



Population Dynamic Models Generating Species Abundance Distributions of the Gamma Type

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This paper deals with processes generating species abundance distributions of the gamma type, including Fisher's logarithmic series model, MacArthur's broken stick model and the extended gamma model. Speciation is described by a Poisson process and density-dependence within species is given by the logistic growth function. Environmental fluctuations are modelled by constant environmental variances in specific rates of population growth. All models are based on diffusion approximations for the abundance of each species. The simplest case of independent identically distributed abundances is generalized in two ways. Interspecific competition is introduced in a way that makes the total abundance for the community constant. The stationary distribution for the corresponding multivariate diffusion for the relative abundances is the Dirichlet distribution, though with a slight reduction in the shape parameter compared to the case of independent abundances. Heterogeneity between the species is discussed in general and exemplified by two types of mixing in Fisher's model leading to Kempton's generalized log-series model.

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Introduction

The models occurring in the literature on species abundance distributions may, in purely statistical terms, be broadly divided into two classes. A large number of data sets from biological communities correspond with the model in which the species abundances are lognormally distributed, first introduced by Preston (1948). Fisher approached the same problem in a classical analysis of community structure in butterflies (Fisher *et al.*, 1943) by considering the gamma distribution for the species abundances.

The frequent difficulty in discriminating between these two distributions is recognized. When fitting the gamma model to data, the shape parameter is usually quite small for most communities, in which case the two distributions are very different, especially for small abundances. However, this difference may be difficult to detect since the statistical analysis must be based on some finite random sample from the

community, which includes only a few representatives from rare species.

Another way of distinguishing these two classes of species abundance distributions, apart from the pure statistical analysis of data, is to consider mechanisms that generate species abundances. In this area there has been most emphasis on the lognormal model, perhaps since it can easily be "explained" by various applications of the central limit theorem through the biological concept of niche-preemption (Bulmer, 1975; May, 1975; Pielou, 1975; Sugihara, 1980). In a recent paper, we have presented various population dynamic models generating the lognormal species abundance distribution (Engen & Lande, 1995). The models are based on diffusion theory and include density-dependence within species given by the Gompertz curve as well as constant environmental noise in the specific growth rates. Mathematically, the models are all closely linked to the Gaussian diffusion process known as the Ornstein-Uhlenbeck process (Karlin & Taylor, 1981). We were also able to include

intraspecific competition and heterogeneity between species, finding that the relative abundances were still distributed as in the case of independent identically distributed lognormal abundances.

In the present paper, we focus on the gamma and related models. The literature does not often refer to the gamma model, but rather to two well-known special cases, Fisher’s model (Fisher *et al.*, 1943) and MacArthur’s broken stick model (MacArthur, 1957). Fisher considered the limiting distribution for a sample where the shape parameter of the gamma tends to zero. To produce a well-defined model he also had to let the number of species tend to infinity, thus deriving what is known as Fisher’s logarithmic series distribution. MacArthur’s model corresponds to the shape parameter being one (Cohen, 1968), although MacArthur only dealt with relative abundances in his niche-preemption model and focused on the expected order statistics. A number of mechanisms generating Fisher’s logarithmic series distribution are given by Boswell & Patil (1971), including birth and death processes with immigration (Kendall, 1948). Most authors actually using the general gamma model refer to it as the negative binomial (Pielou, 1975; Engen, 1974, 1978, 1979), which is the sampling distribution obtained when the number of individuals sampled from any given species is Poisson distributed. Fisher’s model may be extended to include values of the shape parameter in the region $(-1, 0)$ (Engen, 1974, 1977, 1978, 1979), in which case the number of species is also infinite. Many data sets give estimates in this region, and the fit is sometimes remarkably good. The infinite species number in Fisher’s model, as well as the extended gamma, is a theoretical concept required because the lower bound for species abundances is defined to be zero. In practice the smallest abundance is one individual, and the corresponding censored model will only have a finite species number and practically the same sampling distribution.

