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On patterns of temporal and spatial variation in animal populations

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Temporal and spatial variation in populations of insects and birds was analysed with published data on aphids, moths, and birds from Britain, on carabid beetles from the Netherlands, and on moths from Finland. In carabid beetles, temporal variation was affected by some environmental factors, but not by several characteristics of the species; spatial variation was negatively correlated with the intensity of between-site movements and, in moths, with niche width. Environmental stochasticity was sufficient to explain temporal variation in a Finnish moth community, with the exception of added Poisson variance in the rarest species (abundances and trap-catches are integers). A comparison is made between the slopes of (log) variance to mean abundance regressions in intraspecific and interspecific analyses; the latter was calculated from average means and variances for each species. In spatial variation, intraspecific slopes were generally greater than the interspecific slope, suggesting that regionally abundant species are generalists: abundance and niche width are positively correlated. In temporal variation, intraspecific slopes were smaller than the interspecific slope in abundant moths, suggesting a slight density dependence in their population dynamics. This becomes apparent when data from many sites for each species are analysed. No density-dependence was detected in aphids using this method. The results indicate that in the most favourable sites for the species, bird populations tend to be closer to their carrying capacity than do insect populations. Several of the results here do not agree with the model suggested by L. R. Taylor for regional dynamics in abundance and distribution, although the British data are from his studies. A new interpretation is suggested for the slope of the variance to mean regression.

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1. Introduction

One can hardly overestimate the value of L. R. Taylor's work on insect abundance and distribution, which was initiated by Taylor in 1961, conducted by him with many collaborators over the next 20 years (and will hopefully continue), and which is now published in a series of stimulating papers (Taylor 1971, 1974, 1979, Taylor & Taylor 1977, 1978, Taylor R. A. J. & Taylor L. R. 1979, Taylor et al. 1978, 1979, 1980, Taylor & Woiwod 1980, Kempton & Taylor 1979). These papers present, more convincingly than any others, evidence for continuous and interdependent change in abundance and distribution of moths and aphids from the point of view of Great Britain as a whole, and have demonstrated the uniqueness of instantaneous large-scale spatial patterns (for their other main conclusions see Taylor & Taylor 1979: 7).

These well-documented, grand dynamic changes have inevitably — and properly — stimulated speculations and theories about their causes. To explain their observations, Taylor & Taylor (1977) suggested a new model based on individual behaviour. Numerical simulations of the model proved that it was capable of generating patterns observed in nature.

Taylor's model has not met with universal acceptance, however (Iwao 1979, Hanski 1980a), the main cause of criticism being that the model is implausible. Taylor's model is in fact related to optimal foraging models (Hanski 1980a), in which individual movements usually take place within a relatively small area between habitat/resource patches, from high density of individuals per resource to low density, ultimately maximizing individual fitness (e.g. Pyke et al. 1977, Krebs 1978, and references therein). Such a model, though perhaps reasonable within one population site (but see Hanski 1980b, Ollason 1980, and references therein), is inappropriate, for example when applied on the scale of Britain as a whole. After all, there are four causes of population change: natality, mortality, immigration, and emigration. Taylor has focused, in the above-mentioned model (Taylor & Taylor 1977: 418), on the latter two processes.

I have presented another view of these patterns (Hanski 1980a). Specifically, I conjectured that large-scale spatial variation increases primarily because of variation in the reproductive success in space, and decreases primarily because of movements. Data was presented on the between-pasture distribution of dung beetles (Scarabaeidae: *Aphodius*) to support this hypothesis. A simple simulation model was used to demonstrate that these processes, too, like the ones postulated by Taylor, can create the log-linear relationship observed between variance and mean. My results did not show much variation in the regression coefficient, however, which was always close to 2, the null hypothesis. One of the aims of this paper is to clarify this point, and to develop null hypotheses about the regression coefficient, rather than the level of variation (intercept).

This study analyses both spatial and temporal variation in the abundances of moths, aphids, carabid beetles, and birds. It will be shown that patterns exist in Taylor's own data which do not support his model. These patterns nevertheless deserve to be carefully considered, as they throw light on perennial questions about the dynamics of abundance and distribution. Some of the arguments below are conceptually complicated and/or developed here heuristically. This is unavoidable, because of the complexity of the subject matter and because of the lack of earlier work along these lines.

2. Preliminaries and null hypotheses

2.1. Taylor's model

The key observation on which Taylor's work is based is the empirical (Taylor's) "power law" (Taylor 1961),

$$V = a\,x^b,$$

where x is mean abundance and V is the variance in one sample. Several samples are needed to estimate the parameters a and b. They are estimated from log-transformed means and variances using the standard least-squares technique. Samples may be either consecutive abundance values from many populations of one or many species (a_t and b_t, $t =$ temporal), or they may be sets of abundance values from populations at different sites, but sampled at the same time (a_s and b_s, $s =$ spatial). Temporal and spatial scales are not constrained in any way. One could, of course, analyse samples collected from different populations at different times, but such results would be even harder to interpret than the present results.

