amount of surplus energy. The magnitude of reproductive effort coupled with yearly net photosynthetic production determine whether or not a tree can reproduce in successive years. Trees that allocate a small to moderate amount of their energy reserve to reproduction are able to reproduce annually, especially in productive environments, whereas trees that allocate a large fraction of their energy reserves to reproduction often experience consecutive non-reproductive years. Variability annual reproduction is also more pronounced in less-productive environments.

Whole forest patterns of reproductive variability emerge from the dynamics of individual energy-based reproduction and the degree of pollen limitation trees experience. The dynamics of individual reproductive effort are determined by the fraction of stored energy that a tree allocates toward reproduction. This fraction, or depletion coefficient (see below) (Satake and Iwasa, 2000) is directly proportional to the ratio of fruiting to flowering cost (Satake and Iwasa, 2000). As the ratio of fruiting to flowering cost, and hence the depletion coefficient, increases, annual reproduction at the individual scale becomes more variable. Similarly, when the effects of moderate to strong pollen limitation are incorporated into individual reproductive output, annual reproduction at the scale of the entire forest becomes more variable. Below a critical value, determined by the ratio of fruiting to flowering cost, trees in the model reproduce independently which reduces forest level variability in annual reproduction. Pollen coupling must be strong with respect to the ratio of fruiting to flowering cost in order for reproduction to become synchronized and thus more temporally variable. A high degree of pollen limitation forces trees to reproduce simultaneously, and a high ratio of fruiting to flowering cost prevents trees from reproducing constantly through time. The combination of strong pollen limitation and high reproductive cost result in large synchronized bouts of reproduction.

The non-dimensionalized dynamics of the ith tree in a forest (Satake and Iwasa, 2000) are given by

$$Y_i(t+1) = \begin{cases} Y_i(t)+1 & \text{if } Y_i(t)\leqslant 0, \\ -kP_i(t)Y_i(t)+1 & \text{if } Y_i(t)>0 \end{cases} \quad (1)$$

in which

$$P_i(t) = \left[\frac{1}{N-1}\sum_{j\neq i}[Y_i(t)]_+\right]^{\beta} \quad (2)$$

describes the degree of pollen coupling. In Eq. (1), $Y_i(t)$ is the energy reserve of the ith tree at time t, k is the depletion coefficient which is proportional to the ratio of fruiting to flowering cost, β is the coupling strength (acting through pollen limitation), N is the size of the forest, and $[Y_i(t)]_+$ is $Y_i(t)$ if $Y_i(t)>0$ and 0 otherwise. If $\beta=0$, $P_i(t)$ disappears from Eq. (1) and all trees reproduce independently according to Eq. (1) only. But as β becomes more positive, the degree of individual reproductive coupling increases and individual reproduction depends on Eq. (2). The dimensionless $Y_i(t)$ and k are substituted for $(S_i(t)+P_s-L_T)/P_s$ and $a(R_c+1)-1$ respectively in the dimensional form of the model. In the initial model, $S_i(t)$ is the size of the energy reserve of the ith tree at the beginning of year t, P_s is net annual photosynthetic production, L_T is the critical energy reserve threshold below which a tree does not reproduce, R_c is the ratio of fruiting to flowering cost and a determines the proportion of energy excess dedicated to flowering (see Satake and Iwasa (2000) for a full explanation of the model). We recast the model so that energy allocated to reproduction is the quantity of interest, rather than the amount of energy stored and then use it to examine the mean–variance scaling of reproductive output for single trees and for entire forests. Dimensionless reproductive dynamics $R(t)$ are given by

$$R_i(t+1) = \begin{cases} 0 & \text{if } Y_i(t)\leqslant 0, \\ kP_i(t)Y_i(t) & \text{if } Y_i(t)>0, \end{cases} \quad (3)$$

with $P_i(t)$ the same as in Eq. (2).