The Gamma Model with Independent Species

Engen & Lande (1996) defined a general class of abundance models in which the species abundances are described by an inhomogenous Poisson process with rate $\lambda(x)$. The interpretation of this is that the number of species with abundances in any interval, say $[a, b]$, is Poisson distributed with parameter $\int_a^b \lambda(x) dx$. A brief description of Poisson abundance models, and the general class of processes that generates them, is given in the Appendix. For further details the reader is referred to Engen & Lande (1996).

If new species enter the community according to a homogenous Poisson process with rate ω_0 and the species evolve independently according to diffusion processes with infinitesimal mean and variance $m(x)$ and $v(x)$, respectively (Engen & Lande, 1996), then the corresponding Poisson abundance model is

$$\lambda(x) = 2\omega_0 \frac{1}{v(x)} e^{\int_1^x 2m(u)/v(u) du} \tag{1}$$

A more precise definition of the speciation rate ω_0 is given in the Appendix.

The most common stochastic analog to the logistic growth equation

$$\frac{dx}{dt} = rx - \beta x^2 \tag{2}$$

is obtained by replacing the constant growth rate r by the process $r + \sigma_r(x) dB(t)/dt$, where $B(t)$ represents standard Brownian motion. Inserting $\sigma_r^2(x) = \sigma_e^2 + \sigma_d^2/x$ and applying the Ito solution to the corresponding process $\ln(x)$, we find that x is a diffusion with infinitesimal mean and variance

$$m(x) = (r + \frac{1}{2}\sigma_d^2/x + \frac{1}{2}\sigma_e^2)x - \beta x^2 \tag{3}$$

$$v(x) = \sigma_d^2 x + \sigma_e^2 x^2 \tag{4}$$

where σ_d^2 and σ_e^2 are the demographic and environmental variance, respectively (Engen & Lande, 1996). If we adopt the Ito approach to (2) directly without transforming to $\ln x$, the results will be slightly different. However, if σ_d^2 is small or x is large, the infinitesimal variance of the process $\ln x$ is approximately constant, in which case the Ito solution and the Stratonovich solution are identical.

After some algebra we obtain

$$2 \int_1^x m(u)/v(u) du = \ln(x) - \frac{2\beta}{\sigma_e^2} (x-1) + 2 \frac{(r+\beta\epsilon)}{\sigma_e^2} \ln\left(\frac{x+\epsilon}{1+\epsilon}\right) \tag{5}$$

and applying (1) the abundance model takes the form

$$\lambda(x) = a\omega_0(x+\epsilon)^{2(r+\beta\epsilon)/\sigma_e^2 - 1} e^{-2\beta/\sigma_e^2(x+\epsilon)}, \tag{6}$$

for $x \geq 1$, where $\epsilon = \sigma_d^2/\sigma_e^2$ and

$$a = \frac{2 e^{2(1+\epsilon)\beta/\sigma_e^2}}{\sigma_e^2(1+\epsilon)^{2(r+\beta\epsilon)/\sigma_e^2}} \tag{7}$$

This curve is proportional to a gamma distribution

translated to start at $-\epsilon$ rather than at zero. However, unless the demographic variance is very large compared with the environmental variance, this translation can be neglected. If we ignore the demographic variance which has a significant effect only at very small abundances, we arrive at the familiar gamma model

$$\lambda(x) = a_0 \omega_0 x^{2r/\sigma_e^2 - 1} e^{-(2\beta/\sigma_e^2)x} \quad (8)$$

where $a_0 = 2/\sigma_e^2 e^{2\beta/\sigma_e^2}$. It is interesting to note that, although σ_e^2 has practically no effect on the shape of $\lambda(x)$, it affects the constant a defined by (17), and therefore the number of species and the diversity of the community. Engen (1974) found that -1 was the natural lower bound for the shape parameter of the gamma model, corresponding to $2r/\sigma_e^2 > -1$ or $r + \frac{1}{2}\sigma_e^2 > 0$, which ensures that the infinitesimal mean of the diffusion processes, $m(x)$, is positive for small values of x . Notice that Fisher's model corresponds to $r=0$ while MacArthur's broken stick model appears if $r = \frac{1}{2}\sigma_e^2$.

