

## *Taylor's power law and the measurement of variation in the size of populations in space and time*

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**Summary.** The problems of the measurement of variation and the selection of appropriate spatial and temporal units of observation are discussed. Besides theoretical considerations, the performance of variability measures in data on annual catches of noctuid moths was assessed.

Any measure of variability is potentially biased by its dependence on mean population size. The crucial role of dependence of variance on the mean is indicated. Taylor's power law is not a good model when the population mean is low. The potential bias is large when the population mean is small; in real data, the dependence of  $SD[\log(N+1)]$ , CV and Lloyd's index was weak when the mean annual catch was greater than 5 individuals. Lloyd's index was the least dependent on the mean. There is no single appropriate spatial or temporal scale for the analysis of variability. Specific scales are appropriate to specific questions. Multiple scale pattern analyses of time series and transects or grids are informative.

Many ecological theories include hypotheses about the relation of population variability in space and time to the life history traits of species or the successional age of communities (e.g. MacArthur and Wilson 1967, Pianka 1970, Whittaker and Goodman 1979). McArdle et al. (1990) and McArdle and Gaston (1992) have shown that many studies could be seriously biased by difficulties in measuring this variability. Their arguments are based on the assumption that SD of  $\log(N)$  is the appropriate measure of population variability. According to them, measure is unbiased, when it is a good substitute for SD of  $\log(N)$ .

More particularly, these authors have shown that the most commonly used measure of temporal variability, SD of  $\log(N+1)$ , is seriously biased, and that the bias is especially strong when the population mean is less than 50 individuals. They recommend the general use of the coefficient of variation (CV), which is a good substitute for SD of  $\log(N)$ : "The problem of the +1 bias can be

easily overcome by recourse to an alternative measure of variability, namely CV using untransformed data" (McArdle et al. 1990). Conversely, use of SD of  $\log(N+1)$  should be avoided, because "... even in situations where the true variability of the system actually decreases, SD  $\log(N+1)$  can show positive correlation [with the mean]" (McArdle and Gaston 1992). However, what is the "true variability" of the system? I do not know a better answer than that it depends on our definition.

Some features and difficulties are common for measuring variation in population size in both space and time. Description of spatial variability has been the work mainly of plant ecologists (see Greigh Smith 1952, Kershaw 1973a), while variation in time is more the concern of animal ecologists (e.g. Taylor 1961). This is not to say that plant ecologists do not take changes in time into account (they do, but pay attention mainly to directional changes), or that zoologists do not consider spatial variability (they do, but usually not with methods developed by plant ecologists). In fact, many of the problems of analyzing variation in time series in zoological data discussed by McArdle et al. (1990) are analogical to those solved by Pielou (1969, ch. 8) and Hill (1973), analyzing variation in space in botanical data.

The main problems of measuring variability in space and time are:

1. How to quantify variation when the mean and variance of the population (measured over either space or time) are not independent. There is no simple and general method of standardizing variance.
2. Selection of the size of the spatial and/or temporal unit.

The aim of this paper is to review some methods used for measuring temporal and spatial variability and their relationship to Taylor's power law, and to provide recommendations for empirical studies. Besides theoretical considerations, I analyze the performance of selected variability measures using yearly light trap catches of noctuid moths. Finally, I show that a combination of methods used in plant and animal ecology can help to resolve the problem of measuring spatial and temporal variability on various scales.

## Dependence of variation in population size on the mean

In this section, the problem of the dependence of various variability measures on the mean is discussed. The problems of selecting the size of spatial and temporal units, and of using information about the spatial and temporal relationships of these units, are discussed in the next section.

### Current methods

Many different indices are used to measure variation in population size. Those used for variation in time are reviewed by McArdle et al. (1990); the two measures used most often are (1) variance or standard deviation (SD) of log (or log(N+1)) transformed data and the measures derived from SD of log(N), and (2) coefficient of variation (CV). It should be noted that most data sets on the abundance of species contain zeros and, consequently, the log(N+1) transformation is used. If ecologists speak about log-transformed data, they often mean the log(N+1) transformation (although the difference between results based on log(N) and log(N+1) transformed data is often spectacular). Most other coefficients could be expressed using one of the above (e.g. Stability index of Wolda 1983).