2.2. Theoretical predictions for mean–variance scaling exponents

The idea that the exponent of a mean–variance scaling relationship, or alternatively Taylor's power law, is related to the degree of dependence among interacting units has been alluded to by different authors (Sugihara et al., 1990; Keeling and Grenfell, 1999) but can be formalized using random variable theory. By considering individual reproductive output (R_i) a random

variable and population level reproductive output the sum of individual reproductive output ($\sum R_i$), it is easy to show that

$$M_{pop} = N\mu \tag{4}$$

and

$$V_{pop} = V\left[\sum_{i=1}^{N} R_i\right] = NV(R_i) + N(N-1)Cov(R_i, R_j) \tag{5}$$

if the R_i are identically distributed with mean μ and variance V_{ind}. A simple rearrangement of Eq. (5) yields

$$V_{pop} = N[V_{ind} - Cov_{ind}] + N^2 Cov_{ind}, \tag{6}$$

where V_{pop} is the variance of reproductive output for the entire population and Cov_{ind} is the average reproductive covariance between individuals. Eq. (6) is a general relationship that does not depend on any particular underlying model, it only assumes that individuals in a population can be described as random variables. Using Eq. (6) we predict that for the Satake and Iwasa forest model, regions of parameter space resulting in asynchronous reproduction should be characterized by an exponent of one for Taylor's power law because V_{pop} is a linear function of forest size (N) if $Cov_{ind} = 0$. Similarly, parameter combinations leading to synchronized reproduction, or masting, should generate an exponent of two because V_{pop} is a quadratic function of N if $Cov_{ind} = V_{ind}$. We are able to make these predictions because V_{ind} and Cov_{ind} are functions of k and β in the forest model and are constant once k and β are specified. Theory also predicts that mean–variance scaling of individual reproductive variability in the model should be characterized by an exponent of two (Ballantyne, 2005).

3. Power-law scaling of mean and variance for model forests

3.1. Mean–variance scaling for individual trees

For a particular tree species, k, the depletion coefficient is assumed to be constant so the only variable that affects reproductive output is net annual photosynthetic production, P_s. To asses the impact of photosynthetic production on individual reproductive variability, we rescaled $R_i(t)$ in (1) by P_s while holding $\beta = 0$ in 2. Multiplying $R_i(t)$ by P_s explicitly reincorporates the effect of net photosynthetic production because Satake and Iwasa (2000) originally divided by P_s to obtain the dimensionless $Y_i(t)$. This type of linear rescaling of dimensionless models yields a slope of two for Taylor's power law (Ballantyne, 2005) in general, and the Satake and Iwasa model is no exception. Mean reproductive output through time is a linear function of P_s and the variance in reproductive output is a quadratic function of P_s which results is an exponent of two for Taylor's power law. For a given value of P_s, larger k results in higher individual variability (CV_{ind}) in annual reproduction because depletion coefficients of large magnitude prevent trees from reproducing each year. The mean–variance scaling of individual reproductive variability as a function of both k and P_s is plotted in Fig. 1. The exponent of the scaling relationship is clearly two and the value of k determines the normalization constant, which is analogous to CV_{ind}. The different lines correspond to different values of k. Increases in k reflect life-history strategies that favor high-energy investment into reproductive fruits but prevent annual reproduction. The inability to reproduce annually results in more variable reproductive output through time. Thus, CV_{ind} for trees in the model increases as k increases.

3.2. Mean–variance scaling for forests in the absence of pollen limitation

Patterns of reproductive variability become more interesting at the level of the forest even in the absence of pollen limitation. For values of k below one, individual tree dynamics approach a stable equilibrium of constant annual reproduction (Satake and Iwasa, 2000) so different initial conditions for individual trees become virutually irrelevant after initial transient behavior. Several two-point limit cycles exist but are a consequence of particular initial conditions (Satake and Iwasa, 2000). If all trees in a forest exhibit two-point

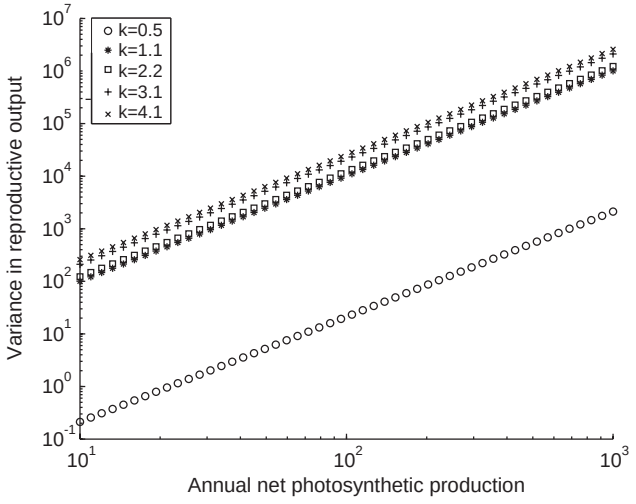

Fig. 1. Mean–variance scaling for individual trees with changing net photosynthetic production P_s. The scaling exponent is two regardless of k. Increasing k increases individual reproductive variability for a given value of P_s. The slope for all scaling relationships is 2 and the normalization constants for ascending k values are −2.67, 0.003, 0.08, and 0.5153.