The Effect of Inter-specific Competition

If we ignore demographic variance, put $\omega_0 = 0$, and define the extinction barrier at zero, there will be no extinction or speciation, and the abundances x comprise s independent gamma distributed variables with shape parameter $2r/\sigma_e^2$ and scale parameter $2\beta/\sigma_e^2$. The expected total abundance is $n = sr/\beta$ and the relative abundances $p_i = x_i/\sum_j x_j$ possess the symmetric Dirichlet distribution

$$f(\mathbf{p}) = \frac{\Gamma(k_s)}{\Gamma(k)^s} \left[p_1 p_2 \cdots p_{s-1} \left(1 - \sum_{i=1}^{s-1} p_i \right) \right]^{k-1}, \quad (9)$$

where $\mathbf{p} = (p_1, p_2, \dots, p_{s-1})$ and $k = k_0 = 2r/\sigma_e^2 > 0$. In accordance with the derivation of (3), (4) and (8), this model is the Ito-solution of the stochastic differential equations

$$dx_i = (r + \frac{1}{2}\sigma_e^2)x_i - \beta x_i^2 + \sigma_e x_i dB_i(t), \quad (10)$$

$i = 1, \dots, s$, where the $B_i(t)$ are independent standard Brownian motions. One way of modelling inter-specific competition is to assume that the species divide the available resources between them so that the sum of species abundances is constant. Let us do this by imposing some effect that is common to all the individuals in the community. This can be obtained by adding a common noise

term to all species proportional to their abundances writing

$$dx_i = (r + \frac{1}{2}\sigma_e^2)x_i - \beta x_i^2 + \sigma_e x_i dB_i(t) + x_i dW(t). \quad (11)$$

Requiring that $\sum x_i = n$, or $\sum dx_i = 0$, we find that the process $dW(t)$ must obey the equation

$$dW(t) = -(r + \frac{1}{2}\sigma_e^2) + \frac{\beta}{n} \sum x_i^2 - \sigma_e \frac{1}{n} \sum x_i dB_i(t), \quad (12)$$

which inserted into (11) gives the equations

$$dx_i = \beta \frac{x_i}{n} \sum_j x_j^2 - \beta x_i^2 + \sigma_e \left[x_i dB_i(t) - \frac{x_i}{n} \sum_j x_j dB_j(t) \right], \quad (13)$$

for $i = 1, 2, \dots, s$. Introducing the relative abundances $p_i = x_i/n$, writing $R = \sum_j p_j^2$ and $\gamma = n\beta = sr$, the equations for the relative abundances are

$$dp_i = \gamma p_i (R - p_i) + \sigma_e p_i \left[dB_i(t) - \sum_j p_j dB_j(t) \right]. \quad (14)$$

The corresponding Ito-solution is a multivariate diffusion in $(s-1)$ variables (since $\sum_j p_j = 1$) with infinitesimal means, variances and covariances

$$m_i(\mathbf{p}) = \gamma p_i (R - p_i) \quad (15)$$

$$v_{ii}(\mathbf{p}) = \sigma_e^2 p_i^2 (1 + R - 2p_i) \quad (16)$$

$$v_{ij}(\mathbf{p}) = \sigma_e^2 p_i p_j (R - p_i - p_j), \quad i \neq j, \quad (17)$$

where $p_s = 1 - \sum_{i=1}^{s-1} p_i$. If there exists a limiting distribution $f(\mathbf{p})$, it must satisfy the forward equation (Karlin & Taylor, 1981)

$$\sum_{i=1}^{s-1} \frac{\partial}{\partial p_i} [m_i(\mathbf{p})f(\mathbf{p})] - \frac{1}{2} \sum_{i=1}^{s-1} \frac{\partial^2}{\partial p_i^2} [v_{ii}(\mathbf{p})f(\mathbf{p})] - \sum_{i < j} \frac{\partial^2}{\partial p_i \partial p_j} [v_{ij}(\mathbf{p})f(\mathbf{p})] = 0. \quad (18)$$