Taylor and his co-workers have shown that, in moths and aphids, sampled with light-traps and suction-traps, respectively, at sites covering the whole of Britain, b has different values in different species. Less notice is taken of variation in a, perhaps because it is difficult to compare intercepts of regressions differing in slope. Nonetheless, both sampling and the environment are assumed to influence a (Taylor et al. 1980), while b is assumed to depend on species-specific behaviour, and *not* on sampling or the environment. The values of b mostly vary between 1 and 3, in both spatial and temporal analyses, though generally $b_t \neq b_s$. To explain this variation, Taylor postulates species-specific parameters in his model of individual movement behaviour (Taylor & Taylor 1977). No ecological correlates of the regression parameters appear to have been searched for or found.

To say the least, Taylor's model is very complicated, as the number of parameters is four times the number of species (four parameters for each species; Taylor & Taylor 1977: 418). Testing that model is going to be difficult! The present approach is based on the question: *What do we expect the patterns of temporal and spatial variation to look like?* Derivation of the following null hypotheses is heuristic, and will hopefully stimulate more fundamental work.

2.2. Temporal variation

When one first considers temporal variation, or normal fluctuation in abundance, in many species living in one place, it seems difficult to construct a simple null hypothesis on how that variation changes with changing mean abundance. Presumably, two of the factors affected by interspecific differences are the level of temporal variation, and the way it reacts to density. But, however different the species and their ecologies are, the rate of change in abundance is proportional to abundance itself in each species. The question therefore is whether the magnitude of multiplicative changes in abundance is, or is not, dependent on mean abundance. There appear to be no reasons why it should be so dependent, unless one assumes that mean abundance in rare species, and hence rarity, is due to causes qualitatively different from causes of mean abundance in abundant species. There may be theoretical reasons to expect this difference (Southwood & Comins 1976), but it has never, to my knowledge, been demonstrated in any real community. Indeed, the argument may be reversed: if the analysis of temporal variation in abundance shows no difference between the rare and the abundant species, the case for a difference in the factors influencing abundance in the two sets of species is weakened. Exactly this result is obtained in Section 4.

For the sake of argument, consider now a hypothetical set of species, each having the same mean abundance, m, but a different level of temporal variation, var_1, $var_2, \ldots,$ var_n, determined by the ecology of the species. The average level of variation is var. Let us then multiply all the consecutive values of abundance by such species-specific constants that some required differences in mean abundance are obtained. Variances become multiplied by squares of these constants, and the variance to mean regression in the derived data is:

$$\log V = \log (var/m^2) + 2 \log x, \text{ or } V = ax^2.$$

The regression coefficient is $b_t = 2$, which is therefore the null hypothesis for the variance to mean regression in a community of many species.

An analogous analysis of temporal variation in many populations of one species differs in two ways from the case just discussed: there is only one species instead of many, but many sites instead of one. What difference, if any, does this make?

Assuming again, to start with, equal mean abundance in all populations, one expects less variation in temporal variances in populations of one than many species, simply because the causes of variation should be more similar in the former case. The scatter around the variance to mean regression should consequently be less in intraspecific than interspecific plots, which, in fact, appears to be true (Kempton & Taylor 1979; but see Section 4).

Another and more significant difference between intraspecific and interspecific analyses is that, at any one site, most species are represented by an average-sized population with respect to all the populations of that species within a large region. There are no reasons to expect that the few exceptional populations in this respect are amongst the smallest or the largest ones in that community. (This may not happen if the site in question is extreme either geographically or ecologically.) But in the regression of populations of one species from many sites, both sparse and dense populations are necessarily included, and these *are* likely to be the smallest and the largest populations in the material, even if we allow for spatial variation in the carrying capacity, numbers of predators and parasitoids, etc. If changes in abundance are density-independent, this does not make a difference. But if changes in abundance are negatively density-dependent, $b_t < 2$ is expected. There is no simpler null hypothesis here.

2.3. Spatial variation

One may distinguish between four (meaningful) types of analysis, which are found as answers to two independent questions. Are the sites in question qualitatively similar to each other "from the species' point of view"? Are the sites so small and so closely situated to each other that individuals move frequently from one site to another? Populations of only one species are considered throughout this section.

The second distinction is necessary because of the significance of intersite movements. This is Hanski's (1980a) behavioural range, on which optimal foraging theories operate. The first distinction is necessary because differences in geographical location, habitat, etc., all increase spatial variation in abundance in all but the most ubiquitous species. Populations occupying similar sites are expected to show only stochastic variation.