limit cycles, any two trees in the forest will either be completely in phase of completely out of phase. Whether or not two particular trees are in phase depends only on their initial conditions. And regardless of phase correspondence, all tree are completely correlated in their annual reproduction. Trees that are out of phase reduce the overall magnitude of forest level variance in reproductive output but do not affect mean–variance scaling of reproductive variability for the entire forest. As k increases past a critical value, individual tree dynamics become chaotic and initial conditions are paramount. Two trees that exhibit chaotic annual reproduction are functionally independent if they are given different initial conditions. Independent reproduction of individual trees in a forest reduces forest level variability in annual reproduction.

The different patterns of reproductive output for entire forests of 5000 trees in constant environments are plotted in Fig. 2 for different values of k. For small values of k, reproductive output of the entire forest is variable and but entirely predictable. The entire forest is acting as one large tree because the temporal reproductive patterns of all individual trees are identical. As k becomes larger, individuals become independent in their annual reproduction, which decreases temporal reproductive variability at the scale of the entire forest.

Based on the predictions above (Eq. (6)), we expect to see the shift from correlated reproductive output to independent reproductive output reflected in the exponent of Taylor's power law. Specifically, forests consisting of trees with subcritical values of k should exhibit mean–variance scaling with an exponent of two and trees with supercritical values of k should exhibit mean–variance scaling with an exponent of one under constant environmental conditions. The exponent of Taylor's power law as a function of k from simulations of the Satake and Iwasa (2000) model is plotted in Fig. 3. There is an abrupt transition in the exponent of Taylor's power law from two to one as k increases past 1.62, which is the approximate value of k at which any semblance of periodic individual reproduction shifts to chaos in the forest model (see Fig. 2 in Satake and Iwasa (2000)). Trees are functionally independent if k is above this threshold because of sensitive dependence on initial conditions. The correspondence of the almost instantaneous change of power law slope and change in qualitative reproductive dynamics confirms the prediction that correlated individuals produce an exponent of

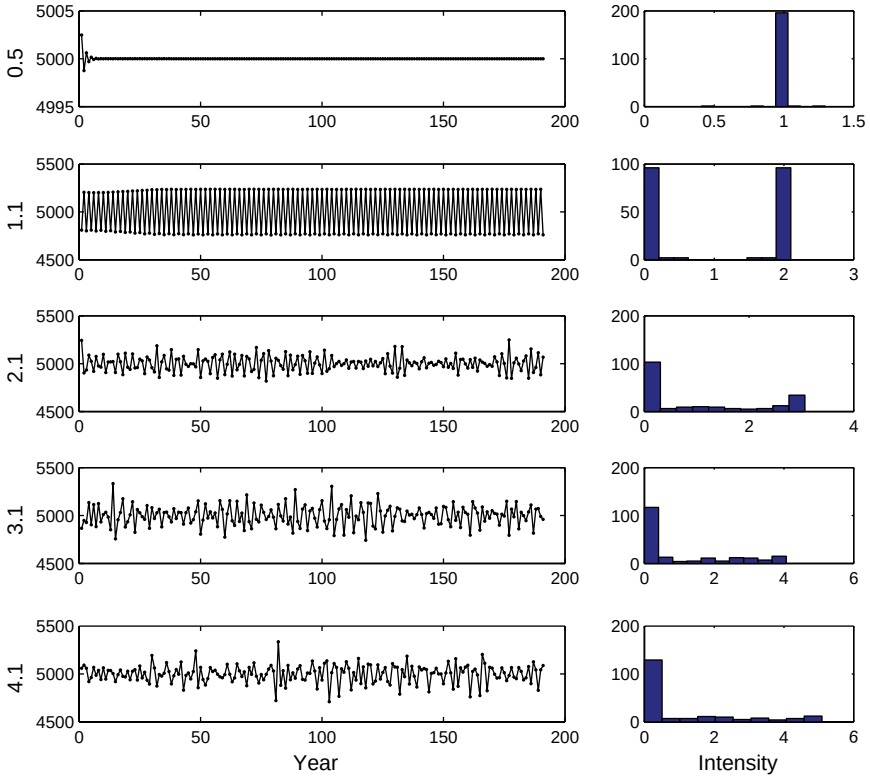

Fig. 2. Reproductive output for entire forests of 5000 trees. The time series are plotted for different values of k, the depletion coefficient, labeled on the y-axis. Once k is larger than approximately 1.62, individual trees are virtually independent in reproductive output and whole forest reproductive variability decreases. The histograms display the distribution of reproductive intensity throughout the forest for the corresponding time series to the left for different values of k.

