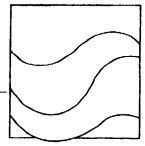
OCEANOLOGICA ACTA · VOL. 24 – No. 5



Detecting changes in diversity in a fluctuating environment based on simulation of stochastic processes

Ola Håvard DISERUD*

Department of Mathematical Sciences, Norwegian University of Science and Technology, Trondheim, Norway

Abstract − In this paper, I present a method developed to detect 'extra', or novel, changes in diversity in a naturally fluctuating environment. When comparing samples in order to evaluate changes in community structure, the sampling procedure will inevitably induce randomness in observed species composition and abundance, so two samples may show considerable differences, even if they come from exactly the same community. Sometimes the effort put into the sampling varies as well, leading to the expectation of a further increase in difference. Finally, if there were a temporal distance between the samples, we would like to correct for variations in species abundance occurring naturally due to fluctuating environmental conditions. The test method presented here includes a model of the sampling procedure, and corrects for differential sampling efforts. The population dynamics is modelled by a diffusion process, its variance mimicking the effect a fluctuating environment has on species abundances. We are thereby able to test the null hypothesis of no unnatural change in diversity, against the alternative of additional changes in community structure due to for example human disturbances. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Résumé − La détection de changements de diversité dans un environnement fluctuant, basée sur la simulation de processus stochastiques. Cet article décrit une méthode pour détecter les changements de diversité dans un environnement fluctuant. Dans la comparaison d'échantillons pour évaluer les changements de structure de la communauté, l'échantillonnage induit inévitablement du « hasard » dans la composition des espèces et de leur abondance. Deux échantillons peuvent présenter de fortes différences même s'ils proviennent de la même communauté. Parfois, l'effort déployé dans l'échantillonnage varie également, ce qui conduit à attendre un nouvel accroissement des différences. Finalement, en cas d'intervalle de temps suffisant entre les échantillons, nous proposons de corriger les données des variations d'abondance des espèces dans ces conditions environnementales fluctuantes. La méthode inclut un modèle de méthodologie d'échantillonnage et corrige les différences dans l'effort d'échantillonnage. La dynamique des populations est modélisée par un processus de diffusion, sa variance simulant l'effet d'un environnement fluctuant sur l'abondance spécifique. Nous sommes à même de tester l'hypothèse nulle d'un changement de diversité qui ne serait pas naturel, en face de changements additionnels hypothétiques de la structure de la communauté dus, par exemple, à l'action humaine. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

community structure / diversity index / environmental variance / population dynamics / species abundance model

structure des communautés / diversité / variance environnementale / dynamique des populations / modèle d'abondance d'une espèce

**Correspondence and reprints: fax:* +47 73 55 09 99.
E-mail address: ola.diserud@pfi.no (O.H. DISERUD).

S0399178401011598/FLA

1. INTRODUCTION

Some of the most pressing ecological problems today are to describe and explain the variety and abundance of species, their expected future development, possibly across centuries (Pimm, 1991), and the prediction of extreme conditions such as species extinction. How are species abundances distributed in nature, and how can they be influenced, or caused, by interactions between individuals or species and by the abiotic forces of their environment? These are all problems where the development and application of an appropriate stochastic model is of great significance. Ecologists are often interested in comparing two, or more, samples in order to test for temporal changes, or spatial differences, in community structure. The samples are either taken at different times from the same community, or from locations spatially separated. For example, we may want to monitor a community over time in order to detect trends or sudden, acute changes, or we may want to compare different habitat types. The major goal is then to infer the possible causes for any observed difference between samples.

Any attempt to study community ecology must first deal with the questions of how to define the term 'community' and how to delimit it, that is, choices of taxonomic, spatial and temporal scales. The most inclusive definition of a community is all the organisms in a prescribed area (e.g. Roughgarden and Diamond, 1986). This definition is in most practical applications restricted along the three scales mentioned above, in order to describe a group of species living closely enough together for the potential of local interaction (Strong, 1984; Claridge, 1987; Southwood, 1987; Magurran, 1988). Caution and 'common sense' must be shown when delimiting the community; the analysis will depend heavily on which species we choose to sample, each of these species will at least have slightly different geographical range and habitat, and the seasonal variation in species abundance may be relatively strong and unsynchronised. Patterns can be apparent if one examines the community over a sufficiently large area or for a sufficiently long time, but not show up if the study is restricted in space and time.

Tolerating uncertainty is often necessary, not only due to lack of information, but also due to the intrinsic stochasticity and unpredictability in many ecological processes. The effects of random sampling may, at least partially, cause an observed difference between samples with regard to community structure. Scientists unfortunately sometimes ignore that they are dealing with a sample rather than the population itself, a mistake which can lead to substantial bias (Solow, 1998). An observed difference may also occur due to possible variations in sample size, or rather, sampling effort. Does a difference in sample size reflect different sampling efforts or an actual difference in community structure? A possible trap here is that an observer who strives to obtain equal sample sizes thereby differentiates the sampling effort and camouflages an actual difference in species abundance. Temporal variations in species abundance may just be reflections of a naturally fluctuating environment. This variance must be included in a dynamical model before any inference on (unnatural) changes in community structure can be performed. When methods for estimation and prediction are constructed, the biological uncertainties as well as statistical uncertainties due to sampling must therefore be taken into account. The observations may also be probable and not certain, for example classification of trophic relations, therefore introducing even more uncertainty. Such uncertainties constitute an essential part of many controversial scientific investigations and policy responses (e.g. global warming). Modelling tools and approaches leading to satisfactory conclusions are therefore of great importance.

The practical implications of stochastic models in biology have recently been questioned (e.g. Caughley, 1994), because the analysis is often based on unrealistic, simplifying assumptions, and on estimates with weak empirical foundation. Another problem is that theoretical models, which are validated in limited domains, are too often generalised on insufficient evidence (Beck, 1997). The search for generality increases our understanding of nature, but this generalisation should be based on solid information and not on excessive and dubious extrapolations. The effect of time and place can often contribute substantially to the variance, and since theories necessarily are simplifications, they cannot be expected to account for all the variance of a noisy world. Finally, the majority of the present models are almost completely biotic in their explanatory variables (Hall, 1988). Abiotic variables are usually better behaved, and may often be just as important in determining the basic properties and the dynamics of community structure. One of the major benefits of modelling is that assumptions must be articulated, and reasoning made explicit. Thus, those participating in the analysis are likely to develop a clearer

perception of the problems and begin to attack them in a more unified manner.