Let us start with the case of similar sites situated far apart from each other. Because the sites are far apart, between-site movements are infrequent, and it is particularly unreasonable to assume that individuals are able to locate the "best" of such sites. In other words, optimal foraging models in general and Taylor's Δ-model in particular are not appropriate here. The crucial question again is whether multiplicative changes in abundance are (negatively) density-dependent or not. If they are, we would expect b_s to be less than 2; if they are not, the null hypothesis is $b_s = 2$.

Taylor and his co-workers are concerned with dissimilar sites which are situated far apart from each other (though the aphid sampling sites differ only in terms of geographical location; Taylor et al. 1980). The point is best made with a simple "thought experiment". Consider two conspecific populations living in different environments, one of which is more favourable to the species than the other (local adaptations are thereby excluded). When conditions of life change, either due to climatic fluctuations, which are known to be important to insect populations (Andrewartha & Birch 1954, Clark et al. 1967), or otherwise, both populations will change. *But which one will change more?* Owing to the assumed difference in the environment, it would be surprising to find an identical (multiplicative) change. Generally, we do not know which population is affected more, but we might expect, though this is only a hypothesis, that the disparity is non-random, one of the populations most of the time varying disproportionately more than the other one.

I shall adopt one possible interpretation in this paper: if the population that is usually larger changes proportionately more than the smaller one, i.e. if $b_s > 2$, the species is called a specialist; but if $b_s < 2$, it is called a generalist. This interpretation is intuitively appealing and open to empirical tests. Naturally, none of the results in this paper are affected by this interpretation, but new fruitful hypotheses are suggested.

If the sites are close to each other and small, optimal foraging models, including Taylor's model, may apply and predict that individuals move to where their expected net energy intake per unit time, and other components of fitness, are highest. If the mean abundance is low, all individuals should congregate to the "best" sites; when density increases, other sites will become profitable as well, in order of decreasing "quality" ("quality" is used, in this context, usually for quantity, and the sites are assumed to be qualitatively similar, i.e. similar in terms of the kinds of resources available but not in their quantities). This should lead to a relative decrease in variance, and the regression slope should certainly be less than 2. Increased movements are expected to lower the level of variation (Hanski 1980a). Any between-site differences in (true) quality should, on the other hand, increase the level of variation, but the slope remains less than 2.

The above arguments are summarized in Table 1 as far as the regression coefficient is concerned. To summarize the expected changes in the intercept, it should decrease with increasing intensity of movements, and should increase with increasing spatial variance in the quality and/or quantity of resources, in the numbers of predators, etc.

Table 1. The null hypotheses about the slope (b_s) of the variance to mean regression in spatial variation.

	Population sites	
	close and small	far apart
Similar sites	$b_s < 2$	$b_s \leqslant 2^a$
Dissimilar sites	$b_s < 2$	$b_s \neq 2$

a) $b_s = 2$ if there is no negative density dependence

Finally, something can be said about spatial variation between populations of many species from many sites, although no study of this case has been published. Populations of randomly chosen species from different communities are perhaps more comparable in terms of adaptations to local ecological conditions than are populations of one species. Hence a slope close to 2 may be expected.

3. Evidence: aphids and moths in Britain

These data, analysed by Taylor and co-workers in two papers (Taylor & Woiwod 1980, Taylor et al. 1980), are very extensive and representative: 97 species of aphids and 263 species of moths are included, and the sample sites cover the whole of Britain over a period of 10 years. Aphids were collected with 8 to 24 suction-traps from equally many sites selected to be as similar as possible. Moths were collected with 21 to 126 light-traps from equally many sites, but the sites were not similar (Taylor et al. 1980).

Noctuidae and Geometridae will be analysed separately, because of the possibility of differences between these morphologically distinct families. All other moths, most of which were rare, are excluded. Altogether there were 116 species of noctuids and 109 species of geometrids.

3.1. Temporal variation

Looking first at the values of the regression coefficient, b_t, which are normally distributed (Taylor & Woiwod 1980: fig. 3), we observe that the means for aphids and moths are different, c. 1.85 and 1.50, respectively (Table 2). Mean abundances of aphids are generally higher than those of moths, which suggests plotting the regression coefficient against the mean abundance in both groups. Taylor & Woiwod (1980) give the means of log-transformed data ($m_{\log}$) for each species, and these data can be used here.

