

Analyzing Spatial Structure of Communities Using the Two-Dimensional Poisson Lognormal Species Abundance Model

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ABSTRACT: The joint spatial and temporal fluctuations in the community structure of tropical butterflies are analyzed by fitting the bivariate Poisson lognormal distribution to a large number of observations in space and time. By applying multivariate dependent diffusions for describing the fluctuations in the abundances, the environmental variance is estimated to be very large and so is the strength of local density regulation. The variance in the lognormal species abundance distribution is partitioned into components expressing the heterogeneity between the species, independent noise components for the different species, a demographic stochastic component, and a component due to overdispersion in the sampling. In disagreement with the neutral theory, the estimates show that the heterogeneity component is the dominating one, representing 81% of the total variance in the lognormal model. Different spatial components of diversity, the alpha, beta, and gamma diversity, are also estimated. The spatial scale of the autocorrelation function for the community is of order 1 km, while sampling of a quadrat would need to be 10 km on a side to yield the total diversity for the community.

Keywords: species abundance distribution, lognormal distribution, spatial scaling, communities of butterflies.

The lognormal species abundance distribution first introduced by Preston (1948) has been widely used to describe

patterns in community structure (Bulmer 1974; May 1975; Pielou 1975; Engen 1978; Ugland and Gray 1982). There are different types of proposed models explaining this pattern, most of which use the concept of niche preemption and rely mathematically on the central limit theorem (Bulmer 1974; May 1975; Sugihara 1980). Engen and Lande (1996*b*) proposed a dynamic model including speciation and extinction, where species abundances were modeled by multivariate diffusion processes. The species could follow different diffusions, and the noise terms acting on the different species could be correlated. In a parallel article (Engen and Lande 1996*a*), a similar model giving the gamma type of abundance model, including Fisher's (Fisher et al. 1943) log-series model and the extended gamma model (Engen 1974, 1978) was presented, and recently Diserud and Engen (2000) defined and fitted a number of data sets to a more general model embracing the gamma as well as the lognormal. All these models use environmental stochasticity (May 1973; Lande 1993; Engen et al. 1998) as the major driving force of the stochastic fluctuations in contrast to Hubbell (1997, 2001), whose approach was based on demographic stochasticity only and therefore can be realistic only for rather small population sizes (Lande 1993).

Community data are usually collected at multiple locations in space at different times, yielding samples that differ considerably. A major difficulty in detecting which differences are due to sampling effects is the fact that a large number of species are usually represented by only one or a few individuals in the samples. Hence, not only the observed number of individuals for each species, but also the list of species represented in the sample, may differ considerably in space and time. The spatial variation in these types of data led early ecologists to define the spatial structure of communities in terms such as alpha, beta, and gamma diversity (Whittaker 1972) or within-habitat and between-habitat diversity (MacArthur 1965). The alpha diversity was defined as the within-habitat diversity, while the gamma diversity is the total diversity of a region in-

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cluding several habitats. The beta diversity was used to describe the differentiation between alpha and gamma diversity. According to Whittaker (1972), the gamma diversity of a landscape, or geographic area, is the product of the alpha diversity of its communities and the degree of beta differentiation among them. In this article, we shall analyze this type of spatial community structure assuming that a lognormal species abundance distribution fits at each local habitat at any time but with some correlation structure between sites. We do this by fitting a two-dimensional Poisson lognormal species abundance model to pairs of communities and finally by analyzing the temporal and spatial structure of correlations estimated from each pair. This enables us to study the temporal fluctuations of diversity and to calculate the alpha, beta, and gamma diversity, including the spatial scaling of the increase in diversity with area.

The underlying model is basically that in Engen and Lande (1996b), with heterogeneity between species but generalized to include spatial structure as well. The fundamental parameter of interest in the lognormal species abundance distribution is the variance parameter that has traditionally been used as a measure of community structure (Patrick et al. 1954; DeVries et al. 1999). Our approach enables us to partition the variance in the lognormal species abundance distribution into four additive components and, thus, to better understand the processes that lead to differences in the relative abundance of species. One component of the variance is the contribution due to the heterogeneity in growth rates and carrying capacities between species. This component reflects innate differences in the biology of each species that influence species density, and its existence contradicts the assumption of neutral-abundance models (Hubbell 2001). Another component, which is the one that also has a spatial structure, is due to the component of the environmental noise acting independently on each species. We are also able to identify an additive component due to demographic stochasticity. If the sampling is overdispersed compared to the Poisson distribution, this component will also be affected by the degree of overdispersion. Finally, we also compute the total variance parameter estimated by fitting the univariate Poisson lognormal distribution to the data, treating all counts for every species at all times and sites as a single sample. This parameter is somewhat larger than the variance parameter of the species abundance distribution since it also includes the component due to heterogeneity in carrying capacities between sites as well as the effect of the noise component that is common to all sites and species.

Spatial aspects of single-species populations have been frequently discussed in the literature (Shigesada and Kawasaki 1997; Tilman and Kareiva 1997; Bascompte and Solé 1998; Turchin 1998). Simulation studies have been

performed to understand the dynamics of spatially structured populations and to link them to basic demographic processes (Ranta et al. 1995, 1997a, 1997b, 1999). In particular, much attention has been given to the spatial scale of synchrony of population fluctuations that is known to influence the risk of local and global extinction (Allen et al. 1993; Bolker and Grenfell 1996; Heino et al. 1997). Lande et al. (1999) and Engen et al. (2002) used linear approximations to spatiotemporal diffusion models with migration to analyze the spatial synchrony of population fluctuations, while Engen (2001) used a nonlinear model with migration to generate the lognormal distribution of population densities in space.

In this article, we analyze the structure of spatially and temporally related communities of butterflies in a Neotropical rain forest. Adult butterflies in the family Nymphalidae that are attracted to, and feed on, the juices of rotting fruits comprise a feeding guild commonly known as fruit-feeding nymphalids (see DeVries et al. 1997, 1999). By employing arrays of traps baited with rotting fruits, these butterflies have recently become an important focal group for assessing spatial diversity of tropical insect communities (e.g., DeVries 1988; Pinheiro and Ortiz 1992; DeVries et al. 1997, 1999; Willott et al. 2000; DeVries and Walla 2001). Using abundance data sampled at 25 locations over a period of 5 yr (fig. 1), we fit a bivariate Poisson lognormal model to 7,750 different community sample pairs and analyze the structure of the correlations between them.