2. MATERIALS AND METHODS

Studies of community patterns usually applies to an assemblage of closely related species, since taxonomically distant taxa often have weak relationships. The kind of data often analysed tends to have relatively vague spatial and temporal boundaries, making a proper definition of the community difficult. For that reason, many ecologists, Fisher included, often referred to 'collections' rather than 'communities'. When the study aims at comparing separate communities in space or the same community over time, it is important that the other scales are fixed throughout the study. The effect of for example seasonal variation could otherwise be severe. When comparing communities, we shall in most cases wish to eliminate differences due to unequal sampling efforts.

2.1. Species abundance models

One aspect of community structure that has been given particular attention is the pattern of abundances of all the species in the community. The species may have a wide range of abundances; some are very common and others are rare. A species abundance model is a statistical model describing this distribution of abundances. When adopting a parametric probability distribution we have parameters to draw inference on, the possibility to test for differences in parameter values between different types of communities, and the data from random samples can be treated statistically. Ecologists often go further to investigate how the structure is generated, and search for processes which can explain the observed pattern.

For all the classical models, it generally applies that the set of observations is treated as a random sample from some indefinitely large population. We further assume Poisson-sampling, that is, if a species with abundance x is represented by X individuals in the sample, then X is a Poisson variate with a distribution

$$P(X = i) = \frac{(\nu x)^i}{i!} \, e^{-\nu x}$$

where ν is a measure of the sampling intensity, $\nu \in [0,1]$. Let S be the number of species in the community. The abundances of all the species in the community can then be regarded as a sample of size S from some probability distribution $f(x)$. The probability that a species will be represented by i individuals in a sample is then

$$p_i = \int_0^\infty \frac{(\nu x)^i}{i!} e^{-\nu x} \, f(x) \, dx$$

for $i = 0, 1, 2, \ldots$, that is, a compound Poisson distribution. We will only observe the truncated form of this distribution, since the number of unobserved species generally is unknown.

Fisher (Fisher et al., 1943) started out by assuming that the abundances could be modelled by a gamma distribution

$$f(x) = \frac{\beta^k}{\Gamma(k)} x^{k-1} e^{-\beta x}$$

where $k, \beta > 0$. He then performed a limiting operation on the compound Poisson distribution by sending the shape parameter k to zero, and the number of species in the sample to infinity, and ended up with Fisher's 'log-series model'. If we instead let the shape parameter equal one, we arrive at MacArthur's 'broken stick model' (MacArthur, 1957), a model often applied due to its niche-partitioning interpretation. When k is not fixed, but allowed to run freely, we obtain the negative binomial model, (e.g. Pielou, 1975; Engen, 1978). I will here choose to denote it the gamma model, since it is the abundance distribution that is interesting not necessarily the compound sampling distribution. The gamma model can be extended to include values of the shape parameter between –1 and 0 (Engen, 1974), but then only the truncated distribution is well defined. In *figure 1*, I have illustrated the limitations caused by fitting the log-series or broken stick models to a real data set instead of applying the general gamma model (here with an estimated $k = 0.19$). The data set presented, Malayan butterflies (Corbet, 1941), was originally used by Fisher et al. (1943) to illustrate the fit of the log-series model.

Preston's (1948) approach was to fit the lognormal distribution to the species abundances instead of a gamma distribution,

$$f(x) = \frac{1}{\sqrt{2\pi}\,\sigma x} e^{-\frac{1}{2\sigma^2}(\ln x - \mu)^2}$$

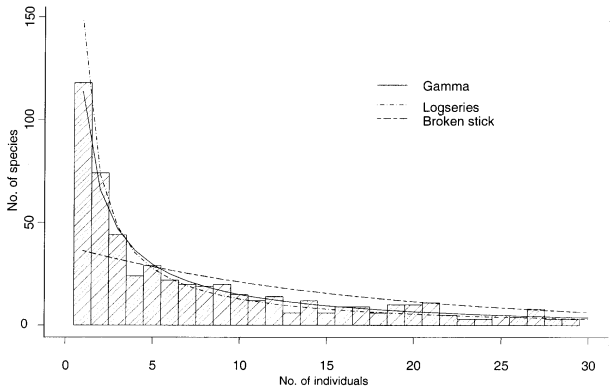


Figure 1. The gamma, log-series and broken stick models fitted to observations of Malayan butterflies (Corbet, 1941). The histogram is truncated at the right; Corbet observed in addition 96 species with counts in the range from 30 to 194.

a model that was later refined by Grundy (1951) and Bulmer (1974), leading to the truncated Poisson lognormal model.

In Diserud and Engen (2000), we have developed a general and dynamic class of species abundance models. Let the expected change in species abundance be modelled as $rx(1 - (x/K)^{\theta})$, that is, θ-logistic density regulation (May, 1981; Hanski, 1994; Sæther et al., 1996; Middleton and Nisbet, 1997) where r is the growth rate at low densities and K the community's carrying capacity defined as the level where the expected change equals 0. With an environmental variance acting simultaneously on all the individuals in the community, the quasi-stationary distribution corresponds to the gamma distribution for $\theta = 1$, and the lognormal distribution in the limit as θ approaches 0.

A complete insight into the pattern of species abundances can only be achieved by studying the full distribution, but in many circumstances it can be helpful to adopt a single summarising statistic, particularly when comparing different communities. Several authors have attempted to find this single index that characterise the whole species abundance distribution, with respect to diversity, evenness and dominance. Engen (1978) gives the relationship between the parameters in species abundance models and different indices of diversity. Diversity indices have traditionally been more appealing to researchers, conservationists and managers of natural resources due to their intuitive interpretation and ease of calculation, while applying species abundance models have been considered a more difficult task (Tokeshi, 1993). Since diversity indices are a one-dimensional description of community structure, we should not expect them to be more than measures of this specific dimension. If we want a more robust analysis, we should either apply several different indices or rely on a more complete description of the community. The diversity index must be able to distinguish between not too different communities, it is the more subtle changes for which we need to discover analytic tools. A diversity index' effectiveness will therefore depend on its ability to discriminate between the possible states of a community, and the precision with which it can be estimated from a sample (Kempton, 1979).