Table 2. Means and standard deviations (*SD*) of b_t and b_s. *SE* is the standard error of the estimate of b_t in Fig. 1.

	b_t			b_s	
	Mean	*SD*	*SE*	Mean	*SD*
Aphids	1.86	0.27	0.25	1.97[a]	0.30
Noctuids	1.50	0.16	0.13	2.07	0.36
Geometrids	1.51	0.14	0.12	2.06	0.34
Birds				1.71[b]	0.38

a) S.E. = 0.03 (Taylor et al. 1980), and the average does not differ significantly from 2.

b) This is slightly different from 1.68, given by Taylor et al. (1980), because the sample is not the same; I have included those species whose average abundance was log $m_s > -0.5$.

There is a significant positive correlation between b_t and $m_{\log}$ in all groups studied (Fig. 1), the proportion of variance in b_t accounted for by the regression being 41.4 % in the noctuids, 25.4 % in the geometrids, and 19.0 % in the aphids. These correlations substantially weaken the case for ecologically significant, density-independent variation in b_t, the hypothesis proposed by Taylor. Some much simpler elements are involved and should be analysed, whatever the explanation of the regression residuals in Fig. 1.

It was pointed out in Section 2 (Table 1) that $b_t < 2$ is expected if there is negative density-dependence in population dynamics. No single value of b_t was greater than 2 in moths, while over 30 % of the aphids had $b_t > 2$ (Fig. 1). The implication from this is clear enough, but it should be noted that no correlation between b_t and abundance was predicted. The positive correlation observed does not support any hypothesis of density-dependence due to resource limitation, because in that case one would expect a *negative* correlation, unless one makes the implausible assumption that rare species are generally closer to their "carrying capacity" than are abundant species. Some other factors are involved and will be analysed in Section 4.

3.2. Spatial variation

There is no correlation between b_s and abundance (Fig. 2), with the exception of a tendency towards smaller b_s (less than 2) in the rare aphids, to which we shall return in Section 7. Abundance was measured here using the mean of the logarithm of mean abundance, which is given for each species by Taylor et al. (1980). This makes a minor scaling difference in comparison

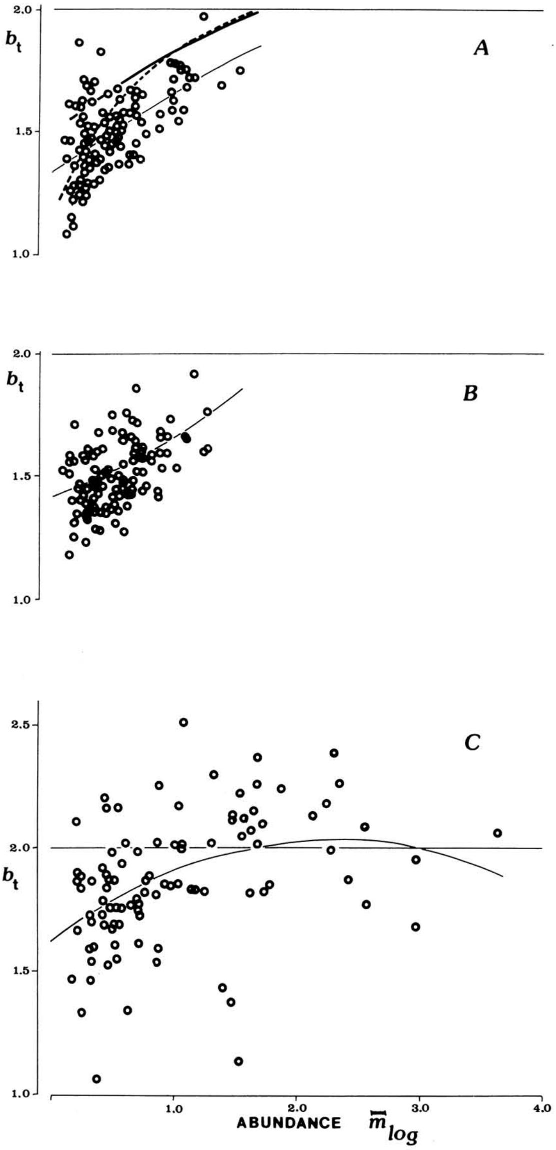

Fig. 1. Relationship between b_t, the slope of the intraspecific temporal variance to mean abundance regression, and abundance (average of mean abundances, log-transformed data) in A) noctuids, B) geometrids, and C) aphids. Data are from Taylor & Woiwod (1980). The regression equations (thin lines) were fitted using Marquardt's iterative algorithm (Conway et al. 1970) and are as follows (percentage of variance accounted for by the regression in parentheses): A) $b_t = 1.32 + 0.36\, m_{log} - 0.03\, m^2_{\log}$ (41.4 %), B) $b_t = 1.41 + 0.14\, m_{\log} + 0.10\, m^2_{\log}$ (25.4 %), and C) $b_t = 1.61 + 0.37\, m_{\log} - 0.08\, m^2_{\log}$ (19.0 %). The thick continuous line in A was derived from the data in Fig. 3, and the thick broken line is the interspecific slope derived from these data as explained in the text (Section 4). The thin line $b_t = 2$ has been drawn for reference.