Solving the equation in the case that $s=2$ and extinction barrier at zero, one can easily see that there exists an equilibrium solution which is the beta-distribution. A natural guess for the general case is then the symmetric Dirichlet distribution given by (9), possibly with $k \neq k_0$, which is the multivariate analogy to the beta-distribution. It is a long exercise, even when using algebraic programming, to show

that this distribution solves the forward equation. Inserting (15) to (17) into (18) produces the expression

$$\gamma \left[\prod_{i=1}^{s-1} p_i^{k-1} \right] [-1 - k + (1 + ks)R] - \frac{\sigma_c^2}{2} \left[\prod_{i=1}^{s-1} p_i^{k-1} (2 + ks) [-1 - k + (1 + ks)R] \right] = 0, \tag{19}$$

with final solution

$$k = k_1 = \frac{2(\gamma - \sigma_c^2)}{\sigma_c^2 s}. \tag{20}$$

It appears that we have an equilibrium distribution which is actually the Dirichlet distribution as in the case of independence, though the shape parameter has changed from k_0 to k_1 where

$$k_1 = k_0 - \frac{2}{s}. \tag{21}$$

Fisher considered the limit $k \rightarrow 0, s \rightarrow \infty$ as $ks \rightarrow \alpha$. Taking the same limit for both models we get from (21)

$$\alpha_1 = \alpha_0 - 2. \tag{22}$$

Fisher called α the index of diversity. It often takes values around, say 40, in which case the inter specific competition only reduces Fisher's diversity by 2.5%. As a further illustration we may compare the expected values of the information index of diversity $H = -\sum p_i \ln p_i$ (Shannon & Weaver, 1963) which is $\psi(ks + 1) - \psi(k + 1)$ (Webb, 1974; Bulmer, 1974; Engen, 1978), where $\psi(x) = d/dx \ln \Gamma(x)$ is the digamma function (Abramowitz & Stegun, 1964). From the recurrence relation $\psi(x + 1) = \psi(x) + 1/x$ we find for example for Fisher's model that the reduction in diversity is

$$EH_0 - EH_1 = \frac{1}{\alpha_0} + \frac{1}{\alpha_0 - 1}. \tag{23}$$

For $\alpha_0 = 40$ this difference is about 0.05, which is considered a very small reduction in the diversity.

In the model with constant total abundance each relative abundance may be approximated by a univariate diffusion. We first write $R = \sum p_i^2$ as

$$R = p_i^2 + (1 - p_i^2)U \tag{24}$$

where $U = \sum_{j \neq i} p_j^2 / (1 - p_i^2)$. If the species number is large, U may be replaced by $EU = (k_1 + 1) / [k_1(s - 1) + 1]$, giving s one-dimensional independent diffusions. The corresponding stationary distribution for the p_i turns out to be the beta-distribution with

parameters k_1 and $k_1(s - 1)$, which is exactly the marginal distributions in (9) with $k = k_1$. This can be used to find the approximate speciation rate required to replace extinct species when the extinction barrier for the relative abundances is at $1/N_0$, corresponding to absolute abundances being 1. The results of those calculations are analogous to the results given by (21) to (23): the effect of inter-specific competition is small if the species number is large. For both models the required speciation rate is approximately

$$\omega_0 = s \frac{\sigma_c^2}{2} \frac{\left(\frac{2\beta}{\sigma_c^2}\right)^{2r/\sigma_c^2}}{\Gamma\left(\frac{2\beta}{\sigma_c^2}\right)} e^{-2\beta/\sigma_c^2} \tag{25}$$

provided that $r > 0$.

Mixing of Gamma Models

The community structure is given by a Poisson abundance model even if the parameters in the diffusion for each species are generated from some distribution. The resulting abundance model is the mixture given by eqn (31) in the Appendix. For further details see Engen & Lande (1996).