The common measures used to describe spatial variability are discussed in many textbooks and papers, as indices of clumping, or of aggregation, or intensity of spatial pattern (e.g. Pielou 1969, Kershaw 1973b, Hill 1973, Ludwig and Reynolds 1988). Those more often used are the variance:mean ratio ( $s^2/\bar{x}$ ) and Lloyd's index of patchiness (Lloyd 1967) (i.e.  $L = 1 + (s^2 - \bar{x})/\bar{x}^2$ ), see Pielou (1969). Lloyd's index is equivalent to the Hill's intensity of spatial pattern (Hill 1973) and moment estimate of negative binomial  $k$ .

Another index of aggregation is that of Green (1966). It is defined as

$$G = \frac{s^2/\bar{x} - 1}{n - 1},$$

where  $n$  is the total number of individuals in the sample (sum of individuals in all the sampling units). This index

is highly recommended by Ludwig and Reynolds (1988: 29). Unfortunately, samples from the same population with differing numbers of sampling units will yield different values for the index ( $s^2$  and  $\bar{x}$  do not change systematically with an increase in the number of sampling units, while  $n$  increases steadily); consequently, this index should not be used.

In both spatial and temporal variability, the fit of the data to some distribution (usually Poisson, negative binomial or Neyman A), and the values of fitted parameters describe variability. Note that the negative binomial and Neyman distributions are generalized Poisson distributions, and consequently should by definition fit the data at least as well as the Poisson distribution (if a good method is used for distribution fitting), without suggesting 'a tendency toward some aggregation' (as in Ludwig and Reynolds 1988).

Plant ecologists measuring spatial variability usually agree that variance can be standardized (by the mean) in various ways, none of which can be preferred a priori (see Pielou 1969). Most often, the standardization assumes random thinning (i.e., a process where each individual has the same probability of dying) as a yardstick neutral process. In this case the relationship between variance and mean is

$$s^2 = c \cdot \bar{x}^2 + \bar{x}, \quad (1)$$

where  $c$  is a parameter determined by the initial conditions. Similarly, this variance-mean relationship could be derived for variations in time (e.g. Routledge and Swartz 1991). Taking Eq. 1 as a yardstick, Lloyd's index and the reciprocal of  $k$  are independent of the mean, the variance:mean ratio has a highly positive correlation to the mean, CV and SD of log(N) are negatively correlated, and the relation of SD of log(N+1) with the mean is humped (rapid increase and then very slow decrease). Standardization based on Eq. 1 has some advantages (see Hill 1973) which are usually considered useful but not necessarily the only ones possible. Similarly, Bliss (1971) concluded that "When comparing negative binomial distributions of the same species, some ecological series could be fitted with a common  $k$ , but in others,  $1/k$  decreases inversely as the  $\sqrt{\text{mean}}$ ". Nevertheless, the variance:mean ratio has a marked dependence on the mean under any feasible assumption and, consequently, is not useful for comparative studies. I will therefore consider further only CV, SD of log(N+1) and Lloyd's index.

Evaluating the variability of animal populations over time, Taylor (1961) has shown that the relationship between variance and mean can be expressed by the power relationship ("Taylor's power law"), i.e.  $s^2 = a\bar{x}^b$ , where  $s^2$  and  $\bar{x}$  are variance and mean, respectively, and  $a$  and  $b$  are parameters. The relationship is usually determined by fitting a linear function to log-log transformed data. (The statistical analysis is further complicated by the fact that neither variable is error-free. In

this paper, I have used the ordinary least square regression, which differs somewhat from geometric mean regression, though not enough to influence conclusions.) The power function was developed to describe the relationship of variance and the mean for populations of the same species in time and in space (Taylor et al. 1978, 1980), but may be applied just as well to the relationship between variance and the mean of various species in space (Chalupský and Lepš 1985) and in time (Kempton and Taylor 1979). One of the reasons for the use of SD of  $\log(N)$  is that it is independent of the mean, when Taylor's power law applies and the  $b$  value equals 2. Nevertheless, the performance of Taylor's power law at low mean population densities is strange. With a decrease in the mean (particularly when  $\bar{x} < 1$ ), the predicted value of variance becomes lower not only than the mean, indicating some degree of regularity, but also lower than the theoretical minimum (where each sampling unit either contains one individual or is empty). Consequently, Taylor's power law is not a good model for populations with low densities. (See Routledge and Swartz 1991 for precise formulas and further references.)