The community characteristic that has been given the most attention is the number of species. Bunge and Fitzpatrick (1993) have written a good and thorough review on existing estimation techniques. They found that the problem is quite resistant to statistical solution, no matter how large the sample is, there will still be a relatively large proportion of unobserved species. Besides species richness, other common diversity indices includes the Shannon index, Simpson's index and Hill's index (e.g. Magurran, 1988). An indication of the lack of information in many samples on the number of species S in the community is shown by the fact that the gamma and lognormal models, while often giving rather similar fits to the species abundance distribution, provide totally different estimates of S (Kempton, 1979). Indeed, when $k \leq 0$, the gamma model presumes an infinite pool of species. The use of this parameter also suffers from the difficulty of delimiting the community from which the sample is drawn, or even accepting that such a discrete community exists. As an illustration, the gamma, the lognormal and our generalised model are fitted to the Malayan butterfly data set (Corbet, 1941). All three models fit reasonably well, but they give radically different estimates of the number of unobserved species. The gamma model estimates that 621 species have not been sampled, the lognormal model estimates this number to be only 89, while our general model estimates 236 unobserved species.

2.2. Community limitation

Observed spatial differences in the value of the diversity index could be due to different community sizes or limitations. The natural, or defined, limitations of the two

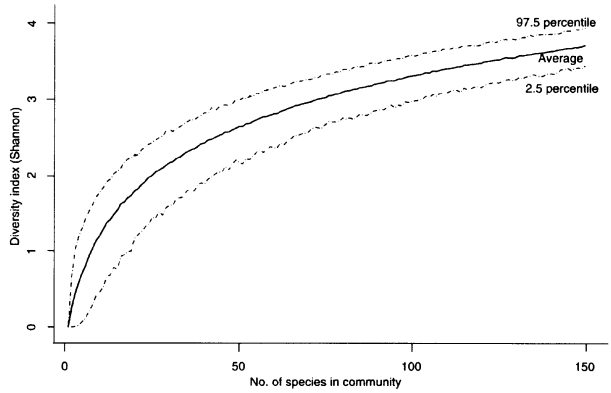


Figure 2. The dependency of the Shannon index on the number of species in the community. The community is described by a fixed lognormal species abundance model.

communities (spatial, temporal or taxonomical) may vary, so we would expect differences in the value of most diversity indices. A specific value of a diversity index may describe an optimal diversity in one community, whereas in another community of different 'size', this value may indicate a rather poor diversity. This is a great weakness when applying diversity indices; we do not always have a clear perception of what is a 'good' or a 'bad' value. In *figure 2*, I have simulated species abundances from a fixed lognormal model. The 'size' of the community is represented by the total number of species *S*. For each chosen value of *S*, I simulated 1 000 communities and calculated the mean and the 95 % confidence interval for the Shannon index. The degree of change will of course depend on choices of model, parameter values and diversity index (*figure 2* is to be regarded as an illustration).

2.3. Sampling effects

Biologists unfortunately often treat the sample as if it were the whole community, either by neglect or as a way to avoid the problems introduced by stochasticity and uncertainty due to sampling. Since censusing all individuals in a community usually is impossible or too expensive, random sampling is considered to be the best alternative; random in the sense that each individual, regardless of the species, has the same probability of being caught. This condition is in practice often hard to achieve, its efficiency depending on the taxonomic distance between species. More often the 'randomness' refers to for example the location sampled which does not necessarily lead to random sampling of individuals. Another possible cause for observational error is that the observer may be eager to sample rare species so that these becomes overrepresented in the sample. When species abundance distributions are fitted, it will then appear as if even more rare species are undiscovered. Uncertain species identification will also lead to sampling bias, since the individuals questioned often are removed from the sample rather than contributing to the rare species. Some authors also mix counts of individuals of species with counts only identified to genera (or a higher taxonomic level) in the same data set. Such mixtures, with possibly very dominant 'genera groups', may have a significant influence on the values of the diversity indices. In order to save time, money, or due to difficulties in identifying the species, some researchers want to perform the analysis of diversity entirely at a higher taxonomic level. Depending on the structure of the change, the same analysis performed on different taxonomic levels could yield radically different results. Diversity indices which handle mixed data sets, or data sets not identified down to species, have been developed (e.g. Warwick and Clarke, 1995), but they are sensitive to the more or less arbitrarily defined weights on the 'taxonomic distances'. Implicit in these indices is the view that species far from each other are valued more than 'close neighbours'. This approach will be in conflict with what I mentioned earlier regarding the taxonomical limitation of the community under study, that is, we are often only interested in studying related species with a potential for local interaction.

2.4. Two samples from the same community

When comparing two samples, we are often interested in whether the two samples are from the 'same' community, or more precisely, if they are sampled from the same species abundance distribution. Even when they are sampled from exactly the same distribution, we expect differences in species number and composition, especially if the sampling intensities are varied.

Assume first that the community structure is such that some species abundance model can describe it, and that the two samples are from the same model and independent. We further assume Poisson sampling; each individual has thereby an equal probability of being sampled, and we expect to sample a proportion ν of the total number of individuals. The sampling intensity may vary

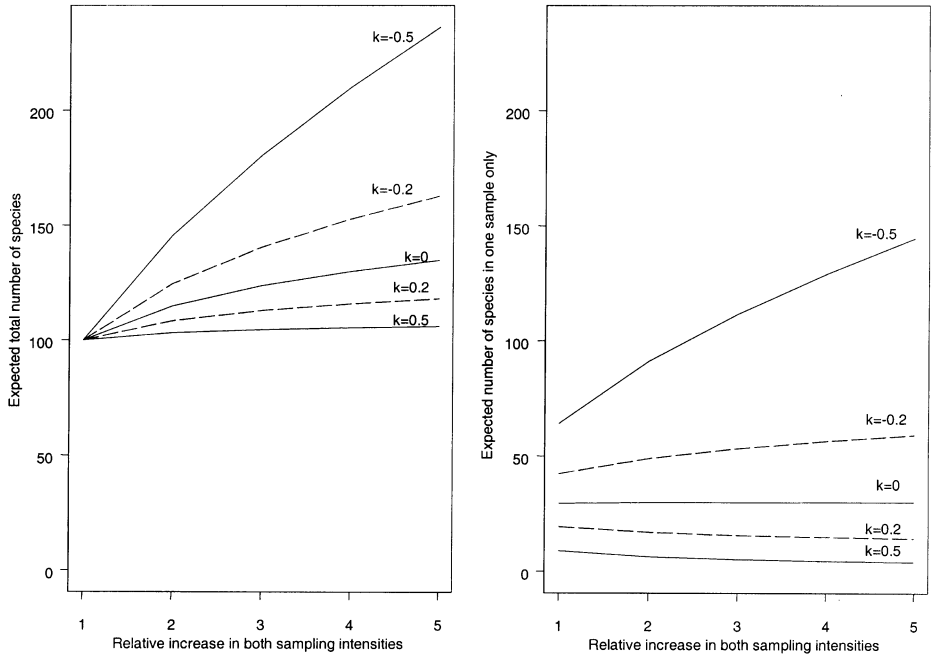


Figure 3. The effect of random sampling when the sampling intensities of the two samples are increased equally. All curves are scaled to start at 100, but the relationship is linear so the curves would have the same relative relationship regardless of initial value of the scale parameter. Note that the expected number of species in one sample only is constant in Fisher's log-series model ($k = 0$). (figure from Diserud, 1999).

