Modeling vertical beta-diversity in tropical butterfly communities

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We present a novel analytical method for assessing spatial and temporal structure in community samples that is useful for comparing large data-sets that include species abundance data. The model assumes that species numbers in two samples are drawn from a bi-variate Poisson log-normal species abundance distribution and parameters from the fitted distribution are estimated to assess community structure. We assessed three tropical butterfly data-sets for spatial structure in the vertical dimension, and tested for changes in structure as a result of temporal variance, disturbance regimes, and geographic location. Our results indicate that the vertical dimension is a major structural component in tropical forest butterfly communities that varies little through time and is not measurably affected by small-scale disturbances. However, there is evidence that the degree of vertical structure may vary among geographic regions. These results are discussed in terms of the mechanisms maintaining vertical structure, and the implications of changes in forest architecture on butterfly communities.

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The distribution of species in time and space is vital for describing ecological communities and developing hypotheses to explain the evolution and maintenance of species diversity (Gleason 1926, Elton 1966, MacArthur 1972, Whittaker 1975, Wiens 1984, Tilman 1994, Brown 1995). Environmental heterogeneity and habitat complexity are important determinants of community composition, and species responses to environmental variation provide insight into ecological and evolutionary processes such as speciation, adaptation, dispersal, and colonization (Hubbell 2001). Recent investigations have also emphasized the influence of environmental heterogeneity on community composition as a critical factor affecting the measurement of species diversity. species area relationships, and the relationship between local and regional diversity patterns (Srivastava 1999, Loreau 2000, Gering and Crist 2002, Wagner and Wildi 2002). Therefore, spatial variation in relative species abundance is critical for understanding community dynamics.

Species respond to the environment in different ways, and spatial scaling or habitat specialization may vary among species in communities. As such, changes in structure among locations within and between communities are generally continuous graded shifts in species composition as opposed to sharply defined boundaries (Pielou 1975, Wilson and Mohler 1983, Williams et al. 1999). Measuring spatial variation is challenging because most communities are comprised of differing numbers of related species that vary in abundance, and include many rare species (Preston 1948, Colwell and Coddington 1994, Novotny and Basset 2000), and evaluation of spatial structure requires estimates of the number of individuals at different locations. Hence, rare species are often excluded from parametric analyses, and species by species assessments. Non-parametric tests for homo-

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geneity of sample composition (chi-square) may include all species and ascertain the significance of structure, but they do not indicate the degree of structure present. Beta-diversity (MacArthur 1965, Whittaker 1975), which is related to measures of community similarity (Lande 1996), describes the difference in species diversity observed between samples. When measured as a function of species richness and relative species abundance, betadiversity can be used to measure community structure in space or time. However, no single measure of betadiversity is universally accepted and few methods support statistical evaluation (Magurran 1988, Vellend 2001, Gering et al. 2003, Lande et al. 2003).

The distribution of species at particular heights within forest communities, referred to here as vertical structure, is a classic phenomena in ecology (Allee 1926, Bates 1944, MacArthur 1958, 1965, Elton 1973, Erwin 1983, Stork 1988, Basset et al. 1992, Wolda 1992, Richards 1996). Vertical structure among samples is manifested as high beta-diversity in the vertical spatial dimension, and accounts for a significant component of species diversity in neotropical fruit-feeding nymphalid butterfly communities (DeVries et al. 1997, 1999, DeVries and Walla 2001). Vertical structure has also been shown among mimetic groups of neotropical butterflies that are not attracted to fruit-baited traps (Papageorgis 1975, Beccaloni 1997). Thus accounting for vertical structure is an essential underlying concern for studies seeking to measure diversity in natural communities. Nevertheless, due to limitations in analytical techniques and availability of appropriate data-sets, vertical structure among butterfly species (and other insects) has not been investigated in terms of how spatial or temporal variance may influence them, or under what conditions vertical structure becomes inconsequential.