If Taylor's power law with  $b=2$  holds, SD of  $\log(N+1)$  is positively correlated with the mean (pronounced for all populations with  $\bar{x} < 50$ ), the CV and SD of  $\log(N)$  are independent of the mean (McArdle et al. 1990), and Lloyd's index increases slightly with the mean (at high mean values it converges to  $1 + CV^2$ ). As there are some sampling problems with the coefficient of variation, SD of  $\log(N)$  is often considered the best theoretical measure, but its applicability is constrained by the presence of zeros. (The problem of zeros is further complicated by the existence of 'true' and 'apparent' zeros. In a sample from a community, that is, not a census – a zero could indicate either low population density or complete absence.) Nevertheless, SD of  $\log(N)$  and CV are independent of the mean if, and only if, Taylor's power law holds and  $b=2$ , which need not be the case. (Consequently, taking the SD of  $\log(N)$  as a yardstick produces the same results as would evaluating the measures on the assumption that Taylor's power law with  $b=2$  holds.) At low population densities, SD of  $\log(N)$  is not applicable because of zeroes, and CV is expected to be positively biased because the variance must be higher than that predicted by Taylor's power law. Indeed, if  $\bar{x} < 1$ , then  $CV \geq \sqrt{(1-\bar{x})/\bar{x}}$  (derived by simple bookkeeping from formulas in Routledge and Swartz 1991). For example, for  $\bar{x} < 0.5$ , CV has to be greater than one (which is more than the majority of species exhibits in Spitzer and Lepš 1988).

Recently, Yamamura (1990) constructed a model that gives rise to the power curve relationship between mean and variance by splitting colonies with increasing numbers of individuals in each colony. Models leading to other functional forms of dependence could also be constructed. It should be noted that the power curve is used in biology for various purposes, e.g. to relate the

number of species to the area or the size of various parts of a body in allometric relations (Gould 1971, 1979). The frequent use of the power function probably reflects the ability of a log-log transformation to linearize monotonous relationships without inflection. Thus the power curve is not specific to the relationship of variance and mean. In the relationship of variance and mean, the value of  $b$  changes from case to case; even though  $b$  often equals 2, it need not be necessarily so. The simplest way to construct a set of samples that conform to the power law with  $b=2$  is to take one sample and generate the others by simply multiplying all the values of the original sample by a constant, i.e. with each new sample having its own constant (it could be interpreted as density independent changes in population size). All samples will have the same CV, and SD of  $\log(N)$ , and will conform exactly  $s^2 = a \cdot \bar{x}^2$ . From this point of view, there is the same amount of variation in series 1, 2, 4, 1 as in series 10, 20, 40, 10, as follows from the use of CV and SD of  $\log(N)$ . Taking into account the stochastic nature of the process (due to the integer nature of the counts, the change from 1 to 2 is the smallest possible change, whereas that from 10 to 20 is not), the first series is more likely to appear simply as a chance event than the second series (as follows from using Lloyd's index). Clearly, what is the null model of variance mean relationship and which measure of aggregation is independent of the mean depends on our definition of the neutral process. Correspondingly, if counts are converted to densities (as in Thomas 1991), CV and SD of  $\log(N)$  do not change, while Lloyd's index and SD of  $\log(N+1)$  do change.