between samples. Regardless of the species abundance model, the number of individuals of a species in the first sample, given the pooled count of this species in both samples, then becomes binomially distributed (Diserud, 1999) with probability

$$\pi = \frac{v_1}{v_1 + v_2}, v \in (0,1)$$

where v_1 and v_2 are the sampling intensities of the first and second sample respectively. If $v_1 = v_2$, then $\pi = 1/2$ as expected. This probability π can be estimated rather straightforwardly as $\hat{\pi} = n_1/(n_1 + n_2)$, where n_1 and n_2 are the total number of individuals in the first and second samples respectively. Note that this estimator may become a pitfall if the size of the samples do not reflect the effort put into the sampling. For example, if you know that the number of man-hours put into collecting the two samples differ significantly, but the sample-sizes come out equal, then the ratio between the number of man-hours spent may be a better estimator.

To illustrate the expected difference between two 'equal' samples, I have carried out a simulation from five related gamma models. The scale parameter in all models is fixed at the same value indicating a low sampling intensity (a small fraction of the community is sampled), while the shape parameter k is varied (values given in *figure 3*). Fisher's log-series model corresponds to $k = 0$, whereas insect communities often yield estimates of k around –0.2. The shape parameter of the gamma model is often used as a diversity index itself. Note then that an increase in k can indicate both a decrease in species richness and an increase in evenness.

If the sampling intensities are unequal, the expected difference between the samples will increase. A relevant question could then be: how large must the second sample be in order to observe almost all of the species from the first? For illustration sake, we still simulate from the same model, but now we keep the intensity of the first sample fixed, while the intensity of the second is increased (*figure 4*). We see that the probability of observing a species in the first sample only first reaches below say 0.05 when $v_2/v_1 = (10, 6, 4, 2, 1)$ for $k = (–0.5, –0.2, 0, 0.2, 0.5)$, respectively. For Fisher's log-series model, the second sample must thereby be more than four times as large as the first in order to observe at least 95 % of the species registered in the first sample.

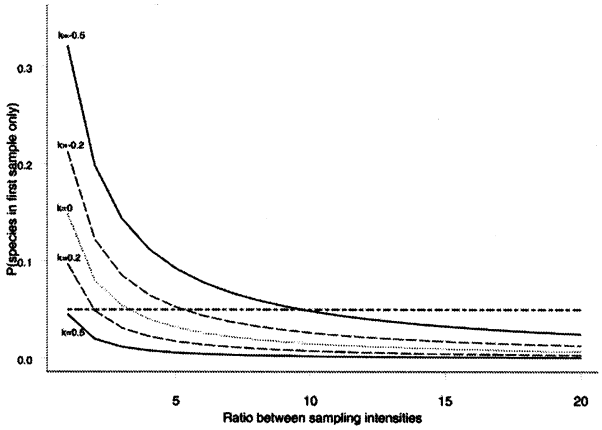


Figure 4. We have again chosen the same five values for *k*, and kept the scale parameter fixed in the gamma model, to show the effect an increase in the second sampling intensity ν_2 has on the probability of observing a species in the first sample only (figure from Diserud, 1999).

2.5. Temporal variability

One of the central problems in ecology is modelling the dynamics of animal populations. Population dynamics is the science of describing and understanding changes in populations over time, alternatively why they do not change but have reached some kind of equilibrium. The classical species abundance models are not dynamic, they just describe the composition of the community correctly at a given point in time. The parameters can be considered as characterisations of the environment, different environmental conditions giving models with different parameter values.

Populations are generally not stable, for some communities each year can be considered almost as a new situation, so we need to provide links between abundance models for the same community at different points in time. Accordingly, the variations can be modelled by assuming that the parameters of the models change stochastically from one year to the next. In conservation biology, it is of major interest to estimate the probabilities of for example reduction in species diversity or a threatened species' expected time of extinction. Both these characteristics are closely linked to the community's stability. The relation between a stable community (in equilibrium) and species diversity has long been a puzzle. Hutchinson (1961) stated that a lack of equilibrium could be an explanation of species diversity. Tilman (1996) has suggested that although diversity may stabilise community properties, it may also be associated with large fluctuation of individual species, so population variations in diverse natural communities may reflect strong connections between species (e.g. compensatory fluctuations due to competition), leading to dynamic and fragile systems (Hanski, 1997).

For a majority of the animal populations surveyed, the stochasticity seems to increase with the length of the study period (Pimm, 1991). Populations tend to vary relatively slightly at some level on short time scales. When the time scale is prolonged, this level itself varies, and even more than the short time variations. A possible explanation was suggested by Davis (1986) who found that climatic parameters also change through time, either in a directional way or as variations around several values rather than around a constant mean. Another possibility is that speciation or extinction may disturb a community's quasi-equilibrium, and induce stepwise changes like the ones observed. Regardless of explanation, this stochastic time dependence makes long time predictions very uncertain.

The understanding of the complex causality of population fluctuations has far-reaching applications in areas ranging from resource management to conservation biology (Dennis et al., 1995). One way to comprehend the observed fluctuations is to compare its pattern with that of a theoretical model. The usual line of attack is to start with a simple, basic model and as knowledge accumulates, it can be generalised and elaborated in order to obtain higher descriptive and predictive power. The next step is therefore to include the dynamic aspect in the stochastic abundance models, that is, modelling the fluctuations in species abundances due to variations in environmental conditions. The importance the environmental variance has on the populations is suggested by the relative fragility of juveniles of many organisms (Chesson, 1986). If an acceptable estimate of this natural variation in species abundance is established for a specific community, we would be able to predict the impact of human interference (habitat reduction, fragmentation or pollution) by performing theoretical calculations on how different external changes represented by changes in model parameters will affect the diversity of the community. The few dynamical approaches that exist have little practical value since they include only demographic stochasticity due to the individual variation in birth and death rates (e.g. Kendall, 1948). Recent research has shown that the stochastic variations in populations are

mainly due to fluctuations in the environment, and that demographic stochasticity is of little importance (Lande, 1993).