Here we present a method for modeling structure in species rich communities that is analogous to measurement of beta-diversity. We model structure between a pair of community samples as a parametric distribution among species with the expected frequency of species in the canopy and understory as the variables of interest, and we estimate the model parameters by fitting a bivariate Poisson log-normal species abundance distribution to two community samples. Unlike most techniques, our novel method of evaluating beta-diversity between community samples makes full use of the information in samples without excluding species on the basis of sample size, and it allows sample pairs to be evaluated statistically for differences in the degree of vertical structure among communities.

After deriving the model we apply it to several large neotropical butterfly data-sets to understand how vertical beta-diversity varies in space and time. We first assess the long-term stability of vertical structure in a community sampled from intact rainforest. We then test the null hypothesis that vertical structure does not change under varying degrees of natural and anthropogenic disturbance. Third, we assess the generality of vertical structure among geographic regions by comparing the vertical structure of rainforest butterfly communities from three different sites, two in eastern Ecuador, and one in Costa Rica. Finally, we discuss the results of our analyses in the context of ecological and evolutionary patterns of community structure, and conservation.

Methods

Study communities

Adult butterflies in the family Nymphalidae that are attracted to and feed on the juices of rotting fruits constitute a feeding guild known as fruit-feeding nymphalids (DeVries and Walla 2001). Data-sets on fruit-feeding nymphalids from three rainforest community studies were used in our analyses: two from the upper Amazon of Ecuador, La Selva Lodge (DeVries and Walla 2001) and Jatun Sacha (DeVries et al. 1997), and one from the Atlantic lowlands in Costa Rica, Finca La Selva (DeVries 1988). All three sites are considered evergreen wet (Costa Rica) or superwet (Ecuador) rainforests (Richards 1996), and have characteristic wet and dry seasons with 3–5 m of rain per year.

Similar sampling methods were applied in all three communities, where traps were placed in replicated pairs, with one in the canopy (15–25 m above ground) and one in the understory (1 m above ground), and baited with fermented bananas (DeVries 1988, DeVries and Walla 2001).

At La Selva Lodge the traps were sampled monthly for five years from August 1994–July 1999 in natural forest habitat. The Jatun Sacha study was designed to sample equally from four different habitat types: primary, secondary, hi-graded forest, and forest edge adjacent to pasture. At Jatun Sacha traps were sampled monthly for one year from August 1992–August 1993. At Finca La Selva five canopy and five understory traps were sampled daily for approximately 2 months from October 1979–December 1979.

The model

We model the structure observed in samples from two points in space or time, and apply the model to canopy and understory samples. The vertical structure of each species is reflected in the proportion of individuals in that species observed in the canopy. For convenience we use the expected frequency of a species in the canopy p as a proportion of the pooled sample to measure vertical structure and model the distribution of p among species to describe vertical structure at the community level. A derivation of the model used in our analyses is presented in the appendix. To summarize, we assume samples from each forest height are drawn from a Poisson log-normal species abundance distribution. The abundance pair for each species (canopy and understory) may then be considered drawn from the bi-variate Poisson log-normal species abundance distribution where every species has a probability of occurring in the canopy (p) versus the understory (1-p). Maximum likelihood was then used to estimate the parameters of the fitted bi-variate distribution, allowing some species to be absent from either the understory and/or canopy samples.

The number of individuals observed in the canopy for a given species may be considered as the number of successes in a bi-nomial sampling experiment with parameters N and p, where N is the number of trials (individuals sampled) and p is the probability of a success (capture in the canopy). The observed frequency of each species in the canopy (number of individuals in the canopy/number of individuals sampled from that species) provides an estimate of p for each species. However, the distribution of p among species, denoted g(p), is obtained from the bi-variate distribution of abundances among species as shown in the appendix. Here g(p) is a function of the five parameters (means, variances, and correlation) from the fitted joint canopy and understory species abundance distribution.