The Bivariate Poisson Lognormal Species Abundance Model

A community of S species fits the lognormal species abundance model if the log of the abundances constitutes a sample from a normal distribution. Different methods

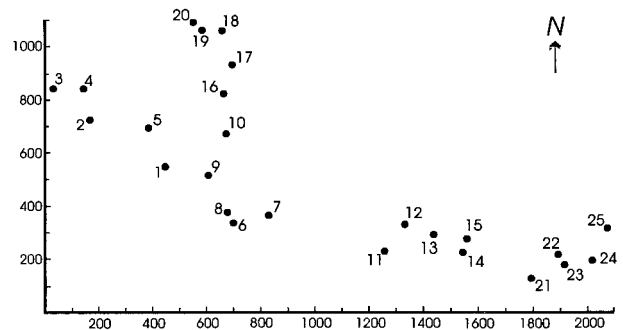


Figure 1: Scale map in meters of butterfly trap locations. Each of the 25 sites represents a canopy-understory trap pair. Modified from DeVries and Walla (2001).

have been used in ecological literature to estimate the parameters of this distribution and to overcome the problem that rare species may not be present in the sample and that more species appear as the sampling intensity increases. Here, we will use a generalization of the statistical approach of Bulmer (1974), which is also the approach adopted earlier by Fisher et al. (1943), when deriving the log-series species abundance distribution. If the sampling distribution conditioned on the abundance is Poisson, then the distribution of counts between species will have a Poisson lognormal distribution as explained in appendix A. Since the zero class is not observable, the truncated form of the distribution must be used in the estimation procedure (Fisher et al. 1943; Bulmer 1974).

When considering two communities jointly, either in two different locations or within the same community at two different points of time, the natural assumption to make is that the log abundances in the pair of communities have the binormal distribution so that the lognormal model still fits each community separately. The correlation of this distribution then serves as a measurement of similarity between communities. If the correlation is 1, then the relative abundance of any species is the same in both communities although samples will still be different due to sampling effects. If sampling from both communities is given by the Poisson distribution, the pair of counts among species will have the bivariate Poisson lognormal distribution. In this case, the zero-zero class is not observable, so the truncated form has to be used in the estimation. The likelihood function must be calculated by numerical integration and maximized numerically with respect to the unknown parameters. When fitting only one data set (two communities) to this model, uncertainties are most conveniently found by performing parametric bootstrapping, that is, simulating new sets of data from the estimated model and calculating bootstrap estimates from each simulated set of data. However, since we will fit the model to a huge number of pairs of sites, we can use the faster approach of bootstrapping by resampling sites (Bjørnstad et al. 1999). For a further description of the bivariate Poisson lognormal distribution, see appendix A.

Spatial Autocorrelation and Variance Decomposition

Let $Y(z, t)$ be the abundance of some species at location z in the plane at time t , and write $X(z, t) = \ln Y(z, t)$ for the log abundance. If the population fluctuations around some carrying capacities are not very large, the dynamics of the log abundances may often be approximated by the continuous Ornstein-Uhlenbeck process

$$dX(z, t) = [r - \delta X(z, t)]dt + \tau dB(z, t), \quad (1)$$

where $B(z, t)$ is a standard Brownian motion (Karlin and Taylor 1981). This model is equivalent to the diffusion with infinitesimal mean and variance $r - \delta x$ and τ^2 , respectively. The parameter δ represents the strength of local density regulation. The stationary distribution is the normal with mean r/δ and variance $\tau^2/2\delta$, and the stationary distribution of $Y(z, t)$ is therefore the corresponding log-normal distribution. The carrying capacity of this population is $K = \exp(r/\delta)$. We write $k = \ln K = r/\delta$ for the corresponding “carrying capacity” on the log scale.

In appendix B, we generalize this model to include a demographic variance σ_d^2 and a corresponding demographic noise term. Here, we also consider the joint dynamics of all species in the community. We first show that if there is some common noise term for all species, this will not affect the correlations between community samples. In addition to such common noise, there may be noise terms that are independent between species. We assume that this noise has the same magnitude for all species determined by a variance parameter σ_s^2 . For all species, this noise is spatially correlated with correlation $\rho(v)$, where v denotes the displacement vector between the locations. Finally, in accordance with Engen and Lande (1996b), we assume that the growth rate r in equation (1) is normally distributed among species with variance σ_r^2 . For any species, this leads to the covariance

$$\text{cov}[X(z, t), X(z + v, t + u)] = \frac{\sigma_s^2 \rho_s(v) e^{-\delta u}}{2\delta} + \frac{\sigma_r^2}{\delta^2},$$

while the variance in log abundance among species can be decomposed into three additive components:

$$\sigma^2 = \frac{\sigma_s^2}{2\delta} + \frac{\sigma_d^2}{2K\delta} + \frac{\sigma_r^2}{\delta^2}, \quad (2)$$

where $1/\bar{K} = Ee^{-r/\delta}$. The first term is the environmental component due to independent environmental noise terms acting on the species, the second term is the demographic component, and the last term is the interspecies heterogeneity component due to the heterogeneity between the species determined by the variance σ_r^2 of r among species. This term may alternatively be expressed by the between-species variance in the carrying capacities on the log scale; that is, $\sigma_k^2 = \text{Var}(k) = \text{Var}(r/\delta) = \sigma_r^2/\delta^2$.

Finally, from the expressions for the variance and covariance, the joint spatial and temporal correlation then takes the form

$$\rho(v, u) = \frac{\sigma_s^2 \rho_s(v) e^{-\delta u} + 2\sigma_r^2/\delta}{\sigma_s^2 + \sigma_d^2/\bar{K} + 2\sigma_r^2/\delta}. \quad (3)$$

If there is overdispersion, there will be an additional term θ^2 in the denominator as explained in appendix C. The correlation given by equation (3) is exactly the correlation parameter in the bivariate Poisson lognormal distribution for samples taken at time difference u from two communities with displacement vector v between them in space.

Temporal Fluctuations and Spatial Scaling of Diversity

According to our model, the estimated variance from the total collection of local samples will have a demographic component. If the number of traps at one location was increased, the demographic component at each trap would represent independent contributions to the fluctuations and would therefore be wiped out relative to the effect of the environmental noise if catches from a large number of traps were added together. When modeling the diversity, we therefore omit the demographic component.

The most widely used index of diversity is the information index (Shannon and Weaver 1948)

$$H = - \sum_{i=1}^S p_i \ln p_i,$$

where the p_i 's are the relative abundances of the species in the community; that is, $p_i = Y_i / \sum_{j=1}^S Y_j$. In our model, the $X_i = \ln Y_i$ follows a multivariate Ornstein-Uhlenbeck process. Hence, when the parameters of the process are estimated, we can easily simulate the process H against time to find the magnitude and speed of the fluctuations in H . In practice, we will then first simulate the carrying capacities on the log scale of each species in the community. These are normally distributed with variance σ_k^2 , while the expectation may be chosen arbitrarily since the relative abundances will not depend on it. Second, we can simulate the fluctuations of each species around its carrying capacity separately as independent processes with infinitesimal variances σ_s^2 using well-known properties of the Ornstein-Uhlenbeck process (see Karlin and Taylor 1981). At each point in time, we then calculate the absolute abundances, the relative ones, and, finally, the value of H .