It should be noted that the power curve fits well the relationship between variance and mean in the course of random thinning (Eq. 1). The value of  $b$  is between 1 and 2, close to 1 when  $c$  is small and values of  $\bar{x}$  are also small, and close to 2 in the reverse case. For example, if we take  $c=2$  in Eq. 1 and fit the relationship for all  $\bar{x}$  from 1 to 100 in steps of 1 by linear regression after the log-log transformation, we get  $b=1.92$ , with a very high correlation coefficient  $r=0.9996$ . (The fact that the value of  $b$  is close to 2 and that the correlation is high suggests that, for reasonably abundant species, the difference in results obtained using CV and Lloyd's index should be small.) If we fit the same relationship for all  $\bar{x}$  between 0.1 and 4, in steps of 0.1, then  $b=1.48$  ( $r=0.9968$ ). The fact that it is difficult to distinguish regression by the power curve from polynomial regression was noted by Taylor (1971).

Those considerations suggest that CV should be negatively, and SD of  $\log(N+1)$  positively, correlated with the mean at low values of the mean.

### Analysis of light trap data

The dependence of variability measures on the mean was analyzed within two extended data sets used by

Table 1. The correlation ( $r$ ) of variability measures with the mean annual catch, mutual correlations of variability measures, and estimate of  $b$  in Taylor's power curve, as depend on the threshold (i.e. the minimum mean annual catch included in the analysis). no. sp. – number of species in the analysis,  $\bar{x}$  – mean annual catch, cv – coefficient of variation, sdl – standard deviation of  $\log(N+1)$  transformed data, Ll – Lloyd's index of patchiness.

Threshold	no. sp.	$r(\bar{x}, cv)$	$r(\bar{x}, sdl)$	$r(\bar{x}, Ll)$	$r(cv, sdl)$	$r(cv, Ll)$	$r(sdl, Ll)$	$b$
Ruderal site								
no	216	-0.752	0.837	0.108	-0.618	0.178	0.265	1.638
1	138	-0.367	0.466	-0.137	0.195	0.925	0.246	1.799
3	99	-0.273	0.149	-0.108	0.531	0.968	0.530	1.827
5	78	-0.220	0.005	-0.096	0.597	0.974	0.556	1.839
10	57	-0.091	-0.092	0.009	0.682	0.973	0.610	1.899
20	35	0.047	-0.059	0.096	0.711	0.976	0.614	2.007
Forest site								
no	174	-0.757	0.571	0.323	-0.290	-0.008	0.672	1.564
1	123	-0.404	0.084	-0.161	0.613	0.931	0.620	1.710
3	90	-0.234	-0.052	-0.107	0.800	0.960	0.731	1.799
5	77	-0.181	-0.073	-0.111	0.823	0.968	0.733	1.840
10	52	-0.288	-0.241	-0.228	0.824	0.969	0.732	1.713
20	31	-0.346	-0.346	-0.287	0.881	0.976	0.844	1.648

Rejmánek and Spitzer (1982) and Spitzer and Lepš (1988). Detailed site descriptions are given by the authors: one site was a mixture of agroecosystems and ruderals and will be referred to as ruderal; the other was a natural alder forest, referred to as 'forest'. Both the localities are close to České Budějovice, South Bohemia, Czech Republic. The ruderal data set consists of a 22-year series of annual light trap catches of 216 noctuid moth species, and the forest data set, of 8 yearly catches of 174 species. The dependency of the variance on the mean, the correlation coefficients of CV, of SD of log