The model distribution g(p) among species is a probability density function expressing the probability that a species chosen at random from the community (independent of species abundance) will exhibit a given frequency in the canopy. If the model shows the mass of the distribution to be concentrated near 0.5, there is a high probability that a randomly selected species will be evenly distributed between canopy and understory; in other words, species specialized to one height class are rare. However, if the mass of the distribution is concentrated in the tails, it forms a U shape, and there is a high probability that a randomly selected species is found mostly at one height. Examples of potential forms of the p distribution are presented in Fig. 1 where all parameters are held constant with the exception of the correlation ρ between samples. All five parameters of the bi-variate species abundance distribution affect the distribution of p, thus the example is a simplification.

Confidence limits for the model are generated through parametric bootstrapping; that is, repeatedly simulating new sets of data from the estimated model and recalculating the parameter estimates from each simulated data-set or bootstrap sample to approximate the sampling distribution of the parameter estimates. For each bootstrap sample the five parameters are estimated by maximum likelihood and the p distribution is modeled; the distribution of parameter estimates among the bootstrap samples provides measures of uncertainty



Fig. 1. Plot of the hypothetical p distributions where correlation ρ is varied from maximum to minimum possible values. The four other parameters in the model are held constant. When ρ is high the p distribution is a bell shaped curve. When ρ is low, the mass of the distribution is concentrated in the tails. Vertical gray lines represent selected α level ($\alpha = 0.2$).

for each of five parameters as well as the distribution of p.

It is not required that sampling effort be equal in the two samples compared, since this will not affect the form of the species abundance distributions. However it is far more informative if both samples are large enough to accurately model species abundance distributions; small sample sizes result in large uncertainty.

A simplified representation of differences in the form of the p distribution between sample pairs from different communities is performed by partitioning the distribution into sections corresponding to three categories of vertical stratification: understory species, unstratified species found at both heights, and canopy species. The cutoffs for the categories (referred to here as α) can be determined based on the biology of the study organisms or the interest of the researcher. Here we consider species with 20% or less of their abundance in canopy samples are vertically stratified understory species. Thus an α level of 0.2 was chosen and applied to both tails of the distribution. Expected p values between 0.2 and 0.8 in the middle section of the distribution correspond to unstratified species found frequently in both canopy and understory samples. Values less than 0.2 correspond to understory species and values greater then 0.8 correspond to canopy species. A species chosen at random from the community has a probability of being in each of the three stratification categories that are equivalent to the areas under each of the three α -defined sections of the distribution (Fig. 1). The results were not sensitive to α , since values of α from 0.1 to 0.3 yielded similar results.

To compare the form of the p distribution among communities graphically, the areas under each of the three curve sections are considered as vectors in an equilateral triangle with axes corresponding to vertices labeled Canopy, Understory, and Both located as a single point in the triangle. If areas under each section of the p distribution are equivalent, the point will plot in the center of the triangle. If a randomly chosen species is more likely to be a "canopy species" then it will be closer to the Canopy vertex.

Conversely when the mass of the distribution is concentrated at 0.5, the point will be closer to the Both vertex, and when the mass of the distribution is concentrated near p = 0, the point will be closer to the Understory vertex (Fig. 2). The confidence region for the bootstrap replicates is plotted on the triangle to indicate the degree of uncertainty.

Comparisons

To test the hypothesis that vertical structure was temporally stable, we modeled five years of monitoring data from La Selva Lodge. The degree of stratification modeled for each year was then compared to the five year combined sample using parametric bootstrapping to estimate confidence intervals for the parameter estimates.

Effects of natural tree fall disturbances on vertical structure were tested by sub-dividing the La Selva Lodge trap samples into those that were adjacent to large tree fall gaps for more than one year during the study period and those that were never adjacent to tree fall gaps. These two groups were then assessed for differences in vertical structure.

To test for effects of human-induced disturbance on butterfly vertical structure, we compared samples from the four habitats at Jatun Sacha representing different



Fig. 2. Triangular plotting surface showing the vertical structure present in the hypothetical communities from Fig. 1. Higher correlations between canopy and understory abundance distributions will move the community closer to the Both vertex. Strongly stratified communities will plot near the center of the triangle. Greater numbers of Canopy or Understory species will shift the community closer to one of the lower vertices.

levels of anthropogenic disturbance ranging from undisturbed forest to pasture edge.