The first-order approximation to the expectation of H that is valid when the number of species is large and the variance parameter σ^2 of the lognormal is small is simply (Bulmer 1974; Webb 1974; Engen 1978)

$$EH \approx \ln S - \frac{1}{2} \sigma^2.$$

To this order of approximation, we find from equation

(2), ignoring the demographic component, that the expected alpha diversity at each location is

$$EH_\alpha \approx \ln S - \frac{1}{2} \left(\frac{\sigma_s^2}{2\delta} + \frac{\sigma_r^2}{\delta^2} \right).$$

For very large areas, the independent fluctuations due to σ_s^2 will practically be wiped out, and the mean log abundances over the area will be constant equal to the log abundances of each species that are normally distributed with variance $\sigma_k^2 = \sigma_r^2/\delta^2$. Hence, for very large areas, the expected value of the diversity corresponding to Whittaker's (1972) gamma diversity is

$$EH_\gamma \approx \ln S - \frac{1}{2} \left(\frac{\sigma_r^2}{\delta^2} \right).$$

As a consequence, the beta diversity, being the difference between the two, has expectation

$$EH_\beta \approx \frac{\sigma_s^2}{4\delta}.$$

Notice that Whittaker (1972) used the term "product" rather than "sum" for the effect of the beta diversity. In this model, this effect will actually be a factor $\exp(\sigma_s^2/4\delta)$ in a product in accordance with Whittaker's (1972) definition if we use $\exp(H)$ rather than H as diversity index.

We can also calculate the spatial scaling of the increase in diversity from EH_α to EH_γ as the area increases. At each point in a quadrat with side a , the abundances are log-normally distributed. If one approximates the distribution of the total abundances in the quadrat by the lognormal, it is straightforward to show that the variance of the corresponding normal distribution is

$$V(a) \approx \frac{\sigma_r^2}{\delta^2} + \ln \int_0^{\sqrt{2}} e^{\rho_s(az)\sigma_s^2/(2\delta)} f(z) dz,$$

where $f(z)$ is the distribution of the distance between two randomly chosen points in a quadrat with area 1, which is actually

$$f(z) =$$

$$\begin{cases} 2z(\pi + z^2 - 4z) & \text{for } 0 \leq z \leq 1 \\ 2z \left[2 \arcsin \left(\frac{2}{z^2} - 1 \right) + 4(z^2 - 1)^{1/2} - 2 - z^2 \right] & \text{for } 1 \leq z \leq \sqrt{2} \end{cases}.$$

Notice that if the area is so small that ρ_s is practically 1 over the entire quadrat, then the variance approaches

$$V(0) = \frac{\sigma_r^2}{\delta^2} + \frac{\sigma_s^2}{2\delta},$$

which is actually σ^2 , while for very large areas where the mean of ρ_s is practically 0, it approaches

$$V(\infty) = \frac{\sigma_r^2}{\delta^2}.$$

The expected diversity in the quadrat is $EH(a) \approx \ln S - (1/2)V(a)$. If the parameters take values so that the approximation for the expected diversity is not valid, then the expectations may alternatively be computed by stochastic simulations.

Fitting the Model to the Tropical Butterfly Data

Estimation

There are 25 sites and 5 yr of data, and the bivariate model has to be fitted to all 7,750 pairs of samples. Since the uncertainty in each estimate of the correlation is fairly large, as seen in figure 2, we cannot expect to find exactly the shape of the function $\rho_s(v)$. However, we will mainly be interested in the scaling of this function, which we can find by assuming an exponential decay. Hence, equation (3) takes the form

$$\rho(v, u) = Ae^{-\eta v - \delta u} + B, \quad (4)$$

where all four constants can be estimated by fitting the curve to the 7,750 estimates. The variance of each correlation estimate is large and varies in an unknown way

with sample sizes and the magnitude of the true correlations. Because this information is not available, we have chosen to fit the curves by simple least squares. Since the variance σ^2 of the lognormal is the same at each location and each point of time, we estimate this by the mean value of the estimated variances. Finally, by combining equations (2)–(4), we can eventually estimate all three terms in the additive decomposition defined by equation (2), together with the parameters η and δ defining the spatial and temporal autocorrelations. We define the spatial scaling of the noise that is specific for each particular species as $d = 1/\eta$ (Roughgarden 1975; Lande et al. 1999; Engen et al. 2002). All confidence intervals given in brackets below are 95% intervals based on 1,000 resamples of populations (sites and times) with replacement (Cressie 1993; Bjørnstad et al. 1999).

Results

The mean value of the variance estimates for all populations was $\hat{\sigma}^2 = 3.418$, with confidence interval (3.385, 3.454). The major component turned out to be the interspecies heterogeneity component estimated as 2.756 (2.706, 2.790). This means that the variance in abundance between species is mainly due to differences between the species, here modeled as a variation in specific growth rate and local carrying capacity among species. This means that species that are among the most abundant at the present time are also expected to be so in the future. Hence, this result is in disagreement with the commonly used assumption of so-called neutral models (see Hubbell 2001). This model is a neutral one only if $\sigma_r^2 = 0$, in which case the variance of the lognormal is determined totally by stochastic factors other than permanent between-species variation in parameters.

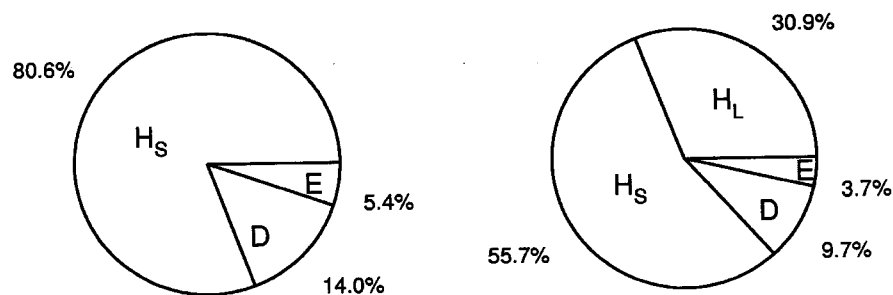


Figure 2: The left panel shows the estimated partitioning of the variance of the lognormal species abundance distribution into three components: the heterogeneity between species (H_s), the demographic component that also may include the effect of overdispersion (D), and the environmental component (E). The right panel shows the estimated partitioning of the variance parameter of the lognormal when the distribution is fitted to the total data set. The additional component (H_L) now represents the effect of heterogeneity between locations as well as the common noise generated by σ_c^2 .

The estimated environmental component of the variance parameter was 0.480 (0.393, 0.575), while the demographic component was 0.183 with confidence interval (0.106, 0.259). We emphasize that this component may be an effect of overdispersion including the term θ^2 defined in appendix C, as well as demographic stochasticity. These components are due to demographic and environmental stochasticity generated by between-years stochastic fluctuations in vital rates. Fitting the univariate Poisson lognormal distribution to the total set of counts for every species at all times and sites gives a variance parameter of 5.045. The difference between this parameter and the variance parameter of the species abundance model (1.527) is a variance component generated by heterogeneity between sites in local carrying capacities as well as the effect of the common noise term σ_c^2 (see app. B). Generally, this component will also be affected by differences in sampling effort between sites and seasons, but for our data set the effort is constant. Figure 2 (*left panel*) shows the estimated partitioning of the variance parameter in the lognormal species abundance model, as well as (*right panel*) the partitioning of the total variance.