Writing eqn (8) as an exponential function, we see that the exponent is linear in r as well as β . Hence we can easily find generalizations for any of the models treated here provided that (r, β) has a bivariate distribution among species with known moment generating function. However, it turns out that well-known bivariate distributions such as, for example, the normal or the gamma, give models that are more complex than those usually dealt with in the literature, except for the case with $r = 0$. In this case we may choose the density-dependence to vary between species assuming that β is gamma-distributed with parameters, say (u, v) , giving

$$\lambda(x) = \frac{2\omega_0}{\sigma_c^2 x} \left[1 + \frac{2}{v\sigma_c^2} (x - 1) \right]^{-u} \tag{26}$$

which is approximately Kempton's generalized log-series model (Kempton, 1975) for $x > 1$. Alternatively, the mixing may be carried out by assuming heterogeneity in the environmental variances acting on each species. If $2/\sigma_c^2$ has a gamma distribution with parameters (u, v) , the corresponding abundance model is

$$\lambda(x) = \frac{\omega_0 u}{xv} \left[1 + \frac{2\beta}{v} (x - 1) \right]^{-(u+1)} \tag{27}$$

which is equivalent to the family of models given above.

Kempton (1975) showed that the generalized log-series model fitted quite well to insect catches from traps at Rothamsted experimental station. Thus, this two-parameter model is an interesting alternative to the more commonly used lognormal and gamma.

Discussion

The birth and death process of Kendall (1948), discussed by Boswell & Patil (1971), may be approximated by the diffusion $m(x)=rx$ with $r<0$ and $v(x)=\sigma_d^2x$. There is no environmental variance, no density-dependence, and the mean growth rate is negative. The demographic variance, σ_d^2 , is the sum of the birth- and death-rate. The corresponding Poisson abundance model given by (1) is

$$\lambda(x) = \frac{2\omega_0}{\sigma_d^2} e^{-2r/\sigma_d^2} x^{-1} e^{(2r/\sigma_d^2)x} \tag{28}$$

which is actually equivalent to Fisher’s log-series distribution.

We have shown that species abundance distributions of the gamma type, with Fisher’s model, can be generated by assuming that each species is subject to intra-specific density-regulation according to the stochastic logistic model with environmental and demographic stochasticity in the specific growth rates. If demographic variances were ignored we found the exact gamma, while in general the model is a translated gamma. The translation is the exact ratio between the demographic and the environmental variance. A similar result was found for lognormal species abundance distributions generated through density-regulation according to a stochastic Gompertz model (Engen & Lande, 1996).

If the mean growth rate, r , is positive, the process will be approximately stationary between speciations and extinctions, and the relative abundances will be Dirichlet distributed. This distribution also arises in population genetics as a stationary distribution of the frequencies of multiple alleles in a single locus under mutation and random genetic drift (Ewens, 1979), or random selection (Gillespie, 1991). Population genetic models of this type have been used to describe neutral models of community structure, producing species abundance distributions that approximate Fisher’s log-series distribution (Caswell, 1976). The diffusions used in these models are, however, different from the process defined by eqns (14–17), derived by modelling population

growth with environmental noise and logistic density-dependence.

The shape parameter, k , of the gamma distribution reflects the population structure. For the model with independent abundances we have $k=2r/\sigma_e^2$. For positive values of r , increasing stochasticity in the environment leads to smaller values of k . This is in agreement with empirical biological studies showing that communities of birds are often well described by MacArthur’s broken stick model ($k=1$), while insect data correspond well to Fisher’s model ($k=0$).

Negative values of k occur when $r<0$. Since the specific growth rate in the stochastic model is $(r+\frac{1}{2}\sigma_e^2)$ for small abundances, invading species are expected to grow in abundance for any $k>-1$. Hence the natural lower limit for the shape parameter is -1 in accordance with the results of Engen (1974, 1978). If $r<0$, the effect of increasing stochasticity in the environment is to increase k towards 0.

In a similar approach to the lognormal species abundance model, Engen & Lande (1996) found that inter-specific density-dependence acting equally on each individual in the community did not change the process for the relative abundances. This is not the case for the diffusions leading to the gamma model. However, if we include terms required to keep the total community size constant, the relative abundances still have a stationary distribution of the Dirichlet type provided that the extinction barrier is at zero and $r>0$. The only effect of this form of density-dependence is that the shape parameter is reduced from $k=k_1$ to $k=k_1-2/s$. We have demonstrated that this is only a minor effect that can be ignored. The effect on expected species diversity is small, as is the effect on the speciation rate required to maintain s species in the community.