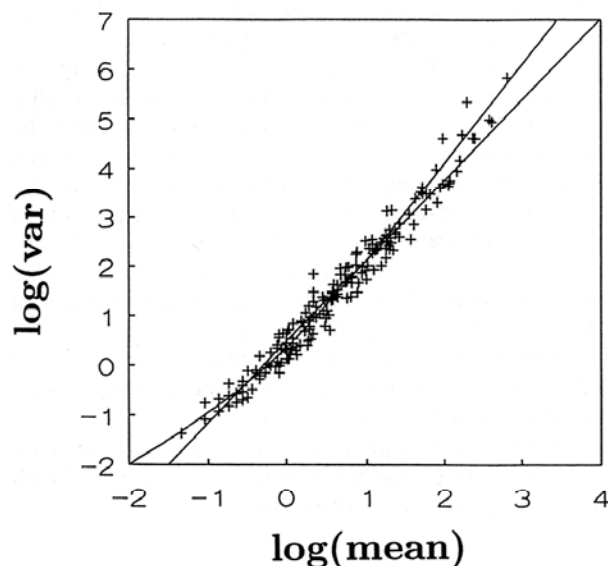


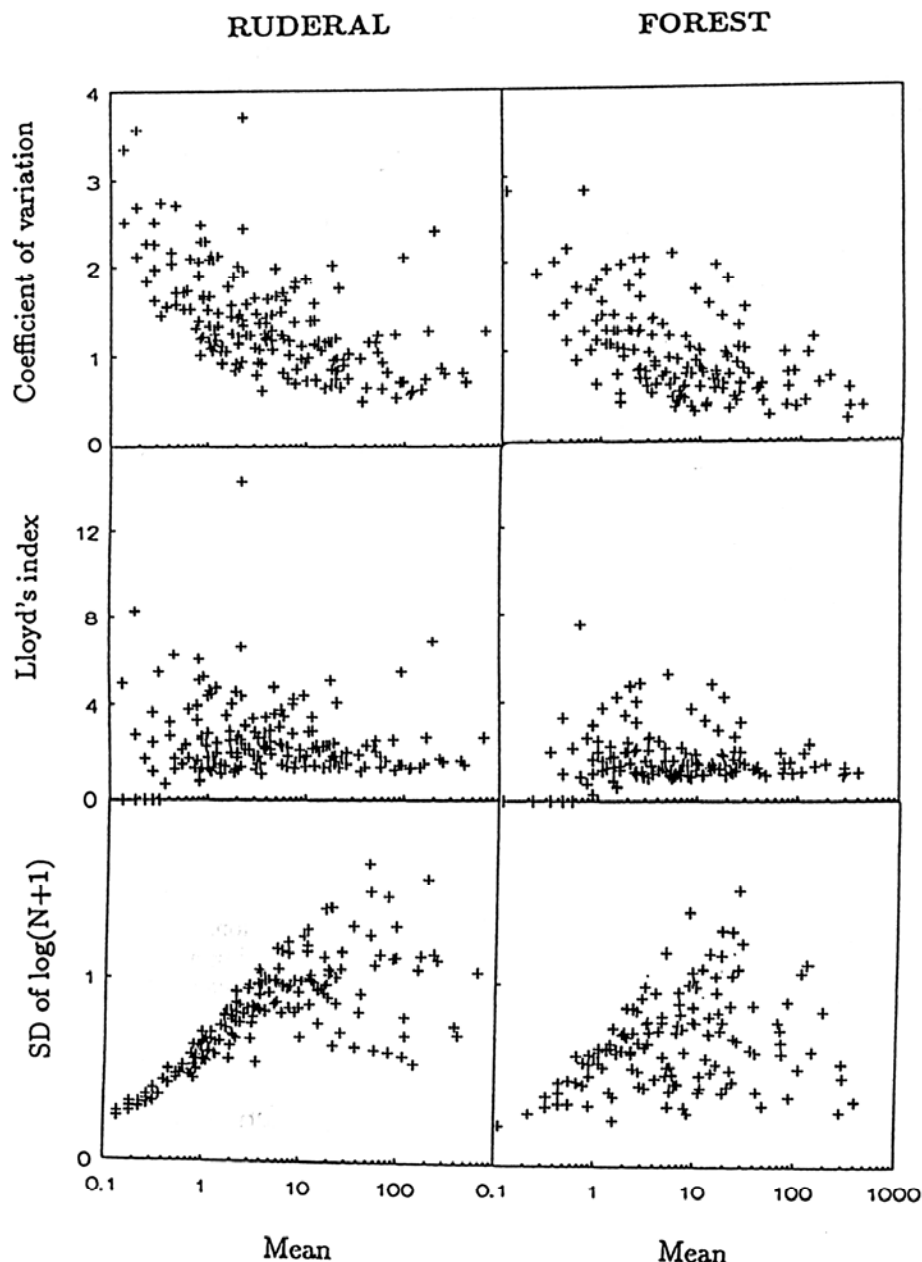
Fig. 1. The relationship between mean annual catch and variance in the ruderal site. The straight line corresponds to fitted Taylor's power law, the curve to the Eq. (1) corresponding to the random dying.