The spatial scaling of $\rho_s(v)$ was estimated as $\hat{d} = 1.04$ km (0.67, 1.61). This means that the environmental noise acting on a single species at locations at distance 1 km will have a significant positive correlation, while the correlation practically will vanish at a distance of 3 km. Another parameter estimated with rather large uncertainty is the strength of local density regulation, which is $\hat{\delta} = 1.610$ (0.577, 2.626). The inaccuracy is due to the fact that the term $e^{-\delta u}$ decays to a very small value already at $u = 1$, which is the smallest value of u that is >0 , in the data we have used. Most observations are for time differences >1 , for which the factor containing δ is practically 0. Hence, the data contain rather little information about this parameter. The large value of this parameter defining the strength of density regulation is equivalent to the return time to equilibrium being small. The species are expected on average to pass the equilibrium abundance more than once a year.

In figure 3, we have plotted all estimated correlations for $u = 0$ and $u = 1$ against the spatial distance v together with the smoothed spatial autocorrelation defined by equation (4) with those two values of u inserted.

In figure 4, we show stochastic simulations of the temporal fluctuations in the information index at local sites. The parameters used are the estimates obtained from the data. The total number of species in the whole community is estimated to be 158 by fitting a Poisson lognormal abundance model to the total accumulated data. Figure 5 gives the histogram for the stationary distribution for the same temporal process. Notice that the temporal fluctuations in

H are fairly large, ranging from about 2.3 to 4.2 with a distribution that is skew to the left.

In figure 6, the expected diversity in quadrats is plotted against the quadrat size. This shows an increase from the alpha diversity that is 3.63 to a gamma diversity of 3.81. The first-order approximation gives the correct shape and scaling of this curve, but the error in absolute value is rather large.

Discussion

In this article, we were able to estimate parameters in the model in Engen and Lande (1996b) that are essential for understanding how communities fluctuate in time and space. We did this by conditioning on the noise term that is common for all species in the community. Engen and Lande (1996b) showed that such a term, which could also depend on the sum of the abundances of all species in the community and hence describe a community-level density regulation as well as common stochastic noise, would not affect the structure of the community. Intuitively, this is obvious, since a multiplication of all abundances by some common factor for all species and all locations only adds a common term to the log of the abundances. Hence, this will affect the mean value parameter of the lognormal but not the variance parameter, which is the one we analyzed. However, such a common factor obviously generates a synchrony in the fluctuations of the populations. This component of the synchrony is not considered in our species abundance model since we have conditioned on this common noise. The synchronies, or spatial autocorrelations, dealt with here are those generated by the independent environmental effects on each species.

The environmental variance for the species in this community is very large. Previously, such variances have been estimated for some bird species (Sæther et al. 1998; Tufto et al. 2000) and are usually found to be of order 0.01–0.1. In this community of butterflies, the environmental variance is $\sigma_c^2 = \sigma_c^2 + \sigma_s^2$. We have not estimated the common component σ_c^2 , but the estimate for σ_s^2 (see eq. [2]) is as large as 2.22 (0.77, 3.65). However, the very large environmental variance does not lead to extremely large temporal fluctuations in abundances. This is due to the fact that the strength of local density regulation is also very large, actually $\gamma = 1.610$ (0.577, 2.626). This parameter turns up in the denominator of the expression for the variance in the stationary distribution of log abundance. For the bird species mentioned above, this parameter is much smaller, actually ranging from about 0.01 to 0.5. The return rate to equilibrium is much shorter for the species in this butterfly community compared to birds and may be a consequence of much shorter generation time as well as larger values of r .

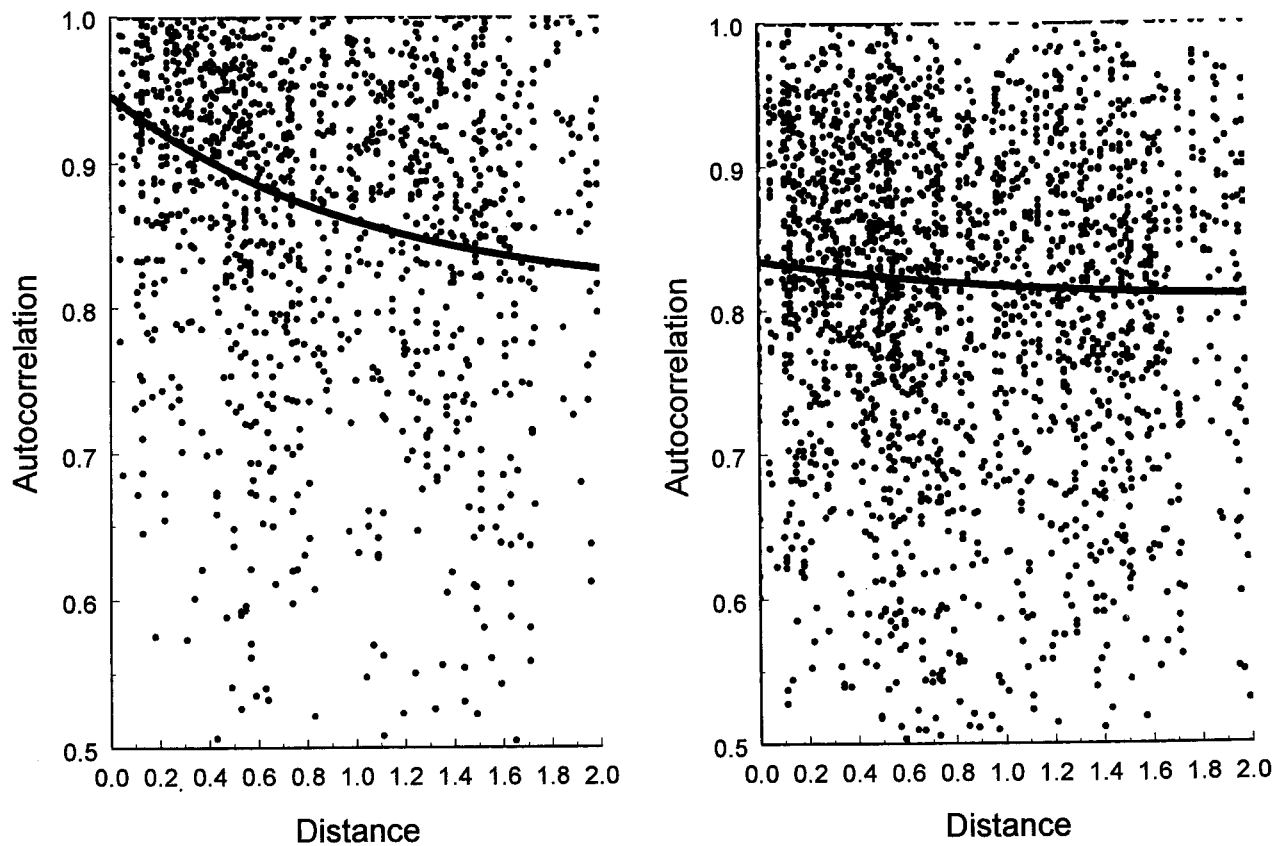


Figure 3: The estimated correlations plotted against spatial distance in kilometers for time differences $u = 0$ (left panel) and $u = 1$ (right panel). The curves are the fitted autocorrelation function given by equation (3) with u inserted as 0 and 1, respectively.