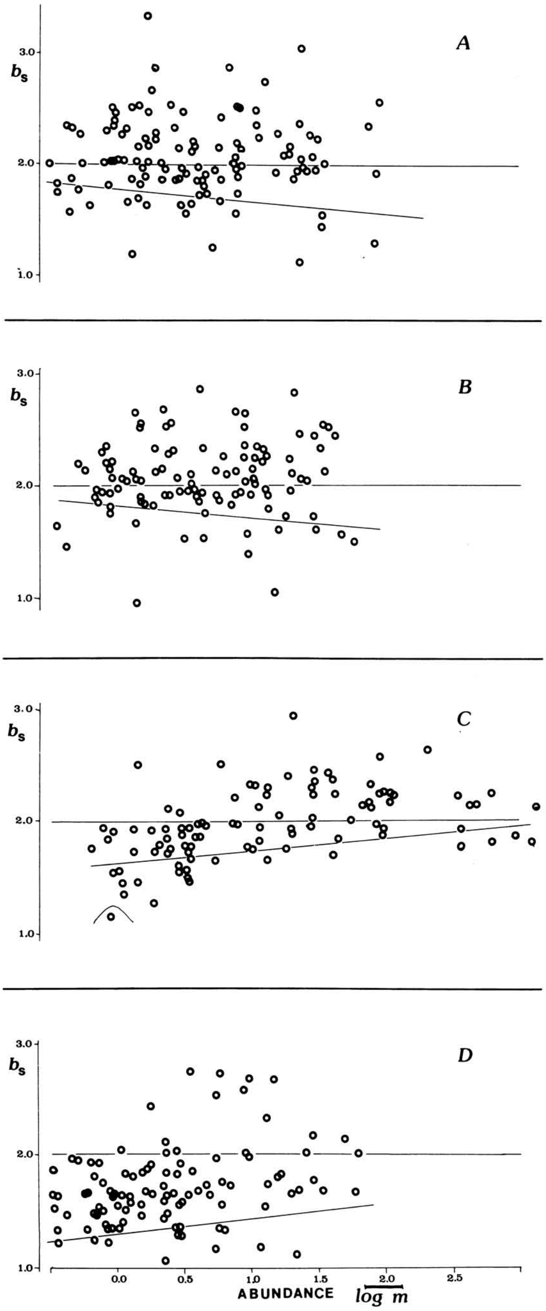

Fig. 2. Relationship between b_s, the slope of the intraspecific spatial variance to mean abundance regression, and abundance (average of logarithm of mean abundance) in A) noctuids, B) geometrids, C) aphids, and D) birds. Data are from Taylor et al. (1980). The thin line $b_s = 2$ has been drawn for reference. The other lines are constructed by regressing each species' average spatial variance with average mean abundance (as further explained in the text). For the statistics see Table 3.

with Fig. 1, but does not change the result qualitatively. There is a genuine difference between the dynamics in spatial and temporal variation, which casts doubt on the hypothesis that "the same behavioural properties are involved in both (temporal and spatial stability)" (Taylor & Woiwod 1980: 216). Three other points are as follows:

1) The average b_s values reported earlier by Taylor et al. (1978) for 156 sets of data, including many different organisms but mostly arthropods, is only 1.45 ($SD = 0.39$), while the average for moths is 2.07, and for aphids 1.97 (Table 2). This substantial disagreement becomes understandable when one realizes that most of the 156 data sets in the earlier study covered a very small area, e.g. a single field (Taylor et al. 1978: 832). The null hypothesis for small areas in $b_s < 2$ (Section 2, Table 1).

2) Most aphids are found throughout Britain (column 5 in the Appendix to Taylor & Woiwod 1980, Taylor et al. 1979), and the aphid sampling sites were selected to be as similar to each other as possible (Taylor et al. 1980: 834). Therefore, it is not surprising that variance in b_s is less in the aphids than in the moths, although exactly the opposite was true for variance in b_t (Table 2).

3) Taylor et al. (1980) give data on birds as well as on moths and aphids. The average b_s for birds is 1.68 (Fig. 2), which is much less than the average for aphids and moths, c. 2 (Table 2). This result confirms the prediction made in Section 2 (Table 1) that for large regions, b_s is not automatically equal to 2; that the means happen to be close to 2 in moths and aphids is, according to this hypothesis, due to their biology. As in insects, there is no correlation between b_s and abundance in birds (Fig. 2D).