When our two samples are taken at different times in a fluctuating environment, we will therefore expect the differences between the values of the diversity indices to be even larger than that due to random sampling alone. My suggested solution is to model the dynamics by a diffusion process, and construct a test that detects if we have observations or differences more extreme than what we would expect under natural levels of environmental fluctuations. This approach is presented in detail in Diserud (1999). As test statistic, a diversity index will be an intuitive choice. Different communities respond differently to a stochastic environment; animal populations may show a rapid response to climatic change, whereas plant populations may respond more slowly. Temporal variability will be greater where critical environmental variables are themselves more variable (Pimm, 1991). Population parameters, especially the growth rate, can modify the variability, since they are able to negate the effect of fluctuating conditions.

A necessary first step is to identify the deterministic processes that are structuring the community. Deterministic growth equations for a species are often written as

$$\frac{\mathrm{d}\ln x}{\mathrm{d}t} = r - g(x)$$

where r is the specific growth rate at small densities, and $g(x)$ the density regulating term defined as an increasing function with $g(0) = 0$. Engen and Lande (1996a, 1996b) and others (e.g. Leigh, 1981; Goodman, 1987), replaced the constant r in the equation above by the process $r + \sigma_r(x)\mathrm{d}B(t)/\mathrm{d}t$, reflecting the temporal stochasticity in reproduction and mortality, and thereby obtained a realistic stochastic analogue to the deterministic growth equation. $B(t)$ is a standard Brownian motion with mean and variance equal to 0 and 1 respectively, so that $\mathrm{d}B(t)/\mathrm{d}t$ is the so-called white noise. The variance in r is usually written as

$$\sigma_r^2(x) = \sigma_d^2/x + \sigma_e^2$$

where σ_d^2 is the demographic variance, and σ_e^2 the environmental variance acting simultaneously on all individuals in the population (e.g. Engen and Sæther, 1998). Lande (1993) also included a term describing the effect of natural catastrophes that produce sudden major reductions in population size. Writing the variance like this is only correct in the case of no demographic covariance, that is, the variance due to interactions between individuals, such as intraspecific competition. Precise definitions of the concepts of demographic and environmental stochasticity have been given by Engen et al. (1998). This definition of the variability of species abundances is approximately in accordance with the argument that populations having identical sequences of growth rates should yield the same variance estimates, regardless of abundance (Gaston and McArdle, 1994). Authors adopting this approach usually assume that σ_d^2 and σ_e^2 are constants not depending on the population size, an assumption which in general is not true (Sæther et al., 1998). Note that a possible temporal or spatial autocorrelation in environmental stochasticity may have major impacts on population viability, but are often ignored due to difficulties in estimation (Lande et al., 1999). Positive temporal autocorrelation increases extinction risks, due to consecutive years with consistently low population growth rates.

Engen and Lande (1996a, 1996b) developed dynamic population models that were based on multivariate diffusion processes, assuming the species to be independent. This assumption can be relaxed to include interspecific density regulation and heterogeneity among species. Diffusion processes are stochastic processes that are continuous in state as well as time (Karlin and Taylor, 1981), but give fairly accurate approximations to discrete population processes (e.g. May, 1973; Turelli, 1977; Lande, 1993). Ignoring the demographic stochasticity, which has little effect on the abundance curve (Engen and Lande, 1996b), and applying the Ito-solution of the corresponding stochastic differential equation for the species abundances x (Karlin and Taylor, 1981), we find that the dynamics of the species abundances can be approximated by a diffusion process where the expected change is described by the infinitesimal mean

$$m(x) = rx - xg(x)$$

and the variance of the change in abundance per time unit is described by the infinitesimal variance

$$\sigma^2(x) = \sigma_e^2 x^2$$

For small populations, notice that the demographic variance can be the dominant form of stochasticity (Lande, 1998). Now assume that new species enter the community at times generated by a Poisson process with parameter ω (the speciation rate). The species abun

dances will then, at a given point in time, be realisations of an inhomogeneous Poisson process (Engen and Lande, 1996b) with the rate

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

The number of species with abundances in any interval $[a, b]$ is then Poisson distributed with parameter $\int_a^b \lambda(x)\,dx$.

In our general species abundance model (Diserud and Engen, 2000), we define the density regulating term $g(x)$ as $r(x/K)^\theta$, where r is the growth rate at low densities, K the community's carrying capacity defined by $m(K) = 0$, and θ a parameter that express the strength of the density regulation around K (e.g. May, 1981; Sæther et al., 1996; Middleton and Nisbet, 1997). It will be the value of θ that is crucial in determining the model; the limit $\theta = 0$ indicates that the species abundances follow the lognormal distribution (Engen and Lande, 1996b), whereas $\theta = 1$ corresponds to the gamma model (Engen and Lande, 1996a). Large values of θ give a strong density regulation above K, while smaller values of θ allow larger fluctuations around K. When it comes to estimation, we treat the species as being independent, and adopt the above class of models based on inhomogeneous Poisson processes. The expected number of species in the community is now given by $ES = \int_0^\infty \lambda(x)\,dx$ while the expected number of individuals becomes $EN = \int_0^\infty x\lambda(x)\,dx$. Note that both the expected number of species and individuals are proportional to the rate of speciation ω. We now have a model that, in addition to covering the classical abundance models as special cases at a given point in time, include dynamic characteristics such as speciation and environmental fluctuation.

By modelling and understanding the dynamics of a community in natural quasi-equilibrium, that is, not disturbed by human activities, we have the needed basic knowledge for developing methods to detect if an observation (a year's abundance) is more extreme that what our model would predict. In Diserud (1999), we illustrate the effect a fluctuating environment may have on a community, and the expected difference between two samples taken from the same location and same taxonomic scale, but at different times. We can also evaluate the probable effects of 'extra' changes in the environmental conditions by changing the corresponding model parameters and then simulate the population dynamics, since extinctions may often be caused by novel variation in the environment such as a deteriorating habitat quality (Hanski, 1994).

3. RESULTS

The method will be illustrated by a constructed example where the model will be kept as simple as possible in order to make the effects of a fluctuating environment more visible. Let us first assume that our simulated populations are large, so that the demographic variance can be ignored ($\sigma_d^2 = 0$). The environment is very variable and the populations respond rather quickly, so we may observe, under 'natural' conditions, that a population doubled or halved from one year to the next. Between the two sampling periods, the government increased our funding, enabling us to double the sampling effort ($v_1/v_2 = 1/2$). We can therefore not compare the samples, or the calculated diversity indices, directly. There exists several methods for manipulating the samples to 'equal sample sizes', but then you throw away a lot of valuable information, and risk falling in the same trap as mentioned previously; by forcing the samples to be of equal sizes, you may camouflage an actual change in diversity. In short, our null-model is now a diffusion process with infinitesimal mean $m(x) = 0$, indicating no deterministic trend, and infinitesimal variance $\sigma^2(x) = \sigma_e^2 x^2$. We thereby illustrate the expected difference between two samples due to sampling and environmental variance alone.