( $N+1$ ) and of the Lloyd's index ( $L$ ) with the logarithm of the mean, as well as the correlation coefficients among various measures of variability, were calculated. In both data sets, the analysis of the entire data set was then repeated for species which exceeded some threshold average annual catch (see Table 1).

Taylor's power law fits well the ruderal data set, with  $b = 1.638$  and  $r = 0.985$ . Nevertheless, increasing the threshold increases  $b$ , which reaches a value of 2 for species with a mean annual catch over 20. This suggests that the relationship is not perfectly linearized by a log-log transformation (Fig. 1). In particular, species with a low mean annual catch had higher variance than was predicted by the relationship derived for species with higher means. (A similar situation hold for the data of Chalupský and Lepš 1985, Fig. 3., on spatial variability of enchytraeids in soil.) This corresponds to the theoretical consideration that, at low means, Taylor's power law underestimates variance. Equation 1 fits better, although there only one parameter is estimated, compared to the two parameters of Taylor's power law. Likewise, the relationship for the forest site is not perfectly linearized by log-log transformation, and the values of variance for the least abundant species are higher than are predicted by the power law. As in the ruderal site, the estimate of  $b$  in the power law depends on the threshold value. The value of  $b$  is lower in the forest than in the ruderal site, and reaches its maximum when the threshold is 5, decreasing with further increase in the threshold; in all subsets except that with threshold 5, the  $b$  values are significantly lower than 2 ( $P < 0.05$ ). (Note that the multiple inference is made for various subsets of the same data set, and thus the probability of Type I error is 0.05 for each particular test.)

Comparison of the two data sets (Fig. 2, Table 1) shows several striking features. At low population

Fig. 2. The relationship between mean annual catch and measures of population variability in the ruderal and forest sites. Species with mean annual catch < 0.1 (five species in the ruderal site) are not displayed.



means, CV is much higher than in the rest of the set, and is negatively correlated with the mean and SD of  $\log(N+1)$  is much lower and is positively correlated with the mean. Consequently, there is a strong negative correlation between SD of  $\log(N+1)$  and CV within the whole data set. These phenomena accordingly appear in both data sets, and were predicted by theoretical analysis as inherent features of the variability measures. Consequently, there is no specifically biological mechanism to be explained behind this increase/decrease. McArdle and Gaston (1992), discussing the problem of variability and rarity concluded: "Thus, when the same study shows that variability, measured as SD  $\log(N+1)$  in-

creases with the mean but when measured as CV it decreases with the mean we have no hesitation in saying that the CV is more likely to be correct." On the contrary, my conclusion is that both trends could easily be spurious correlations. Lloyd's index does not show any such bias. Excluding very rare species, all the measures examined are reasonably well-correlated, and probably express similar features of variation in both data sets.

In the ruderal habitat, the dependence of variability on the mean is negligible when rare species are excluded. On the contrary, in the forest a slight but significant decrease of variability with an increasing mean is demonstrated for common species by all three indices

(the higher threshold, the closer the correlation). The difference between the ruderal and the forest site data sets corresponds to the difference in  $b$  values of variance-mean relationship, and probably results from the difference in life history strategies of the species abundant in these two sites (Spitzer and Lepš 1988). On the ruderal site, the mean annual catch is positively correlated with the population growth rate (estimated independently from female fecundity), whereas in the forest this correlation is negative; the 'r-strategists' are more abundant in the ruderal site, the 'K-strategists' more abundant in the forest. As all the variability measures are positively correlated with the population growth rate, the above-mentioned difference could be explained by the difference in prevailing life history strategy. Note that the pattern of decreasing variability with increasing abundance in the forest was shown concordantly by all the three indices and has a feasible ecological explanation.