To evaluate the consistency of vertical structure among geographic regions where forest structure is similar, we compared the vertical structure at La Selva Lodge (Ecuador), Jatun Sacha (Ecuador), and Finca La Selva (Costa Rica).

Results

Sample size and number of species sampled from each community are reported in Table 1. The high species richness from the Ecuadorian samples was characteristic of most Amazonian forest sites, and the Costa Rica site was comparatively species poor due to its geographical location, shorter sampling period, and small sample size.

Fitting the La Selva Lodge samples to the model resulted in a U-shaped g(p) distribution that indicated a strongly stratified species community (Fig. 3). We found no evidence to reject the null hypothesis that the distribution of vertical structure among species was consistent across all five years. The vertical structure was similar among years despite considerable annual variance in overall abundance of butterflies. However, the variance of the species abundance distributions in the canopy and the understory increased through time, and the correlation ρ decreased after the first year (Table 2). These observations reflect subtle changes in the distribution of abundance among species at both forest heights that did not significantly affect the vertical structure of the community (Fig. 4).

We found no evidence that natural disturbance affected vertical distribution at La Selva Lodge. Traps from within closed canopy forest and traps in tree fall gaps showed no significant differences in vertical structure (Fig. 4, Table 2).

The four habitat types at Jatun Sacha showed no significant differences in vertical structure (Fig. 4). Only the edge habitat had distinctive parameter estimates, showing a comparatively larger variance of the understory fitted species abundance distribution, and a greater correlation, ρ (Table 2).

Comparison among geographic regions suggested that vertical structure may vary regionally. Although Jatun Sacha and La Selva Lodge had similar vertical structure,

Table 1. Summary of data-sets used for analysis of vertical structure.

	LSL Ecuador	JS Ecuador	FLS Costa Rica
Canopy sample size	5840	1173	129
Canopy species richness	87	86	31
Understory sample size	6021	5517	53
Understory species richness	96	105	22
Total sample size	11861	6690	182
Total species richness	128	130	46



Fig. 3. Plot of the probability density function of the p distribution for La Selva Lodge total community. The concentration of mass at the tails of the distribution shows considerable vertical structure among species. The y-axis is truncated at 30

the La Selva CR site showed a significantly different pattern (Fig. 5, Table 2). In Costa Rica the distribution of p showed more mass under the canopy tail of the curve compared to the understory. In other words, a species chosen at random in Costa Rica had a higher probability of being a canopy species relative to the Ecuadorian sites. Thus Costa Rican fauna had a significantly greater proportion of canopy species than the other two sites.

Discussion

Natural patterns of spatial structure in communities have been described in terms of alpha and beta-diversity, where alpha diversity describes the average diversity within homogenous sites and beta-diversity describes diversity between sites (MacArthur 1965, Whittaker 1975, Wilson and Mohler 1983, Lande 1996). Ecologists have not previously developed methods of measuring spatial changes in relative abundance of species that simultaneously account for unequal sample sizes, sampling error, and the range of abundances among species including large proportions of singletons (reviewed Magurran 1988). The primary contribution of this work is the presentation of a novel method for analyzing differences in the relative abundance of species among samples. We used a community-level analysis and derived a model that maximally utilizes the information in the data. The model provides a description of the structure between two samples that may be interpreted as a measure of beta-diversity, independent of sample size, and may be generalized to evaluate temporal and spatial community structure. The model also can be used to generate measures of statistical uncertainty in the results. Given these properties, we expect it may prove useful for quantifying the magnitude of differences in species abundances among areas separated by ecological