A major result in this article is the theoretical decomposition of the variance of the lognormal species abundance model into four additive components, and the estimation of these components from data shown in figure 2 (left panel). We did not attempt to estimate the component due to overdispersion, which must be done by performing a number of parallel samples. However, we have estimated the sum of this term and the demographic component that in the end will make it possible to estimate both of them by estimating θ^2 . Even if our model leads to communities where the abundances are random samples from lognormal distributions, our findings contradict the concept of neutral models. In the model defined by Engen and Lande (1996b), the species abundances have different lognormal distributions since the parameter r differs between them. The r values are actually a sample from a normal distribution. Our investigation shows that the heterogeneity component of the variance created by interspecies heterogeneity in growth rates is much larger than the other components. Here, the interspecies heterogeneity component is estimated to be around 81% of the variance

of the lognormal. As a consequence, there are a large number of species with small values of r and small carrying capacities, and these may be predicted to be threatened by extinction if the community is disturbed, for example, by fragmentation. This emphasizes the importance of monitoring multiple species for conservation where the r values of the species selected to assess communities are critical. As we show, focusing only on abundant species with high r values will underestimate the extinction probabilities of other, less abundant species. The component of the variance due to independent environmental noise between the species only accounts for 14% of the variance; the final 5% is demographic noise and/or overdispersion in the sampling.

The correlation estimated from two community samples collected at different times or sites will not be affected by heterogeneity in local carrying capacities or differences in sampling effort between sites or times. Neither will it be affected by the common noise term defined by the parameter σ_c^2 . Such types of heterogeneity will only have a common multiplicative effect on all species, and the com-

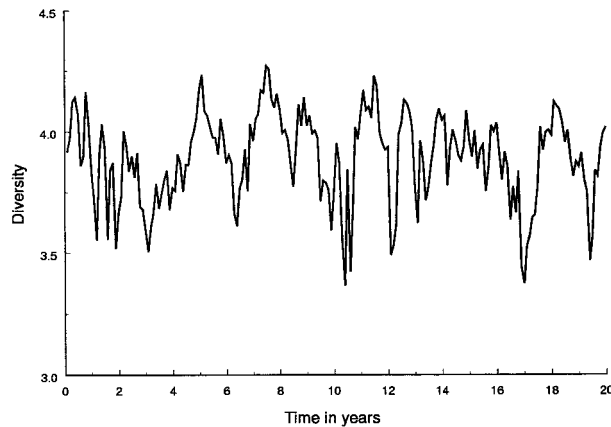


Figure 4: Temporal fluctuations in the information index of diversity. The graph is a simulation from the theoretical model with the estimated parameters inserted. The applied estimate of the number of species in the community is 158.

munity structure revealed by the lognormal abundance model will therefore remain unchanged. The total variance parameter of the univariate Poisson lognormal estimated by treating the complete data set as a single sample is, however, affected by such heterogeneity. This is demonstrated in figure 2 (*right panel*), which shows the partitioning of total variance in which the heterogeneity between locations and the effect of σ_c^2 together accounts for 31% of the total.

The second main result is the theoretical modeling of spatial structure in the correlation of the bivariate lognormal species abundance distribution, and the method of estimating basic spatial and temporal parameters jointly. Although each estimated correlation is rather uncertain, all 7,750 estimates considered together make it possible to draw some statistical inference about the parameters, including the spatial scaling of the autocorrelation. We find that the autocorrelation $\rho_s(v)$ decays to $1/e \approx 0.37$ at a distance of about 1 km (0.67, 1.61). Although we have not attempted to model migration here, it is interesting to view this result in light of the findings of Lande et al. (1999), Engen (2001), and Engen et al. (2002), who analyzed in theoretical models how different factors are expected to affect the spatial scaling of the correlations between population sizes. Migration tends to increase the scaling, in particular when there is weak local density regulation. Since we found a strong density regulation here, migration probably has a rather small impact (Lande et al. 1999). However, it would still be useful to compare the scaling to other communities in the light of information available on migration rates and distances for different communities.

From our data set, we cannot determine the extent to

which different parameters used to describe migration rates and distances, habitat heterogeneity, and autocorrelations in the environmental noise affect the observed scaling. We do, however, know that the effects of migration can vary among species. For example, our preliminary population analyses indicate that individuals of *Nessaea hewitsoni* and *Myscelia capenas* move <50 m during their lifetimes, whereas individuals of *Historis acheronta* and *Morpho achilles* may move across the entire study area (about 2 km) in a single day. Thus, we suspect that the importance of migration in estimating spatial structure may depend on the particular species being considered. Measures of temperate-zone population synchrony in butterflies and local spatial scaling in tropical communities appear to be roughly equivalent. An investigation of 21 butterfly species in Great Britain (Sutcliffe et al. 1996) found that average population synchrony decreased up to 1–2 km and that synchrony was evident up to 4 km for highly mobile species. In another study, Thomas (1991) reported population synchrony for *Plebejus argus* at distances up to about 600 m, but because it is a relatively sedentary species and occurs in successional habitats, it may be expected to show a smaller spatial scale of synchrony. The spatial scaling of autocorrelation of approximately 1 km estimated for our tropical forest community includes both sedentary and mobile species and is slightly smaller than what Sutcliffe et al. (1996) estimated from patchy habitats typical of Britain. We might expect habitat fragmentation to decrease the observed scale of spatial synchrony through reduction in migration distance across unsuitable habitats, and if continuous habitat types are

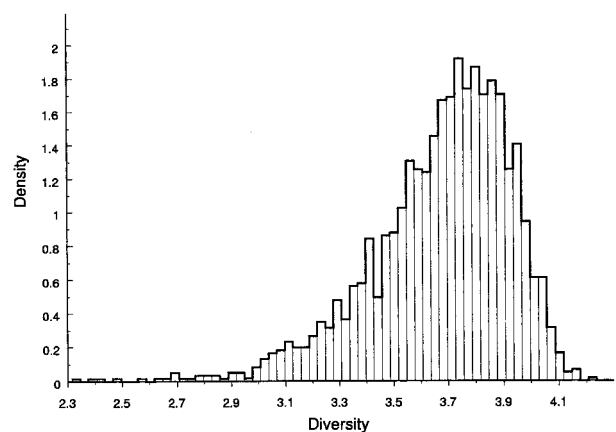


Figure 5: The stationary distribution of the information index of diversity. The histogram is based on 2,000 simulations from the stationary distribution of the index. The parameters in the simulations are those estimated from the data, and the applied estimate of the number of species in the community is 158.

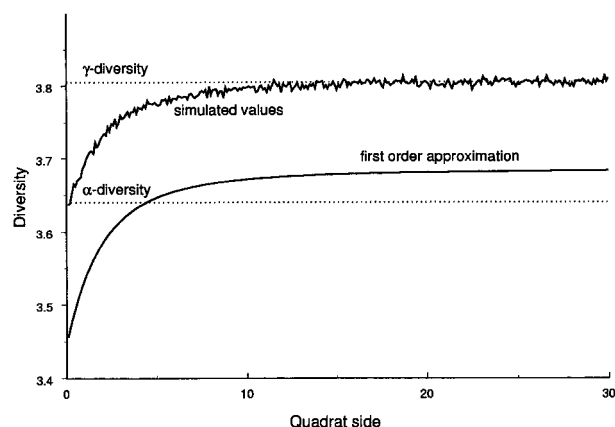


Figure 6: The expected diversity in quadrats plotted against the side length of the quadrat. The smooth line is the first-order approximation, and each point on the oscillating curve is the mean of 10,000 simulations from the model. The dotted lines reflect the within-habitat alpha diversity and large-scale gamma diversity.

compared, tropical butterflies may, in fact, show a smaller spatial scale of autocorrelation than temperate butterflies.