The between-species variance-mean relationship depends on the habitat type and on the set of populations under investigation. A similar rationale could be given for the within-species variance-mean relationship: it depends not only on the species, but also on the set of habitats investigated. There is no variance-mean relationship characteristic for a species per se (i.e. independent of the set of habitats investigated). Both the differences in species abundance as well as in species variability in various habitats are influenced by the differences between habitats.

### Recommendation for applications

Population variability expressed as a single number is a simplification useful for comparing populations or habitats within a data set. The variance-mean relationship is a useful way of describing the relationships within such a data set. Correlations are usually sought between the measure of variability and some characteristic of a species or its habitat.

A very simple pragmatic solution, used by Rejmánek and Spitzer (1982), is to check the data for the dependence of the coefficient of variation on the mean population density. If there is effectively no such dependence for species with a mean annual catch over  $y$  individuals, then these rarer species (catch  $< y$ ) can be excluded from the analysis;  $y=5$  in Rejmánek and Spitzer (1982). This is reasonable also because of the low reliability of any estimate of the population size of a rare species. (In rare species, the error in the population size estimate might influence the variability measure more than the variation itself.) Similarly, Spitzer and Lepš (1988) checked the independence of variability measures from the mean within the data set under consideration prior to further analyses. Wolda (1983) for similar reasons omitted from his analyses all the popula-

tions for which the mean of the natural log of their abundance was smaller than 0.6.

Results based on all the measures could potentially be confounded by dependence on the mean. In principle, there are two possibilities – either we assume that one of the measures is not biased and expresses true variability, and use it; or we accept that any measure is potentially biased and compare results based on various measures. I prefer the second possibility. The spurious correlation of CV and SD of  $\log(N+1)$  with the mean is usually of opposite sign. This demonstrates that some species characteristic could hardly be positively correlated with both CV and SD of  $\log(N+1)$  due to the dependence of the variability measure on the mean. For example, Spitzer and Lepš (1988, Table 4) demonstrated that geographic range and population growth rate are significantly positively correlated with both CV and SD of  $\log(N+1)$ . Although this is just a correlation, it is reasonable to expect some biological mechanisms to explain this correlation, as it was done in the paper.

If a dependence is indeed found, one can use the mean density as a covariable in a regression analysis or in an ANCOVA of population variability coefficients. A similar possibility is to calculate the regression of a variability measure, linear or nonlinear, on the population density, and use the residuals as adjusted variability measures. Similar idea was suggested by Taylor (1971: 376): '...the deviation of the points, each of which represents a population, from the line, which represents the species norm, is presumably a measure of the local environmental effect on disposition'. Similarly, the deviations of points representing species from a line representing a habitat norm could each be considered as a characteristic of a species.

### Temporal and spatial scale

The methods discussed in the previous section are based on a single fixed sampling unit size, and ignore the spatial or temporal arrangement of these units. It has been demonstrated many times that the degree of spatial pattern intensity or aggregation depends on the size of a sampling unit. In classical 'pattern analysis' (Greigh Smith 1952, Kershaw 1973a), the basic sampling units, located in a transect or in a grid, are blocked step by step, and the dependence of pattern intensity on the block size is studied; in this way, the spatial dimension of aggregations is determined. These methods are commonly used in quantitative plant ecology; the literature is extensive (see Lepš 1990 for review and references). It is generally accepted that there is no single appropriate spatial sampling scale.

For temporal variation it is often accepted that the appropriate sampling scale is generation time (e.g. McArdle et al. 1990, Connell and Sousa 1983). However, this approach presents some problems. The first is



practical: for polyvoltine species with overlapping generations it is not always feasible to distinguish particular generations. The other problems are conceptual. For instance, from the point of view of the impact of a species on an ecosystem, it is less important whether the species has one or several generations per year than how much it fluctuates in abundance between years. Generation time is difficult to apply as an appropriate unit to organisms with complicated life cycles (e.g. aphids with many parthenogenetic generations, but relatively regular yearly cycles). Moreover, in ecosystems species with differing generation times interact, and as a result the variability in population size could exhibit some phenomena on a time scale different from generation time. Although from the viewpoint of population dynamics generation time is perhaps the appropriate unit, population behaviour could show some longer term phenomena (as cycles over several generations, trends). When only mean and variance are used, such information is lost.