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	ρ	0.08	0.25	0.25	0.25	0.31	0.35	0.39	0.23	0.16	0. 4	0.24	0.19	0.10	-0.22
	Ι	3.14	3.65	3.90	5.17	5.27	6.21	6.24	4.36	4.73	5.22	3.54	3.01	3.30	0.52
	+	9.25	10.22	9.81	12.20	12.25	13.06	13.01	11.65	9.55	13.85	10.16	8.21	9.47	4.68
	σ_{u}^{2}	5.64	6.63	7.14	6.63	8.90	9.33	9.95	8.55	7.13	9.67	6.84	5.51	6.44	2.30
	Ι	0.25	4.73	5.00	6.13	6.10	6.91	6.42	6.10	3.10	2.02	2.53	2.68	2.95	0.97
	+	9.75	11.84	11.17	12.92	12.77	13.70	13.01	12.45	7.07	6.77	8.11	8.38	9.07	5.08
onon engre	σ_c^2	7.37	8.55	9.38	8.55	10.44	10.78	10.92	11.14	4.84	4.20	4.94	5.25	5.96	2.64
	-	-1.84	-1.45	-2.34	-2.04	-2.10	-0.78	-1.57	-2.04	-0.06	-2.19	-2.19	-1.84	-2.48	-2.57
	+	0.17	0.55	-0.12	0.12	0.08	0.99	0.36	-0.05	1.37	0.45	0.21	0.22	-0.23	-0.39
u canopy ar	μ	-0.74	-0.39	-1.39	-0.39	-1.42	0.13	-0.82	-1.31	0.71	-0.86	-0.91	-0.74	-1.40	-1.26
	Ι	-2.53	-2.11	-3.13	-2.15	-2.18	-1.22	-1.95	-2.77	-0.91	-2.61	-2.87	-2.80	-3.02	-1.84
л <i>у</i> , р — сонс	+	-0.27	-0.02	-1.05	-0.15	-0.18	0.38	-0.06	-0.87	0.33	-0.52	-0.79	-0.66	-0.73	0.29
	μ	-1.28	-1.08	-2.47	-1.08	-2.06	-0.45	-1.28	-2.23	-0.22	-1.43	-1.72	-1.66	-1.90	-0.51
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Fig. 4. Vertical structure of communities in different disturbance regimes. Dashed ellipse includes 95% of the 500 bootstrap estimates for the total La Selva Lodge community. None of the communities plotted exhibit significantly different vertical structures compared to other Ecuadorian communities.

or environmental gradients. This approach has been generalized by Engen et al. (2002a), and Lande et al. (2003).

This study provides the first comparisons of vertical structure among tropical communities. We found surprisingly robust vertical structure among fruit-feeding nymphalid butterfly communities; neither small-scale disturbance nor temporal fluctuations in abundance influenced vertical structure. The consistency of this



Fig. 5. Community comparison of vertical structure among the three locations. Dashed ellipse includes 95% of the 500 bootstrap estimates for the total Finca La Selva community. The results indicate significant differences between the Finca La Selva site and the Ecuadorian sites. Finca La Selva has more species in the canopy compared to the understory and slightly less vertical stratification.

pattern confirms that vertical structure is an important component of tropical forest butterfly communities (DeVries and Walla 2001).

Despite dynamic changes in community abundance among years presumably caused by disturbance to the forest by large storms at the La Selva Lodge (DeVries and Walla 2001), we found that the overall vertical structure of the butterfly community remained unaffected. Our model of g(p) distribution for each year was similar in form to the total community and showed a large proportion of the distribution concentrated at the tails (Fig. 3). We also found that natural small-scale disturbance due to tree falls did not disrupt vertical structure within the intact forests. No significant difference in structure was observed between samples taken adjacent to tree fall gaps and those within the forest (Fig. 4, Table 2). This contrasts with observations suggesting that canopy species may show a propensity to fly at ground level in forest gaps (DeVries 1988). Our results suggest small-scale disturbances are not sufficiently frequent to significantly alter the overall community vertical structure.

At Jatun Sacha where four habitats represented varying degrees of anthropogenic disturbance we found that vertical structure was equivalent in all habitats. Even at the forest edge adjacent to the cattle pasture there was no evidence of a change in the distribution of p among species. The raw data showed that some common canopy species were more abundant in the understory at the forest edge, but concurrently some rare species were more frequent in the canopy than in less disturbed habitats. The mean and variance of the p distribution for the edge sample is similar to the other three habitats, thus generating a non-significant difference in vertical structure (Table 2, Fig. 4).