The tree falls so common in tropical forests are known to create small-scale disturbances that may pass quickly from open to closed (Denslow 1994). It has been suggested that tree-fall frequency maintains plant diversity in tropical forests by precluding the dominance of any one species and creating microhabitats suitable for colonizing species (Connell 1978; Hubbell et al. 1999). In our community, we found that a sample from a single location and time provides little information about the composition of a sample taken the following year (fig. 1*b*). This may, in part, be due to tree falls changing the composition of local vegetation necessary for butterflies and contributing to the short temporal scale of autocorrelation observed within the study area. For example, butterfly larvae that depend on abundant new growth of host plants in recently formed gaps (DeVries 1987) may increase in density during a favorable temporal window, but, due to succession, the same gap may be unacceptable 2 yr later. Conversely, subpopulations on healthy shade-tolerant host plants one year may be adversely affected by tree falls in the following year. Thus, our results are consistent with the idea that tropical forests are constantly undergoing low levels of disturbance that preclude the long-term persistence of spatially structured populations.

A third result of our analysis is the derivation of the relation between the temporal and spatial model and the well-established concepts like the alpha, beta, and gamma diversity of Whittaker (1972). By applying the information index of diversity, we are able to calculate how the diversity of subcommunities defined by quadrats is expected to in-

crease with the size of the quadrats. The scaling of this function can be defined as the quadrat side required to obtain a diversity equal to the mean of the local alpha diversity and the large-scale gamma diversity. By inspection of figure 6, we see that this scaling is about 3 km, which is actually much larger than the scaling of the autocorrelation $\rho_s(v)$ for the local populations. This is due to the fact that the total diversity for a quadrat comes out as an integral over all pairs of points in the quadrat, and there will be a large number of combinations of points within a quadrat that have distances between them that are much shorter than the side length of the quadrat.

There have been different proposals on how to partition the total diversity of a community into Whittaker's (1972) spatial components of diversity using different diversity indices (Routledge 1977, 1979; Lande 1996). Lande (1996) defined the similarity among multiple communities as the proportion of the total diversity found within communities. By applying this definition and using the information index, we see from figure 6 that the similarity between the local communities is estimated to be 0.95 (3.63/3.81). However, this parameter does not give any information about the spatial scaling revealed by figure 6. In a similar type of analysis based on diversity indices, DeVries et al. (1997) estimated the variance of the lognormal for the same kind of communities of butterflies in a different part Ecuador by the method of Pielou (1975) to be 3.28, using base 3 in the logarithmic grouping of species. Converting this to the variance using natural logarithms as we have done implies multiplying the estimate by $(\ln 3)^2 = 1.207$, which gives an estimate of 3.96 that is a bit larger than our estimate of 3.42. This difference may partly be due to the fact that the Poisson sampling of individuals is included in the variance by Pielou's (1975) method, while the method used here estimates the variance in the underlying lognormal correcting for the sampling variance.

Previous work on this community illuminated the heterogeneity in species diversity among different areas of the same forest (DeVries and Walla 2001). The analysis here provides a more general perspective regarding the nature and scale of within-habitat heterogeneity. Estimates from our model indicate that even measures based on a diversity index reducing the need for equal sample sizes among quadrats would require larger sampling areas to approach the estimated gamma diversity. For example, figure 6 shows that a single quadrat would need to be 10 km on a side to yield the expected gamma diversity for this community. Thus, it is not surprising that DeVries and Walla (2001) found heterogeneity among forest areas separated by <500 m. However, this also suggests that understanding tropical community diversity may require sampling on spatial scales upward of several square kilometers in order

to distinguish between heterogeneity within habitats and larger-scale differences in gamma diversity.

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APPENDIX A

The Bivariate Poisson Lognormal Distribution

Under the assumption of random sampling, the number of individuals sampled from a given species with abundance y , say N , is Poisson distributed with mean, say ωy , where the parameter ω expresses the sampling intensity. If $\ln y$ is normally distributed with mean μ and variance σ^2 among species, then the vector of individuals sampled from all S species then constitutes a sample from the Poisson lognormal distribution with parameters $(\mu + \ln \omega, \sigma^2)$, where μ and σ^2 are the mean and variance of the log abundances. For $\omega = 1$, this is the Poisson lognormal distribution with parameters (μ, σ^2) , which may be written in the form

$$P(N = n; \mu, \sigma^2) = q(n; \mu, \sigma^2) = \int_{-\infty}^{\infty} g_n(\mu, \sigma, u) \phi(u) du,$$

where $\phi(u)$ is the standard normal distribution and

$$g_n(\mu, \sigma, u) = \frac{\exp[u\sigma n + \mu n + e^{-(u\sigma + \mu)}]}{n!}.$$

Since S is usually unknown, we only consider the observed number of individuals for the observed species. With a general sampling intensity ω , the distribution of the number of individuals then follows the zero-truncated Poisson lognormal distribution

$$\frac{q(n; \mu + \ln \omega, \sigma^2)}{1 - q(0; \mu + \ln \omega, \sigma^2)},$$

defined for $n = 1, 2, \dots$. The maximum-likelihood estimation of the parameters of this distribution was derived by Bulmer (1974).

Now consider two communities jointly and assume that the log abundances among species have the binormal distribution with parameters $(\mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \rho)$. Using index $i = 1, 2$ to denote the communities and first assuming

that the sampling intensities $\omega_1 = \omega_2 = 1$, samples from the communities have the bivariate Poisson lognormal distribution

$$q(n_1, n_2; \mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \rho) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} g_{n_1}(\mu_1, \sigma_1, u) g_{n_2}(\mu_2, \sigma_2, v) \phi(u, v; \rho) du dv,$$

where $\phi(u, v; \rho)$ here denotes the binormal distribution with zero means and unit variances and correlation ρ . In the general case with sampling intensities ω_1 and ω_2 , it is easy to check that the μ_i should be replaced by $\mu_i + \ln \omega_i$. In this case, some species will be missing from both samples. The number of individuals for observed species then have the truncated distribution

$$\frac{q(n_1, n_2; \mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \rho)}{1 - q(0, 0; \mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \rho)}.$$

APPENDIX B

Spatial Community Dynamics

Demographic stochasticity may be included by replacing $\tau dB(z, t)$ in equation (1) in the main text by $\sigma_e dB_e(z, t) + \sigma_d/[Y(z, t)]^{1/2} dB_d(z, t)$, where $B_e(z, t)$ and $B_d(z, t)$ are now independent standard Brownian motions. For small fluctuations, we may further replace Y with K , which again gives equation (1) with $\tau^2 = \sigma_e^2 + \sigma_d^2/K$. The parameters σ_e^2 and σ_d^2 are commonly known as the environmental and demographic variances, respectively (Athreya and Karlin 1971; Turelli 1977; Leigh 1981; Lande 1993; Engen et al. 1998). The corresponding approximation to the stochastic differential equation is then

$$dX(z, t) = [r - \delta X(z, t)]dt + \sigma_e dB_e(z, t) + \sigma_d dB_d(z, t)/\sqrt{K}.$$

Now, writing $z + v \neq z$ for another position in the plane, we assume that the demographic noise processes $B_d(z, t)$ and $B_d(z + v, t)$ are independent of each other and independent of the processes defining the environmental noise, while the environmental noise processes have some spatial autocorrelation depending on the distance v between the sites.