Let X_{i1} be the number of individuals of species No. i in the first sample, and m_i the total number of individuals of species i in both samples. I showed in Diserud (1999) that $X_{i1} \sim \text{Bin}(m_i, \pi_i)$ regardless of the underlying type of species abundance model, where π_i is the probability that an observed individual of species No. i will be in the first sample. Note that π_i can vary between species since the species may respond differently to the fluctuating environment. Let further x_{i1} and x_{i2} be the abundances of species i at the times of the first and second sample respectively, then

$$\pi_i = \frac{v_1 x_{i1}}{v_1 x_{i1} + v_2 x_{i2}} = \frac{v_1/v_2}{v_1/v_2 + x_{i2}/x_{i1}}$$

Note that we do not need to know the absolute values of the sampling intensities, only their relative ratio. What remains then is to model the relative change in abundance

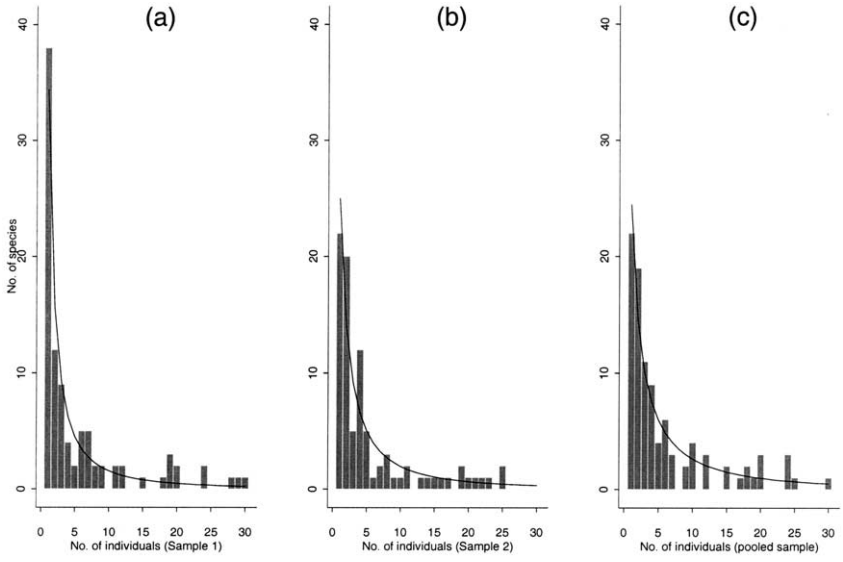


Figure 5. Histograms showing the species abundance distributions of (**a**) S1, (**b**) S2 and (**c**) the 'original' pooled sample respectively. The histograms are truncated at 30 in order to get a more readable figure. The additional observations in S1 were (52, 76, 77, 307, 349) and in S2 (31, 32, 32, 32, 37, 47, 51, 71, 85, 296, 351).

x_{i2}/x_{i1} as a function of σ_e^2. By transforming $y = \ln x$ and from general properties of the diffusion process, we get, as an approximation, $\Delta y_i = y_{i2} - y_{i1} \sim N(0,\ \sigma_e^2(t_2 - t_1))$, where t_1 and t_2 are the times of the first and second sample respectively (Diserud, 1999). If the species' responses to the environmental fluctuations are correlated, that is, they are not independent, we can write

$$\Delta y_i = \left(\rho U + \sqrt{1-\rho^2}\ V_i\right)\sigma_e \sqrt{t_2 - t_1}$$

where U and V_i are i.i.d. N(0,1), and ρ describes the correlation between species with regard to the effect of a fluctuating environment. U will here describe the common response, while V_i denotes the species-specific response.

I have chosen not to use a real pair of samples to illustrate my method, but rather two reference samples, S1 and S2, simulated from a null model of no unnatural change. This is done in order to show what effect random sampling and a naturally variable environment alone may have on the structure of the samples. In order to obtain good estimates of σ_e^2 and ρ we would need long-time series observations, they will here just be assumed as known. An illustration of the method's robustness with respect to uncertain estimates of σ_e^2 and ρ is given in Diserud (1999).

From a pooled sample **m** with 116 species, and a total of 2 935 individuals, I thereby simulated S1 and S2 with $\nu_1/\nu_2 = 1/2$, $\sigma_e^2 = 0.5$ (since $x_2/x_1 \sim 2 \Rightarrow \Delta y = \ln x_2 - \ln x_1 \sim \ln 2 \sim \sqrt{0.5}$) and $\rho = 0.5$. The 'seed' of my simulations, the pooled counts m for the 116 species, is a collection of Chironomidae-observations from the Norwegian river Rauma (Arnekleiv et al., 1997). The actual values are shown in *figure 5C*, but are of minor importance to my example. First, the number of individuals of species No. i in S1 was generated according to $X_{i1} \sim \text{Bin}(m_i, \pi_i)$, where $\pi_i = \dfrac{\nu_1/\nu_2}{\nu_1/\nu_2 + e^{\Delta y_i}}$. The number of individuals of species No. i in S2 is then merely $X_{i2} = m_i - X_{i1}$. In a fixed community ($\sigma_e^2 = 0$) with relatively low sampling intensities, we would expect $n_1 = 978$ and $n_2 = 1\,957$. What we 'observed' was 1 386 individuals distributed among 100 species in S1, and 1 549 individuals from 98 species in S2, so the effect of the fluctuating environment is obvious. If the environmental variance had been ignored, a tempting conclusion would be that there had been a reduction in diversity, based on the fact that we had doubled the sampling intensity and observed fewer species. The whole species abundance distributions for S1, S2 and the pooled sample are shown in *figure 5* with the general species abundance model (Diserud and Engen, 2000) fitted (solid line).