Why are most b_s values less than 2 in birds? If the argument in Section 2 is correct, this indicates that bird — but not insect — populations inhabiting the optimal habitats of the species tend to be so close to the carrying capacity that regional mean abundance can increase only if the density in the sub-optimal habitats increases disproportionately. A contributing factor is that birds are better able to move between the sites than are insects. In fact, it can perhaps be argued that from the birds' point of view Great Britain is a small area, and the optimal foraging theory prediction, $b_s < 2$ (Table 1), applies. This does not seem to be a very likely explanation, however.

The next step in the analysis is to derive an interspecific regression for the four groups in Fig. 2 by calculating for each species the variance corresponding to the mean abundance, log m_s,

Table 3. Interspecific regressions of spatial variation, calculated as explained in the text. The proportion of variance explained by the regression is given in the fifth column. See also Fig. 2.

	a	bx	cx^2	n	%
Aphids	0.61	1.65	0.05	97	97.8
Noctuids	0.99	1.77	−0.05	116	95.0
Geometrids	1.05	1.81	−0.05	109	94.5
Birds	0.96	1.29	0.06	116	98.8

given by Taylor et al. (1980: Appendix). In each of the groups studied — aphids, noctuids, geometrids, and birds — most of the intraspecific regression coefficients are greater than the interspecific b_s (Fig. 2, Table 3). Unfortunately, Taylor and Woiwod (1980) do not give log m_t values, which makes it impossible to calculate an accurate interspecific regression for temporal variation. Taylor & Woiwod (1980) give means of log-transformed data, $m_{\log}$, and because the relationship between log m_t and $m_{\log}$ is non-linear, it is not possible to derive, analytically, log m_t from $m_{\log}$. Empirical data for noctuids in the following Section enable us to calculate log m_t from $m_{\log}$ and thereby to obtain an approximate interspecific regression.

4. Causes of temporal variation

Due to the generosity of Mr. S. Muurimaa, I have been able to analyse his trapping results of noctuids from one locality in south-west Finland (Kakskerta near Turku). Trapping was carried out from early spring to late summer between 1969 and 1979, and all catches were recorded, except in 1974 and 1975. Therefore, data exist for 9 years, and for 221 species, including the very rare ones.

A somewhat varying number of light-traps of two types were used in collecting. I have assumed that the efficiency of the 500 W blended-light lamp is twice the efficiency of the corresponding 160 W lamp (K. Mikkola unpubl.). Expressed in units of 160 W lamps, the number of traps used was, during the 9 years, 5, 11, 7, 8, 13, 3, 5, 7, and 6. To obtain comparable figures, I have multiplied the catch for each year by 7/"number of units used". This would clearly be an invalid procedure were the number of species in the catches of any interest, but for the present purpose this correction is justified.

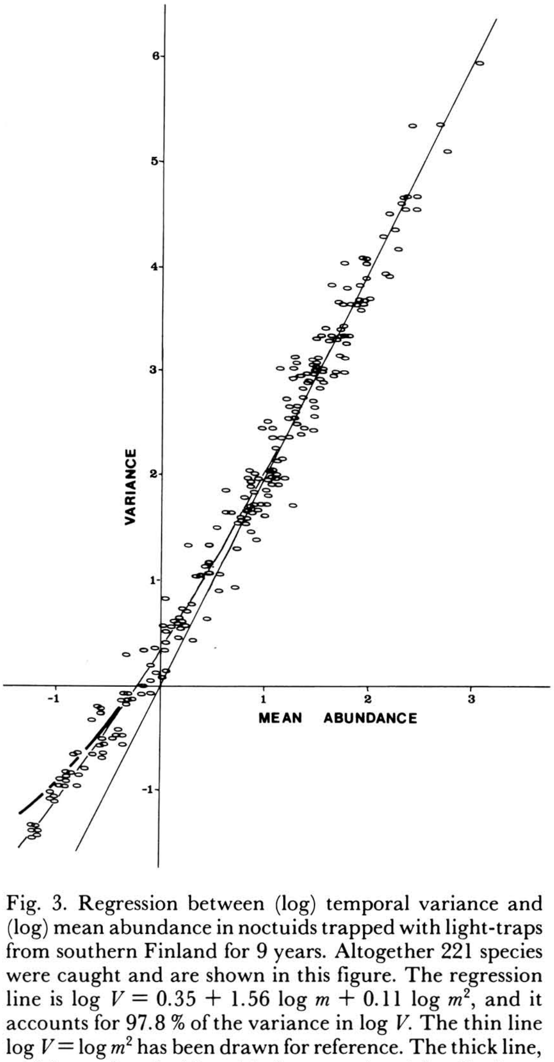

Fig. 3. Regression between (log) temporal variance and (log) mean abundance in noctuids trapped with light-traps from southern Finland for 9 years. Altogether 221 species were caught and are shown in this figure. The regression line is $\log V = 0.35 + 1.56 \log m + 0.11 \log m^2$, and it accounts for 97.8 % of the variance in log V. The thin line $\log V = \log m^2$ has been drawn for reference. The thick line, which mostly coincides with the regression, is $\log V = \log m + \log(m+1)$. The rarest species do not agree with this model because of the correction made for the varying trapping effort.