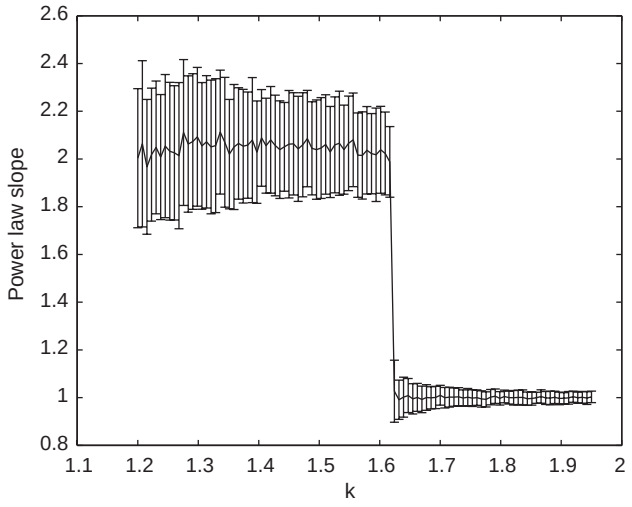

Fig. 3. The slope of Taylor's power law for a range of k values. Simulations were performed with forests of 5000 trees all with the same k value but with different initial conditions. The abrupt transition from a slope of two to one occurs at approximately $k = 1.62$. Error bars represent two standard errors of the mean for 100 simulations at each value of k.

two for Taylor's power law and that independent individuals produce an exponent of one.

3.3. Mean–variance scaling for trees coupled by pollen limitation

The addition of pollen limitation in the Satake and Iwasa forest model has little effect if reproductive cost is relatively high but it acts to correlate individual reproductive output if it is strong relative to reproductive cost. When the effects of pollen coupling (β) are weak, individual trees become rapidly uncorrelated as fruiting cost (k) increases, which results in a exponent of one for Taylor's power law. As pollen coupling becomes stronger, clusters of reproductively autocorrelated trees emerge (Satake and Iwasa, 2000). Further increase in pollen coupling with respect to the ratio of fruiting to flowering cost results in synchronous, or completely correlated, reproduction throughout the forest. The mean–variance scaling exponents generated by the forest model are plotted in Fig. 4 as a function of pollen coupling and depletion coefficient along with a figure reproduced from Satake and Iwasa (2000) that illustrates qualitative forest dynamics for the same parameter range. The shift from asynchronous to synchronous reproduction is less abrupt than the transition in Fig. 3 which indicates that coupling through pollen limitation ($\beta > 0$) blurs the effects of the depletion coefficient k. However, the exponent of Taylor's power law exhibits a pattern similar to the original Satake and Iwasa figure. This correspondence between the degree of reproductive correlation and the exponent of Taylor's power law is precisely the predicted relationship from theory (Ballantyne and Kerkhoff, in prep.).

3.4. Power-law exponent and the Lyapunov spectrum

Satake and Iwasa (2000) use the Lyapunov spectrum to distinguish regions of qualitatively distinct reproductive dynamics so the correspondence of the two panels in Fig. 4 suggests a possible link between the exponent of Taylor's power law and the Lyapunov spectrum. A link between the exponent of Taylor's power law and the Lyapunov spectrum would be interesting because although these two characterizations of dynamics have very different bases, they ultimately result in the same qualitative description. The Lyapunov characterization is based on the correspondence between the number of positive Lyapunov exponents and the number of clusters within a forest (Kaneko, 1990; Satake and Iwasa, 2000), whereas the Taylor's power-law characterization is based on observed reproductive covariance.

Linking the Lyapunov spectrum to Taylor's power law is potentially quite powerful because it allows one to relate population level patterns of reproductive output to individual level reproductive dynamics. In the case of the Satake and Iwasa (2000) model, the exponent of Taylor's power law indicates the threshold in parameter space at which individual initial conditions begin to influence patterns of whole forest reproductive variability. Below a critical threshold, individual trees exhibit periodic cycles of reproduction and whole forests reproduce coherently. But above the critical threshold, individual trees reproduce chaotically, which means that two trees with different initial conditions are completely decoupled and therefore, functionally independent. Fig. 4 illustrates how the stabilizing influence of individual level chaos on the forest is mediated by correlation at the population level. Stronger coupling through pollen limitation ($\beta > 0$) delays the onset of asynchronous reproduction, which reduces population level reproductive variability. The Satake and Iwasa (2000) model is an example of how chaos can affect population dynamics in a nonintuitive way. Dynamic instability at the individual level can lead to increased population level stability.