Let us continue by estimating ν_1/ν_2 straightforwardly as $n_1/n_2 \approx 0.9$, still assuming σ_e^2 and ρ to be known. When simulating 1 000 new pairs of samples from a model with these parameters, we would not see anything suspicious. The differences in the values of the three

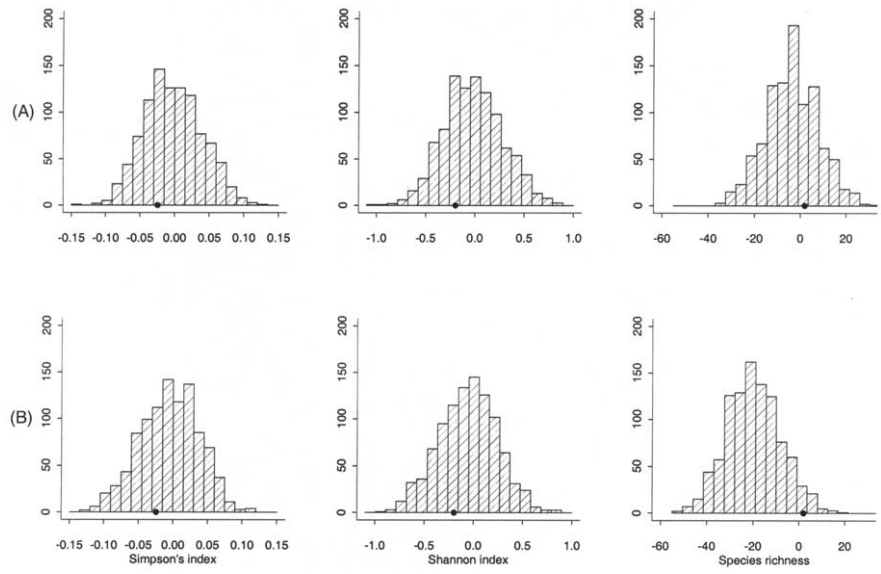


Figure 6. Histograms showing the difference in the calculated value of the diversity index between the pairwise simulated samples. The filled circle indicates our 'observed' difference. The upper row (**A**) shows the difference when ν_1/ν_2 is estimated by $n_1/n_2 \approx 0.9$, and the bottom row (**B**) when ν_1/ν_2 is estimated as 1/2.

most common diversity indices (Simpson, Shannon and species richness) between the simulated pairs are presented in the histograms of *figure 6A*. The difference in diversity between S1 and S2, indicated by the filled circle, are placed neatly in the centre of the simulated differences. Testing the null hypothesis of no unnatural reduction in diversity, with the alternative hypothesis being reduction in diversity, the Simpson's index give a *P*-value of 0.68, Shannon 0.71, and the species richness 0.30. If we instead use our information on the amount of effort (e.g. in man-hours) put into sampling S1 and S2, we estimate ν_1/ν_2 to be 1/2. The histograms in *figure 6B* present the results from these new 1 000 simulations, represented by the difference in the diversity indices. We see that the Simpson and Shannon indices are robust regarding the estimate of ν_1/ν_2, with *P*-values now equal to 0.67 and 0.68, respectively, whereas the species richness count now gives a *P*-value of 0.03, that is, below the typical significance level of 0.05.

The quick lesson to be learned from this simulation example is how much the value of some diversity indices may change under naturally fluctuating environmental conditions. The Simpson index may for example naturally change as much as $\pm$ 0.15 from one sample to the next under our choice of model. The Simpson and Shannon indices also behave well for poor estimates for the ratio between the sampling intensities, while analysis based solely on the species count may be far from the 'right' conclusion.

4. CONCLUSION

Biodiversity is now often considered a human resource, our 'insurance policy' (e.g. Stork, 1993). Amongst ecologists there is a disagreement on the role of diversity in ecosystem functioning. Some consider all species essential and important, while others believe that many species, with the exception of some key species, could be lost without much damage to the ecosystem. It is nevertheless important to know the number of species and how their distributions are changing, since diversity is under continuous threat as more natural ecosystems are polluted, destroyed or affected by climate change. I believe that our methods may help to map to what scale biodiversity will be altered by these environmental changes.

Models will always be simplifications of the investigated system, ignoring several variables that may be important, but the models will hopefully give new insight and understanding of the real world. The quality we realistically can expect from a data set is seldom so good that a more complex model will give any significant improvement regarding estimation and prediction. The variables in dynamical abundance models are by nature stochastic (Engen and Sæther, 1998), so no model can correctly predict the dynamical changes in species abundance but rather present a prediction with intrinsic uncertainty, even if all the parameters are known. The parameters in the model can in general not be considered as constants, but rather as variables in both time and space. This renders it

difficult, or unrealistic, to generalise, so we should expect differences in organising forces rather than any single globally dominant factor. This stochasticity, together with the statistical uncertainties due to sampling, can not be ignored when developing methods for prediction. Even so, if the application of stochastic models is to be successful, we are strongly dependent on the availability of good long-term data sets from a variety of communities.

The diversity indices applied as test statistics in this paper are just simple examples, the method is by no means limited to, or dependent on, these indices. They inevitably throw away a lot of information since they are invariant under permutation of the species in the samples. Better and more sensitive results could be obtained by applying more advanced diversity indices, such as the entropy or the G.S. index by corresponding Rao's diversity indices (Rao, 1982; Nayak, 1986).

We have so far assumed that independent diffusion processes with equal parameters give all the species' dynamics, an assumption that may often be erroneous. The models can in that case be further elaborated (Engen and Lande, 1996a, 1996b). Let Φ be the vector of parameters of the diffusion, and $\lambda(x; \Phi)$ the corresponding abundance model. If the parameters Φ for each new species are drawn from a distribution $f(\Phi)$, the abundances in the community would still be given by an inhomogeneous Poisson-process with a rate that is a mixture of the rates of each species with regard to $f(\Phi)$, that is,

$$\lambda(x) = \int \lambda(x; \Phi)\, f(\Phi)\, \mathrm{d}\Phi$$

The growth rate r could for instance vary between the species. If we assume that $r_i \sim \mathrm{N}(r, \delta^2)$, where i denotes the species number, we can now test if δ^2 is zero or positive, that is, if the growth rates are equal or if at least one r_i differs from the others. We can also include interspecific density regulation in addition to the intraspecific one. The complexity of the model would then increase since the species diffusion processes are no longer independent. If this effect were assumed equal for all individuals in the community, the distribution of the relative abundances in the lognormal model would not be changed even if the distribution of the absolute abundances would. In practice, this model still gives observations fitting the lognormal model (Engen and Lande, 1996b). The same result can be approximated for the gamma model when the number of species is large (Engen and Lande, 1996a).

Evolutionary ecology will therefore necessarily be characterised by mixtures of pattern and uncertainty. Even when patterns and trends can be extracted from the data, predictions will need to be probabilistic statements. Environmental decisions therefore need to be made with full recognition of the limitations posed by the stochastic terms of the models, the assumptions needed and the scale dependency of the sampled data.

Acknowledgements

I would like to thank Steinar Engen and Kaare Aagaard for discussions and valuable advice.