In order to construct an abundance model for the community of species, we first consider two species jointly at

position z and $z + v$, writing $X_1(z, t)$ and $X_2(z + v, t)$ for their log abundances. We assume that the environmental component of the noise for each of the two species may be split into two components: $\sigma_c^2 = \sigma_c^2 + \sigma_s^2$. This is in agreement with the relation

$$\sigma_c dB_c(z, t) = \sigma_c dB_c(z, t) + \sigma_s dB_1(z, t)$$

for species 1 and, correspondingly, for species 2, where the different Brownian motions are independent. Here, $B_c(z, t)$ is a noise process that is common for all species, while $B_1(z, t)$ is a noise for species 1, independent of the noise $B_2(z, t)$ for the other species. The specific species noise processes $B_1(z, t)$ and $B_2(z, t)$ both have the same spatial autocorrelation function $\rho_s(v)$ defined by the relation $E dB_1(z, t) dB_1(z + v, t) = \rho_s(v) dt$, and the same applies for the second species. The subscript c stands for “common” and indicates a common noise term, while s stands for “species” and indicates independent noise terms that are characteristic for each species. The variance of these noise terms is assumed to be the same for each species.

Due to simple linear properties of the Ornstein-Uhlenbeck process, the noise term that is common will actually give the same additive stochastic contribution to the log abundance of all species and will therefore be confounded with the expectation. In the long run, however, this contribution will be close to 0. Neither will this term have any effect on the shape of the abundance model when S different species are included (Engen and Lande 1996b). We therefore consider the model obtained when conditioning on this noise, remembering that a stochastic part generated by this noise is then included in the expectation, which is now only approximately equal to r/δ .

It follows from these assumptions that the bivariate stationary distribution of $[X_1(z, t), X_1(z + v, t)]$ in this conditional model is the bivariate normal and the same as the corresponding distribution for the other species. The variance of each component is $[\sigma_s^2 + (\sigma_d^2/\bar{K})]/2\delta$, while the covariance is $\sigma_s^2 \rho_s(v)/2\delta$. Using known general properties of the Ornstein-Uhlenbeck process (Karlin and Taylor 1981), we find for a time difference u between the observations that

$$\text{cov}[X_1(z, t), X_1(z + v, t + u)] = \text{cov}[X_1(z, t), X_1(z + v, t)] e^{-\delta u}.$$

Engen and Lande (1996a, 1996b) pointed out that one would also obtain the lognormal species abundance model if heterogeneity between species was introduced by assuming that the parameters r for each species were chosen independently from a normal distribution with mean, say \bar{r} , and variance σ_r^2 . For this model, including heterogeneity between species modeled by between-species stochasticity in r , it is straightforward to show that

$$\text{cov}[X_1(z, t), X_1(z + v, t + u)] = \frac{\sigma_s^2 \rho_s(v) e^{-\delta u}}{2\delta} + \frac{\sigma_r^2}{\delta^2},$$

while the variance of any X_i can be decomposed into three additive components:

$$\sigma^2 = \frac{\sigma_s^2}{2\delta} + \frac{\sigma_d^2}{2\bar{K}\delta} + \frac{\sigma_r^2}{\delta^2},$$

where $1/\bar{K} = E e^{-r/\delta}$. From the expressions for the variance and covariance, it follows that the joint spatial and temporal correlation then takes the form

$$\rho(v, u) = \frac{\sigma_s^2 \rho_s(v) e^{-\delta u} + (2\sigma_r^2/\delta)}{\sigma_s^2 + (\sigma_d^2/\bar{K}) + (2\sigma_r^2/\delta)}.$$

If there is overdispersion, there will be an additional term θ^2 in the denominator as explained in appendix C.

Finally, we expand the model to include S species rather than two, writing $\mathbf{X}(z, t)$ for the vector of log abundances at location z at time t . In our conditional model, the pairs $[X_i(z, t), X_i(z + v, t + u)]$ and $i = 1, 2, \dots, S$ are then independent bivariate normally distributed variables with variance $[\sigma_s^2 + (\sigma_d^2/\bar{K}) + (2\sigma_r^2/\delta)]/2\delta$ for each component and a correlation $\rho(v, u)$ between them. Hence, the components of the two vectors $\mathbf{X}(z, t)$ and $\mathbf{X}(z + v, t + u)$ are each independent and normally distributed with the same parameters, while the components with the same subscript, representing log abundances of the same species at the two locations, have correlation $\rho(v, u)$. The components of the vectors of population sizes $\mathbf{Y}(z, t)$, representing the same species, possess the corresponding bivariate lognormal distribution. Assuming Poisson sampling of individuals at the locations z and $z + v$, or possibly sampling with overdispersion as defined in appendix C, a two-dimensional zero-zero-truncated Poisson lognormal model may be fitted to the vectors $[\mathbf{N}(z, t), \mathbf{N}(z + v, t + u)]$, which gives an estimate of the correlation $\rho(v, u)$ and the variance for each possible combination of v and u provided by the data.

APPENDIX C

Overdispersion

Individuals are often clustered, due to dependent behavior or small-scale heterogeneity in the environments. Then, the sampling distribution of N given the abundance y is not Poisson but will often show some overdispersion; that is, the variance in the sampling distribution of N is greater than the mean. Overdispersion only changes the parameter values in our abundance model and not the mathematical

form, if we assume that the sampling distribution itself is Poisson lognormal; that is,

$$P(N = n | Y = y) = \int_0^{\infty} \frac{(\omega y v)^n}{n!} e^{-\omega y v} f(v) dv,$$

where $f(v)$ is some lognormal distribution with mean 1 so that we still have $E(N|y) = \omega y$. Hence, using the general expression for the mean of a lognormal distribution, the distribution of $\ln v$ must be the normal with mean $-\theta^2/2$ and variance θ^2 . The parameter θ is then a measure of overdispersion. More precisely, conditionally on the abundance, we have

$$\frac{\text{var}(N|Y) - E(N|Y)}{[E(N|Y)]^2} = e^{\theta^2} - 1.$$

If $\theta = 0$, we are back to Poisson sampling. When using this sampling distribution rather than the Poisson, it is easy to see that the distribution of N is still the Poisson lognormal, but the parameters are $(\mu + \ln \omega - \theta^2/2, \sigma^2 + \theta^2)$ rather than $(\mu + \ln \omega, \sigma^2)$. Hence, if θ can be estimated from data (e.g., by repeated measurements at the same locations), we can perform our analysis as if θ were 0 and just correct the parameters in the end using the estimate of θ .