Time series data are similar to transect data. For the pattern analysis of transect data, the same mathematical methods were used as in time series analysis (Yarranton 1969). Unfortunately, the majority of time series available are too short for time series analysis techniques. As a rough alternative, some of the methods developed in spatial pattern analysis could be used. One simple possibility is to replace the variance by 'local variance' or 'two term variance' (Hill 1973), based on the mean square of the difference between neighbouring values, i.e. the average of  $(x_i - x_{i+1})^2$ , which reflects the year to year fluctuation, and is far less influenced than the variance by the trend (systematic increase or decrease of species abundance over time or through the transect) and by the size of a sample (i.e., length of the time series or transect). Hill's method also enables us to detect longer term phenomena by blocking sample units. If the value of ordinary variance or a variability measure based on it increases systematically with the increasing length of a time series (as demonstrated by Hanski 1990), the data quite probably reveals a trend. Although other explanations exist (see Pimm and Redfearn 1988, McArdle 1989), a trend is usually the simplest and the most feasible, particularly when the time series is long. In many cases the time series are too short to detect cyclic phenomena of longer periodicity; nevertheless, random and directional changes can always be distinguished (see Wolda et al. 1992). If we ignore the trend, we get high values of all variability indices for species with small year to year changes, but steadily decreasing (increasing) in population size (the longer the time series, the higher the variability indices).

The interaction between temporal and spatial scales of variation is also interesting, containing important biological information. For example, in the context of r- and K-selection theory it was predicted that r-strategists fluctuate more than K-strategists. Spitzer et al. (1984) have indeed shown that variability in moth population

size at a single locality is positively correlated with potential population growth rate. Nevertheless, this is not necessarily so when summarized over many localities. For example, pest species, which are usually r-strategists, might exhibit asynchronous outbreaks caused by local events which result in a relatively stable total population size. The relatively small but synchronized local fluctuations of K-strategists might result in larger fluctuations in total size.

Given available time series from many locations (an unfortunately rare phenomenon), it is possible to carry out more informative analyses than simple plotting of spatial and temporal variance-mean graphs. In particular, it is possible to test explicitly-stated hypotheses, e.g. whether fluctuations, and particularly outbreaks, are synchronized or not, or whether optimum habitats are temporarily stable (see Thomas 1991). If it seems that there are some refugia where species could survive during bad years, it is reasonable to search for the characteristics of refugia (which habitat type) and of bad years.

## Conclusions

1. There is no single best way of standardizing variance which would yield a measure of variability in time or space independent of the mean. Any measure is potentially biased. The variance and mean are mutually dependent, but the functional form differs from data set to data set. The applicability of Taylor's power law is limited, particularly for rare species.

The variance:mean ratio is positively correlated with the mean and the value of Green's index depends on the sample size; use of these measures is not recommended. SD of  $\log(N)$  is not applicable if the data set contains zeroes (as the majority of data sets do). Lloyd's index, CV and SD of  $\log(N+1)$  seem to be more acceptable. Of those, both the CV and SD of  $\log(N+1)$  have some drawbacks, and, indeed, they show close correlation with the mean at low population densities, independent of the biological character of the data. It is often useful to omit populations with a mean lower than certain threshold (3 or 5 individuals per year in our data sets). After this, the dependence of variability on the mean very often disappears. Should populations with low means be included, the use of Lloyd's index seems to be the only admissible solution. Nevertheless, comparison of results based on various variability measures helps to draw the most unbiased conclusions.

2. Variability depends on the spatial and temporal scales used. There is no single most appropriate spatial or temporal scale. Multiple scale analysis provides better insight than analysis on a single scale.
3. Many data sets are either in the form of a spatial

transect or time series. Particular sampling units are not entirely independent in this case, but form spatial or time series. Consequently, special statistical methods, which use information on the spatial or temporal relationships of particular units, should be used. Methods used in plant ecology for pattern analysis are recommended. Trends (directional changes) or cyclic changes should be distinguished from random variation.

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