REFERENCES

Arnekleiv, J.V., Dolmen, D., Aagaard, K., Bongard, T., Hanssen, O., 1997. Rotenonbehandlingens effekt på bunndyr i Rauma- og Hensvassdraget, Møre og Romsdal. Zoologisk serie 1997-8, Vitenskapsmuseet, Norwegian University of Science and Technology.

Beck, M.W., 1997. Inference and generality in ecology: Current problems and an experimental solution. Oikos 78, 265–273.

Bulmer, M.G., 1974. On fitting the Poisson log-normal distribution to species abundance data. Biometrics 30, 101–110.

Bunge, J., Fitzpatrick, M., 1993. Estimating the number of species. J. Am. Stat. Assoc. 88, 364–373.

Caughley, G., 1994. Directions in conservation biology. J. Anim. Ecol. 63, 215–244.

Chesson, P.L., 1986. Environmental variation and the coexistence of species. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper & Row, New York, pp. 240–256.

Claridge, M.F., 1987. Insect assemblages - diversity, organization, and evolution. In: Gee, J.H.R., Giller, P.S. (Eds.), Organization of Communities: Past and Present. Blackwell, Oxford, pp. 141–162.

Corbet, A.S., 1941. The distribution of butterflies in the Malayan Peninsula. Proc. R. Entomol. Soc. Lond. (A) 16, 101–116.

Davis, M.B., 1986. Climatic instability, time lags, and community disequilibrium. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper & Row, New York, pp. 269–284.

Dennis, B., Desharnais, R.A., Cushing, J.M., Costantino, R.F., 1995. Nonlinear demographic dynamics: Mathematical models, statistical methods and biological experiments. Ecol. Monogr. 65, 261–281.

Diserud, O.H., 1999. The analysis of Community Structure – Stochastic Models, Estimation and Simulation, Ph.D. thesis, NTNU. Norwegian University of Science and Technology, Trondheim, Norway.

Diserud, O.H., Engen, S., 2000. A general and dynamic species abundance model, embracing the lognormal and the gamma models. Am. Nat. 155, 497–511.

Engen, S., 1974. On species frequency models. Biometrika 61, 263–270.

Engen, S., 1978. Stochastic Abundance Models. Chapman & Hall, London.

Engen, S., Lande, R., 1996. Population dynamic models generating species abundance distributions of the gamma type. J. Theor. Biol. 178, 325–331.

Engen, S., Lande, R., 1996. Population dynamic models generating the lognormal species abundance distribution. Math. Biosci. 132, 169–183.

Engen, S., Sæther, B.E., 1998. Stochastic population models: Some concepts, definitions and results. Oikos 83, 345–352.

Engen, S., Bakke, Ø., Islam, A., 1998. Demographic and environmental stochasticity - concepts and definitions. Biometrics 54, 840–846.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample from an animal population. J. Anim. Ecol. 12, 42–58.

Gaston, K.J., McArdle, B.H., 1994. The temporal variability of animal abundances: measures, methods and patterns. Phil. Trans. R. Soc. Lond. Ser. B 345, 335–358.

Goodman, D., 1987. The demography of chance extinction. In: Soule, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 11–34.

Grundy, R.M., 1951. The expected frequencies in a sample of an animal population in which the abundances are lognormally distributed. Biometrika 38, 427–434.

Hall, C.A.S., 1988. An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. Ecol. Model. 43, 5–31.

Hanski, I., 1994. Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. Biol. Conserv. 68, 167–180.

Hanski, I., 1997. Be diverse, be predictable. Nature 390, 440–441.

Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145.

Karlin, S., Taylor, H.M., 1981. A Second Course in Stochastic Processes. Academic Press, New York.

Kempton, R.A., 1979. The structure of species abundance and measurement of diversity. Biometrics 35, 307–321.

Kendall, M.G., 1948. On some modes of population growth leading to R.A. Fisher's logarithmic series distribution. Biometrika 35, 6–15.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nat. 142, 911–927.

Lande, R., 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. Oikos 83, 353–358.

Lande, R., Engen, S., Sæther, B.E., 1999. Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. Am. Nat. 154, 271–281.

Leigh, E.G., 1981. The average lifetime of a population in a varying environment. J. Theor. Biol. 90, 213–239.

MacArthur, R.H., 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. Washington 43, 293–295.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Chapman & Hall, London.

May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ.

May, R.M., 1981. Theoretical Ecology, Principles and Applications. Blackwell, Oxford.

Middleton, D.A.J., Nisbet, R.M., 1997. Population persistence time: Estimates, models, and mechanisms. Ecol. Appl. 7, 107–117.

Nayak, T.K., 1986. An analysis of diversity using Rao's quadratic entropy. Sankhya Series B 48, 315–330.

Pielou, E.C., 1975. Ecological Diversity. Wiley, New York.

Pimm, S.L., 1991. The Balance of Nature? Ecological Issues in the Conservation of Species and Communities. The University of Chicago Press, Chicago.

Preston, F.W., 1948. The commonness and rarity of species. Ecology 29, 254–283.

Rao, C.R., 1982. Diversity: its measurement, decomposition, apportionment and analysis. Sankhya Series A 44, 1–22.

Roughgarden, J., Diamond, J., 1986. Overview: The role of species interactions in community ecology. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper & Row, New York, pp. 333–343.

Sæther, B.E., Engen, S., Lande, R., 1996. Density-dependence and optimal harvesting of fluctuating populations. Oikos 76, 40–46.

Sæther, B.E., Engen, S., Islam, A., McCleery, R., Perrins, C., 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. Am. Nat. 151, 441–450.

Solow, A.R., 1998. On fitting a population model in the presence of observation error. Ecology 79, 1463–1466.

Southwood, T.R.E., 1987. The concept and nature of the community. In: Gee, J.H.R., Giller, P.S. (Eds.), Organization of Communities: Past and Present. Blackwell, Oxford, pp. 3–27.

Stork, N.E., 1993. How many species are there? Biodivers. Conserv. 2, 215–232.

Strong, D.R., 1984. Natural variability and the manifold mechanisms of ecological communities. In: Salt, G.W. (Ed.), Ecology and Evolutionary Biology. The University of Chicago Press, Chicago, pp. 56–80.

Tilman, D., 1996. Biodiversity: Population versus ecosystem stability. Ecology 77, 350–363.

Tokeshi, M., 1993. Species abundance patterns and community structure. In: Begon, M. (Ed.), Advances in Ecological Research, vol. 24. Academic Press, London, pp. 111–186.

Turelli, M., 1977. Random environments and stochastic calculus. Theor. Pop. Biol. 12, 140–178.

Warwick, R.M., Clarke, K.R., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Progr. Ser. 129, 301–305.