Fig. 3 shows the usual regular increase in variance with increasing mean abundance in this set of data. Several points deserve to be emphasized.

Firstly, 97.8 % of the variance is accounted for by the regression. Kempton & Taylor (1979) reported more scatter in interspecific than intraspecific plots, and for unknown reasons the scatter in Fig. 3 is in fact less than that observed by them (see their fig. 6).

Secondly, the null hypothesis for an interspecific regression, $b_t = 2$ (Section 2), is confirmed by the data for abundant and relatively abundant species; Taylor's data (Kempton & Taylor 1979) give the same result, as do data for carabid beetles in Section 6.

Thirdly, it is interesting to note that small, but not large, populations deviate from the null hypothesis. The mean abundance of the deviating species is less than 10 individuals per year (Fig. 3), which is so low that any biological variation is appreciably enhanced by Poisson variation resulting from only using integers for abundances and trap-catches. Total variance S is then

$$S = V + P,$$

where V is biological variance and P is Poisson variance. Assuming the model in Section 2,

$$V = ax^2,$$

where a is a constant and x is mean abundance. In Poisson distribution,

$$P = x.$$

Addition of these two yields

$$S = ax^2 + x = ax(x + 1/a), \text{ or}$$
$$\log S = \log a + \log x + \log (x + 1/a).$$

From Fig. 3 we find that, in this material, $a \sim 1$, and hence

$$\log S \sim \log x + \log (x + 1).$$

This line has been drawn in Fig. 3; it fits the data quite well, and an even better fit could undoubtedly be obtained by rigorously estimating the value of a from the data (but this does not concern us here).

The regression slope in Fig. 3 increases with abundance. In the simple model above,

$$b_t = \frac{d \log S}{d \log x} = 1 + x/(x + 1/a),$$

which shows that the derivative $b_t \to 1$ when $x \to 0$ and $b_t \to 2$ when $x \to \infty$. In Section 3 (Fig. 1) we also found an increase in b_t with increasing mean abundance. Can these observations be explained by the same factors?

As Taylor & Woiwod (1980) do not give log m_t values, I used the present data to calculate the relationship between $m_{\log}$ and log m_t. It is nonlinear ($m_{\log} = 0.25 + 0.42 \log m_t + 0.17 \log m_t^2$), but the second order polynomial fits well, 97.7 % of the variance being attributable to the regression. Using this relationship, and the knowledge that $b_t = 1.56 + 0.22 \log m_t$ (the regression in Fig. 3), I constructed the line shown in Fig. 1A. There is an almost constant difference of c. 0.15 between this line and the regression line for the data, but I conclude from the overall similarity of the lines that the increase in b_t with increasing mean abundance in Taylor's data is explicable by Poisson variation due to sampling, and conceivably also by demographic stochasticity in the populations. The difference between the lines must be explained in some other way.

Using the Finnish data, I calculated log m_t as a function of $m_{\log}$; and an interspecific regression was then calculated from the data in Fig. 1A (as explained in Section 3 for spatial analysis). An interesting pattern emerges (Fig. 1A). In the rare species, the average intraspecific slope agrees with the interspecific one, but in the abundant species the latter is greater. This suggests density-dependence in the abundant species. Reasons for the disagreement between the two interspecific regressions in the rare species are unknown. The difference may be due to some site-specific factors in the Finnish material rather than to the techniques of deriving the regressions.

The question of density-dependence can also be approached with the model

$$S = ax^2 + x.$$

Parameter a can be estimated from Taylor's data separately for each species; and b_t can then be calculated as above and compared with the value reported by Taylor & Woiwod (1980). The results agreed with the comparison of the interspecific slope and the intraspecific slopes: calculated and observed values of b_t were similar in the rare species, suggesting that the model is valid for them; but the observed values were systematically lower than the predicted ones in the abundant species, indicating a deviation from the assumed density-dependence in the model. I shall return to this point in Section 7.