Notice that if the above mixing density $f(v)$ is the gamma distribution, then the distribution of N is the more commonly used negative binomial. However, when the y 's are lognormally distributed, it is mathematically more preferable to use the lognormal as the mixing distribution.

Literature Cited

- Allen, J. C., W. M. Schaffer, and D. Rost. 1993. Chaos reduces species extinction by amplifying local population noise. *Nature* 364:229–232.
- Athreya, K. B., and S. Karlin. 1971. On branching processes with random environments: extinction probabilities. *Annals of Mathematical Statistics* 42:1499–1520.
- Bascompte, J., and R. V. Solé, eds. 1998. Modeling spatiotemporal dynamics in ecology. Springer, Berlin.
- Bjørnstad, O. N., R. A. Ims, and L. Xavier. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution* 14:427–432.
- Bolker, B. M., and B. T. Grenfell. 1996. Impact of vaccination on the spatial correlation and persistence of measles dynamics. *Proceedings of the National Academy of Sciences of the USA* 93:12648–12653.
- Bulmer, M. G. 1974. On fitting the Poisson lognormal distribution to species abundance data. *Biometrics* 30: 651–660.
- Connell, J. H. 1978. Diversity in rain forests and coral reefs. *Science* (Washington, D.C.) 199:1302–1310.
- Cressie, N. A. C. 1993. *Statistics for spatial data*. Wiley, New York.
- Denslow, J. S., and G. S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. Pages 120–127 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. *La Selva: ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago.
- DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history. I. Papilionidae, Pieridae and Nymphalidae. Princeton University Press, Princeton, N.J.
- . 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera* 26:98–108.
- DeVries, P. J., and T. R. Walla. 2001. Species diversity and community structure in Neotropical fruit-feeding butterfly. *Biological Journal of the Linnean Society* 74:1–15.
- DeVries, P. J., D. Murray, and R. Lande. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62:343–364.
- DeVries, P. J., T. R. Walla, and H. Greeney. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society* 68:333–353.
- Diserud, O. H., and S. Engen. 2000. A general and dynamic species abundance model, embracing the lognormal and the gamma models. *American Naturalist* 155:497–511.
- Engen, S. 1974. On species frequency models. *Biometrika* 61:263–270.
- . 1978. *Stochastic abundance models*. Chapman & Hall, London.
- . 2001. A dynamic and spatial model with migration generating the log-Gaussian field of population densities. *Mathematical Biosciences* 173:85–102.
- Engen, S., and R. Lande. 1996a. Population dynamic models generating species abundance distributions of the gamma type. *Journal of Theoretical Biology* 178:325–331.
- . 1996b. Population dynamic models generating the lognormal species abundance distribution. *Mathematical Biosciences* 132:169–183.
- Engen, S., Ø. Bakke, and A. Islam. 1998. Demographic and environmental stochasticity—concepts and definitions. *Biometrics* 54:840–846.
- Engen, S., R. Lande, and B.-E. Sæther. 2002. Migration and spatio-temporal variation in population dynamics in a heterogeneous environment. *Ecology* 83:570–579.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The

- relation between the number of species and the number of individuals in a random sample from an animal population. *Journal of Animal Ecology* 12:42–58.
- Heino, M., V. Kaitala, E. Ranta, and J. Lindström. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London B, Biological Sciences* 264:481–486.
- Hubbell, S. P. 1997. A unified theory of biogeography and species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16:9–21.
- . 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, N.J.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science (Washington, D.C.)* 283:554–557.
- Karlin, S., and H. M. Taylor. 1981. *A second course in stochastic processes*. Academic Press, New York.
- Lande, R. 1993. Risk of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- . 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Lande, R., S. Engen, and B.-E. Sæther. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *American Naturalist* 154:271–281.
- Leigh, E. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90: 213–239.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews of the Cambridge Philosophical Society* 40:510–533.
- May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. *American Naturalist* 107: 621–650.
- . 1975. Patterns of species abundance and diversity. Pages 81–120 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- Patrick, R., M. Hohn, and J. Wallace. 1954. A new method for determining the pattern of the diatom flora. *Nootulae Naturae* 259:1–12.
- Pielou, E. C. 1975. *Ecological diversity*. Wiley, New York.
- Pinheiro, C. E. G., and J. V. C. Ortiz. 1992. Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography* 19:505–511.
- Preston, F. W. 1948. The commonness and rarity of species. *Ecology* 29:254–283.
- Ranta, E., V. Kaitala, J. Lindström, and H. Lindén. 1995. Synchrony in population dynamics. *Proceedings of the Royal Society of London B, Biological Sciences* 262: 113–118.
- Ranta, E., J. Lindström, and E. Helle. 1997a. The Moran effect and synchrony in population dynamics. *Oikos* 78: 136–142.
- Ranta, E., V. Kaitala, and P. Lundberg. 1997b. The spatial dimension in population fluctuations. *Science (Washington, D.C.)* 278:1621–1623.
- Ranta, E., V. Kaitala, and J. Lindström. 1999. Spatially autocorrelated disturbances and patterns in population synchrony. *Proceedings of the Royal Society of London B, Biological Sciences* 255:1851–1856.
- Roughgarden, J. D. 1975. A simple model for population dynamics in stochastic environments. *American Naturalist* 109:713–736.
- Routledge, R. D. 1977. On Whittaker's components of diversity. *Ecology* 58:1120–1127.
- . 1979. Diversity indices: which ones are admissible? *Journal of Theoretical Biology* 76:503–515.
- Sæther, B.-E., S. Engen, A. Islam, R. McCleery, and C. Perrins. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *American Naturalist* 151:441–450.
- Shannon, C. E., and W. Weaver. 1948. *The mathematical theory of communication*. University of Illinois Press, Urbana.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions*. Oxford University Press, Oxford.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance pattern. *American Naturalist* 116:770–787.
- Sutcliffe, O. L., C. D. Thomas, and D. Moss. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* 65:85–95.
- Thomas, C. D. 1991. Spatial and temporal variability in a butterfly population. *Oecologia (Berlin)* 87:577–580.
- Tilman, D., and P. Kareiva, eds. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Tufto, J., B.-E. Sæther, S. Engen, P. Arcese, K. Jerstad, O. W. Røstad, and N. M. Smith. 2000. Bayesian meta-analysis of demographic parameters in three small, temperate passerines. *Oikos* 88:273–281.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer, Sunderland, Mass.
- Turelli, M. 1977. Random environments and stochastic calculus. *Theoretical Population Biology* 12:140–178.
- Ugland, K. I., and J. S. Gray. 1982. Lognormal distributions and the concept of community equilibrium. *Oikos* 39: 171–178.

- Webb, D. J. 1974. The statistics of relative abundance and diversity. *Journal of Theoretical Biology* 43:277–291.
- Whittaker, R. H. 1972. Evolution and measurements of species diversity. *Taxon* 21:213–251.
- Willott, S. J., D. C. Lim, S. G. Compton, and S. L. Sutton. 2000. Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology* 14:1055–1065.

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