Current hypotheses explaining vertical structure in tropical butterflies cite mechanisms associated with potential differences in predator communities (Papageorgis 1975), light levels (DeVries 1988), and host plant availability at different heights in the forest (Beccaloni 1997). Our results suggest that vertical stratification is not likely to be maintained solely by differential light levels, which are known to be associated with canopy cover (Richards 1996). If this were the case we would have expected to see a significant number of canopy butterflies captured at the forest floor near gaps and along the forest edge (Table 2, Fig. 4). We cannot dismiss the role of predators and host plant availability since either factor could potentially be maintained in the face of changing habitat structure. It is also possible that under both natural and anthropogenic disturbance, individuals descend to the forest floor in gaps but they are simply not attracted to baits in this alternate habitat. In any case, we present strong evidence that fruit-feeding behavior shows a strong relationship with height in the

forest, regardless of the forest maturity or uniformity of canopy structure.

Community disturbance or pollution may increase the variance of the species abundance distribution by releasing some species to high abundance while others become or remain relatively rare (Patrick et al. 1954, Gray and Mirza 1979, Ugland and Gray 1982). This pattern was noted in the Jatun Sacha butterfly community (DeVries et al. 1999) where there was a significant increase in the variance of the understory species abundance distribution at the forest edge. However, we note that in the same study there was no measurable effect at the other levels of disturbance (i.e. higrade and secondary habitats). We suggest that changes in community structure that are reflected by an increased variance of the species abundance distribution may only be evident in cases where disturbance is particularly severe. Although this investigation does not address the impacts of broad scale habitat disturbance as induced by clear-cutting and forest conversion to agriculture, it shows that intermediate disturbance is unlikely to affect the degree of vertical structure in butterfly communities.

It is well known that geographic location has a large influence on the richness and structure of butterfly communities. Analysis of a limited data-set from Costa Rica showed that butterflies exhibit a vertical distribution of species significantly different from those in the Ecuadorian samples (Fig. 5). Like the other sites, most species were specialized to one height, but the probability that a species selected at random from the Costa Rica sample is a canopy species was much higher. This suggests that the canopy fauna in Costa Rica may be more important in determining overall community composition and diversity than in Ecuadorian faunas. It may be that during the short period of the Costa Rican study, many of the understory species were not present. Nonetheless, effects of seasonal bias are mitigated somewhat by the theoretical underpinnings of the species abundance distributions that permits accounting for the species that are not observed in samples (Appendix 1). The canopy bias of species preference in Costa Rica is probably not due to limited sample sizes since this only affects the degree of certainty in estimates, but not the expectations. Neither is it due to intraspecific variation among regions in height preference; inspection of the raw data shows that all species shared among sites exhibited similar patterns of vertical structure.

Conclusions

The comparative analyses performed here were possible through an integration of long-term studies of species diversity and advances in statistical analyses of community structure (Engen 1978, 2001, Engen and Lande 1996, Engen et al. 2002a, b, Diserud and Engen 2002, Lande et al. 2003). This study indicates that while vertical patterns in species distributions are robust to changes in forest architecture, the underlying components of the canopy and understory communities may vary among regions. Future comparative work using similar community-level analyses may reveal further patterns among ecoregions that provide a broader understanding of community structure useful for testing ecological theory and its application to conservation.

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Appendix

If $\ln \lambda$ is a normally distributed variable with mean μ and variance σ^2 and the distribution of X conditioned on λ is the Poisson distribution with parameter λ , then the unconditional distribution of X is the Poisson lognormal distribution

$$\begin{split} P(X = x; \mu, \sigma^2 = q(x; \mu, \sigma^2) \\ = \int_{-\infty}^{\infty} \frac{exp(z\sigma x + \mu x + e^{-(z\sigma + \mu)})}{x!} \varphi(z) dz \end{split}$$

where $\phi(z)$ is the standard normal distribution.