4. Discussion

The dynamics of reproduction in forests, as described the Satake and Iwasa (2000) model, support predictions that the degree of reproductive correlation among individuals in a population directly influences the exponent of Taylor's power law. For the Satake and Iwasa model, regions of parameter space that result in

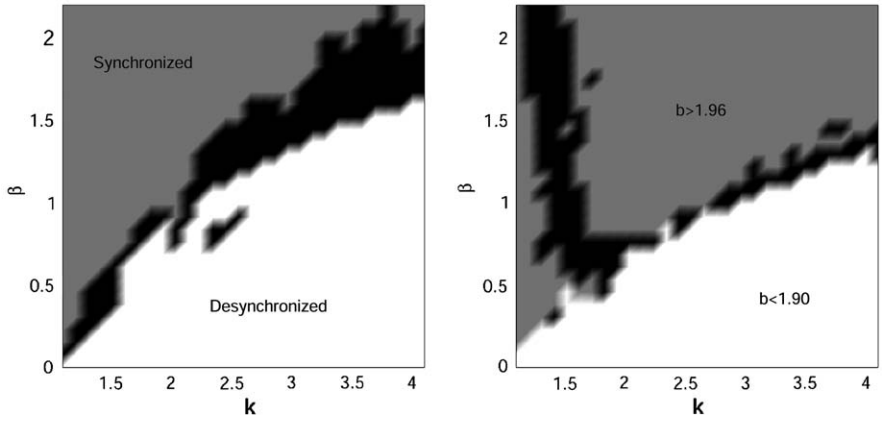

Fig. 4. The relationship between qualitative dynamics and the slope of Taylor's power law. The left panel is reproduced from Satake and Iwasa (2000) to show the qualitative dynamics of forest reproduction. The right panel is the slope of Taylor's power law for the same parameter space. The higher degree of variability in the right panel stems from the fact that each parameter combination was simulated only once. Each combination for the left panel was simulated 100 times and averages are plotted.

asynchronous reproduction produce values of approximately one for the exponent of Taylor's power law. Regions of parameter space that result in synchronous reproduction, produce exponents of approximately two. This is exactly the scaling behavior predicted by Eq. (6). In the absence of synchrony ($Cov_{ind} = 0$), Eq. (6) predicts an exponent of one and for complete synchrony ($Cov_{ind} = V_{ind}$) it predicts an exponent of two. It is easy to recast these predictions in terms of the general mean–variance scaling equation $V = aM^b$ by substituting $a = V_{ind}/\mu$ and $b = 1$ in the former case and substituting $a = Cov_{ind}/\mu^2$ and $b = 2$ in the latter.

The exponent of Taylor's power law also reflects the transition between different regimes of qualitative dynamics exhibited by the model. The transition in reproductive synchrony depicted by the original Satake and Iwasa phase diagram in Fig. 4 is reproduced by the change in power-law exponent as a function of the depletion coefficient k and the degree of pollen limitation β. Within each of the two qualitatively different regions of parameter space, the exponent of Taylor's power law b is virtually invariant but the normalization constant a varies. This means that increasing the intensity of reproductive output k only increases a and does not affect b, except when k approaches a critical value, which is dictated by the degree of pollen limitation β. At this critical value, increasing k qualitatively alters reproductive dynamics at the level of the forest and this qualitative change is bourne out by b. In the case of no pollen limitation, this critical value is approximately 1.62 (see Fig. 3). In the case of pollen limitation, the dependence of this critical value depends on β and is seen in the right panel of Fig. 4. As β increases, the critical value of k also increases. Once k exceeds the critical threshold set by β, reproduction of trees in the forest shifts from synchronous to asynchronous and b changes from two to one. Further increases in k will only increase a and will not affect b. We have therefore decomposed variability in reproductive output for populations into two components that affect mean variance scaling of reproductive variability in different ways. Reproductive intensity only affects individual variability as long as forests are not at the critical threshold and pollen limitation intuitively changes the correlation of reproduction among individuals.