The general theory on mixing of abundance models may also be applied to the gamma model. Kempton’s generalized log-series model can be generated by introducing heterogeneity between the species either in the density-regulating term in the population growth, or in the environmental variances. We can easily perform other types of mixing, though this will give different abundance models to those found in the literature.

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extinct. Engen & Lande (1996) showed that if the species are independent, these assumptions are sufficient to ensure that the abundances of the species in the community at time zero are generated by an inhomogeneous Poisson process with rate

$$\lambda(x) = \int_0^\infty \omega(-t)p(t)f(x; t) dt, \quad (\text{A.1.})$$

for $x > 0$. The interpretation of this process is that the number of species with abundances in any given interval, say $[a, b]$, is Poisson distributed with parameter $\int_a^b \lambda(x) dx$. With a constant speciation rate, say ω_0 , we get $\lambda(x) = \omega_0 \int_0^\infty p(t)f(x; t) dt$. If the processes are diffusions and new species are introduced at abundance x_0 , the last integral multiplied by dx represents the expected total time the process for each species is in $(x, x + dx)$ before it goes extinct, and is called the Green function for the process. Using the notation of Karlin & Taylor (1981), with x_0 as the initial population size at the time of speciation, we have $G(x_0, x) = \int_0^\infty p(t)f(x; t) dt$, and

$$\lambda(x) = \omega_0 G(x_0, x) \quad (\text{A.2.})$$

so that the abundance model is fully specified by the Green function $G(x_0, x)$ and the speciation rate.

Engen & Lande (1996) gave examples demonstrating that this formulation also includes the case of heterogeneity, that is, each species may evolve according to quite different stochastic processes. Assuming that the processes for the different species are members of some family of processes parameterized by $\theta \in \Theta$, the values of θ being generated independently by some distribution $\pi(\theta)$, we still have a Poisson abundance model. Writing $\lambda(x; \theta)$ for the model obtained when θ is constant, the model for the heterogeneous case may simply be written as the mixture

$$\lambda(x) = \int_\Theta \lambda(x; \theta)\pi(\theta) d\theta. \quad (\text{A.3.})$$

If $\int_1^\infty \lambda(x) dx$ is finite, the number of species in the community, say S , is Poisson distributed with parameter $A = \int_0^\infty \lambda(x) dx$. If the integral diverges, then the expected number of species is infinite. If A is finite, then conditioned on $\{S = s\}$, the abundances are independently distributed random variables with distribution $\lambda(x)/A$, even in the case of heterogeneity. The expected number of individuals is given by $EN = \int_0^\infty x\lambda(x) dx$.

If the process for each species is a diffusion process

APPENDIX

Poisson Abundance Models

Here we give a brief introduction to the concept of Poisson abundance models.

Let the present time be zero and suppose that new species enter the community at times generated by a Poisson process, possibly inhomogeneous, with rate $\omega(t)$. Let the distribution of the abundance $X(t)$ at time zero of a species entering at time $-t < 0$ be $f(x; t)$ conditional on still being present in the community, and let $p(t)$ be the probability that it has not become

with infinitesimal mean and variance $m(x)$ and $v(x)$, respectively, then the corresponding abundance model is (Engen & Lande, 1995)

$$\lambda(x) = 2\omega_0 \frac{1}{v(x)} e^{\int_1^x 2m(u)/v(u) du}. \quad (\text{A.4.})$$

The speciation parameter ω_0 may be interpreted as

follows: if speciation is defined to occur at abundance $1 + \delta x$, then the speciation rate is $\omega_0 \delta x$ (in the limit as $\delta x \rightarrow 0$). Hence, ω_0 is approximately the speciation rate for $\delta x = 1$, that is, when the speciation rate is defined as the rate at which new species first reach abundance 2 [see Engen & Lande (1996) for further details].