Consider a community of s species with abundances $\lambda_1, \lambda_2, \dots, \lambda_s$. In the log-normal species abundance model the abundances are modeled as independent observations from the log-normal distribution (Preston 1948, Grundy 1951, Bulmer 1974, Engen and Lande 1996), which is equivalent to the $\ln \lambda$ being normally distributed, say N(μ , σ^2). A dynamic process leading to this model was given by Engen and Lande (1996). For a given abundance λ , the corresponding number of individuals observed is commonly assumed to be Poisson distributed with parameter $\lambda \omega$, where ω is a parameter characterizing the sampling effort. Since $\ln(\lambda \omega)$ is normally distributed with mean $\mu + \ln \omega$ and variance σ^2 it follows from the above definition that the observed number of individuals for each species are independent variables with the Poisson log-normal distribution (x; $\mu + \ln \omega$, σ^2). Notice that the first parameter in this distribution depends on the sample size, while the second

parameter, which is the variance of the log of the abundances, takes the same value regardless the sampling effort.

Since s is usually unknown, we only consider the observed number of individuals for the observed species. The distribution of the number of individuals then follows the zero truncated Poisson log-normal distribution

$$q(x; \mu + \ln\omega, \sigma^2)/(1 - q(0; \mu + \ln\omega, \sigma^2))$$

defined for x = 1, 2, ... The maximum likelihood estimation of the parameters of this distribution based on S observed species was derived by Bulmer (1974). The idea of using the truncated distribution was first put forward by R.A. Fisher in the classical paper on logseries species abundance distribution (Fisher et al. 1943).

If the abundance structures at two different locations, say A and B, are to be analyzed, one may define a twodimensional abundance model giving a joint description of the two sites. Suppose there are s species in the joint community, and let (λ_i, v_i) , for i = 1, 2, ..., s, be the abundances of the species at A and B, respectively. The natural generalization of the log-normal species abundance model is then to make the assumption that for each pair of log of abundances at A and B, $(\ln \lambda_i, \ln \nu_i)$, are generated by a bi-variate normal distribution. The corresponding pair of abundances then has the bi-variate log-normal distribution. Assuming that the sampling intensities at A and B are ω_A and ω_B , respectively, the observed number of individuals at A and B for this set of species is a sample of independent observations from the corresponding bi-variate Poisson log-normal distribution.

Writing $(\mu_A, \mu_B, \sigma_A^2, \sigma_B^2, \rho)$ for the expectations, variances and the correlation of the underlying bi-variate

normal distribution, the straightforward generalization of the one-dimensional case leads to the two-dimensional Poisson log-normal distribution with parameters $(\mu_A + \ln \omega_A, \mu_B + \ln \omega_B, \sigma_A^2, \sigma_B^2, \rho)$. Again, we would have to consider the truncated form, including only species that are observed at least at one of the sites.

In order to estimate the parameters in the twodimensional case, the likelihood function for the zerotruncated bi-variate distribution has to be computed by performing the two-dimensional integrations numerically, and finally the likelihood function must be maximized numerically with respect to the unknown parameters. Uncertainties are most conveniently found by performing parametric bootstrapping, as described in the main text.

For a given species with given abundances in two samples, say (λ, ν) , the number of individuals observed at site A, say X, given the total number of individuals observed from this species, say N = X + Y, is bi-nomially distributed with parameters N and $p = \lambda/(\lambda + \nu)$, which is equivalent to logit (p) =ln λ -ln ν . Hence, the distribution of logit (p) among species is the normal distribution with mean $\mu = \mu_A - \mu_B$ and variance $\sigma^2 = \sigma_A^2 + \sigma_B^2 - 2\rho\sigma_A\sigma_B$. From this we find the distribution of p among species to be

$$g(p) = \frac{1}{\sqrt{2\pi}\sigma p(1-p)} \exp\left\{-\frac{1}{2\sigma^2} \left[\ln\left(\frac{p}{1-p}\right) - \mu\right]^2\right\}$$

Notice that if the sampling intensities at A and B are the same, that is, $\omega_A = \omega_B$, then the parameter μ and σ^2 are estimable by observations from the bi-variate Poisson log-normal distribution. Otherwise, ω_A/ω_B must be known in order to estimate the parameter μ in the distribution of p.