In relating the normalization constant and exponent of Taylor's power law to individual reproductive variability and reproductive covariance, we are able to link the three components of masting previously thought to be unrelated (Hererra, 1998; Koenig et al., 2003; Buonaccorsi et al., 2003). And in the specific case of the (Satake and Iwasa, 2000) model, we can relate the components of masting to particular life-history parameters, namely pollen limitation and fruiting and flowering costs. Recently, Buonaccorsi et al. (2003) show that through a one-way ANOVA sum of squares decomposition, CV_{ind}, CV_{pop} and synchrony cannot be related to one another from empirical data. We are able to link these three components of masting through Taylor's power law. Taylor's power law is the key ingredient to make this linkage because it explicitly expresses the relationship between individual variability, synchrony and population variability. Individual variability, V_{ind} in Eq. (6) is reflected in the normalization constant of an empirical relationship (for example a in $V = aM^b$), and is predominantly a function of k in the (Satake and Iwasa, 2000) model (see Fig. (1)). However, when a forest is at a critical state, k also affects the correlation of reproductive output (Satake and Iwasa, 2002) and therefore population synchrony. Synchrony is

always reflected in the scaling exponent b (the extreme cases of one and two are represented in Eq. (6)) and does not depend on the underlying mechanics of masting. For the forest model considered here, synchrony is a function of β for fixed k. Population variability is shown to be a function of both individual variability and synchrony in Eq. (6). An exponent of two reflects synchrony whereas an exponent of one reflects asynchrony.

Taylor's power law further describes how CV_{pop}, the third commonly used measure of masting (Hererra, 1998; Koenig et al., 2003; Buonaccorsi et al., 2003), scales with population size and is related to synchrony. Eq. (6) shows the functional dependence of V_{pop} on forest size (N), which is a surrogate for the mean since all trees are identical in their dynamics. Synchronously reproducing forests ($Cov_{ind} = V_{ind}$) exhibit a quadratic dependence of V_{pop} on N and asynchronously reproducing forests ($Cov_{ind} = 0$) exhibit linear dependence of V_{pop} on N. This result has important implications for empiricists using CV_{pop} to describe masting. If $b = 2$, CV_{pop} is a scale invariant measure of variability but if $b = 1$, it is not. This is easily seen by remembering that if $V_{pop} \propto N^b$, then

$$CV_{pop} = \frac{\sqrt{V_{pop}}}{N} \propto N^{b/2-1}. \quad (7)$$

Therefore, $b = 1$ means that variability of populations of different sizes is not directly comparable using CV_{pop}. However, because b, which reflects the degree of reproductive synchrony, describes how CV_{pop} changes with respect to population size, the necessary transformation can easily be made. The functional dependence of CV_{pop} on forest size is critically determined by the degree of reproductive synchrony in the forest. Thus, the exponent of Taylor's power law, which describes explicitly how V_{pop} and implicitly how CV_{pop} scale with forest size, reflects the degree of reproductive synchrony in forests. Here we have only explored the extreme cases of complete synchrony and complete asynchrony and an in depth discussion of intermediate levels of reproductive synchrony will appear elsewhere.

Our analysis is an example of how a macro-scale descriptor, the exponent of Taylor's power law, can be related to individual scale dynamics. The exponent of Taylor's power law indicates the degree of correlation among population constituents and here, we are able to interpret correlation in terms of life-history attributes, namely pollen limitation and the ratio of fruiting to flowering cost (a measure of reproductive intensity). Pollen limitation and reproductive intensity, defined as the fraction of stored energy allocated to reproduction, interact to produce different degrees of reproductive correlation among trees in the Satake and Iwasa forest model. The reproductive correlation inferred from Taylor's power law constrains combinations of pollen limitation and reproductive intensity to those corresponding to a particular power-law slope. Knowledge of species-specific life-history allows one to further restrict parameter space and draw more specific conclusions about reproductive dynamics.

The exponent of Taylor's power law is a general description of correlation in populations and is a robust link between large-scale patterns of population fluctuations and individual behavior. Although we have only discussed the relationship between power-law exponents and reproductive synchrony, power-law exponents can be related more generally to the dynamics of aggregated individuals in other systems (Ballantyne and Kerkhoff, in prep.). Correlation at the individual scale is extremely difficult or impossible to measure but mean–variance scaling provides us with an appealing alternative. We are able to infer the degree of individual correlation directly from the exponent of Taylor's power law. Rescaling ecological systems has proved to be very difficult but Taylor's power law is an intuitive metric with which to predict how the relative magnitude of reproductive output scales with population size.

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