Taking into account that no abundance data are available for 1974 and 1975, there are a total of seven times 221 (= 1547) annual abundances that follow another annual abundance of the species in the previous year. Of these, 438 or 28 % followed a zero abundance, and of these, 283 or 65 % were zero, leaving 155 "colonizations" (Fig. 4). One hundred (100) of the "colonizations", or 65 %, were catches of one specimen, and most of the catches consisted of less than 10 individuals. One very exceptional case was observed, however (Fig. 4). *Agrochola circellaris* (Huf.) was absent in

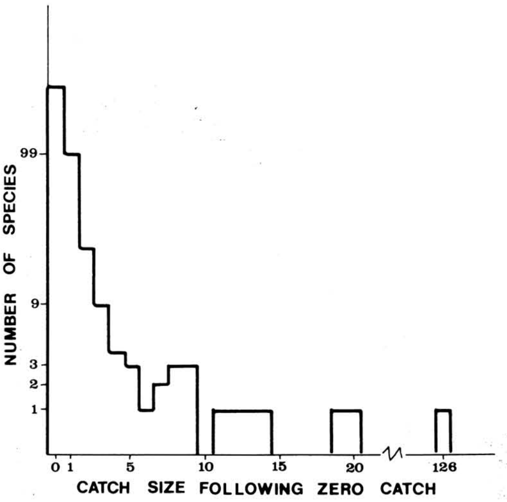

Fig. 4. Size distribution of yearly catches following a zero catch of the species. Data are the same as in Fig. 3. The exceptional species, of which a catch of 126 specimens was caught following a zero catch, is *Agrochola circellaris.*

1971, but 144 individuals were caught in 1972 (126 individuals per standardized trapping effort). It is significant that in only 3 of the 116 species in Taylor's data (Taylor et al. 1980) spatial regression accounted for less of the variance than in *A. circellaris* (55 %).

5. Patterns of large-scale spatial variation

One may doubt the value of analysing spatial variation with data covering as large an area as Britain; the data are collected from many habitats, and include species whose feeding habits, to mention just one aspect of their ecology, are widely different. Besides stochastic variation, such data can be expected to incorporate variation due to many other factors, including those mentioned above. Nevertheless, spatial variation is expected to increase with increasing degree of ecological specialization, i.e. with decreasing niche width, regardless of the type of spezialization. A start can be made on the analysis without making a distinction between the different kinds of specialization, or between the components of spatial variation caused by them. Here I attempt to outline some connections between large-scale spatial patterns, as studied by Taylor, and general ecological theory. A much more elaborate analysis is possible but beyond the scope of this paper.

To start with, we need a measure of spatial variation. Because of the relationship between variance and mean, Taylor has objected to using any single figure for spatial (or temporal) variation. However, this need not be wrong in itself, if the limitations of such figures are appreciated. I shall distinguish between two measures of variation. *An absolute measure of variation* is the deviation of the average spatial variance, corresponding to the average mean abundance, from the line $\log V = 2 \log x$, i.e. $a \log m_s^b - \log m_s^2$, where a and b are the species-specific parameters and $\log m$ is the average log-abundance. *A relative measure of variation,* not influenced by abundance, is the residual from the appropriate interspecific regression (which are given for the present data in Table 3). Absolute measures are comparable between different sets of data, but relative measures are not. The merit of the latter is that density dependence, if it exists, can be removed. Naturally, analogous measures can be used for temporal variation, and in practice "average variance" is simply variance, as only one set of figures (sample) is usually available.

Absolute spatial variation decreases with increasing abundance in moths, aphids, and birds (Table 3: $b < 2$; cf. correlation coefficients in Table 4). The steepest decline ($b = 1.29$) was found in birds, reflecting their low b_s values (Section 3). With respect to the argument in the beginning of this section — that increasing ecological specialization increases spatial variance — the result indicates, in short, that abundance and niche width are positively correlated.

Interestingly enough, the same conclusion emerges from a slightly different argument. In all groups studied, the intraspecific regression coefficient (b_s) was, in most species, greater than the corresponding slope of the interspecific regression (Fig. 2). To see the significance of this difference, consider two species, A and B, of which A has a slightly greater average abundance than B. Every now and then, B increases up to the level of average abundance of A, but because of its large regression coefficient, B is then more patchily distributed than A. This suggests that a permanent increase in average abundance is associated with a decrease in the level of spatial variation, which means, on the scale of an area the size of Britain and in the kinds of samples analysed by Taylor, a decrease in the degree of specialization. This observation, too, amounts to a large-scale demonstration of positive correlation between niche width and abundance. There is nothing surprising in that idea itself (Levins 1968), but it is encouraging that it emerges from the present analyses.

The level of spatial variation is clearly less in aphids than in moths at any level of abundance. This was actually expected, because the aphid samples, unlike the moth samples, come from similar habitats (Section 3). The aphid samples do not, therefore, include variation due to habitat selection and related factors, though they include stochastic variation and variation due to restricted geographical ranges. It is more surprising that the difference between noctuids and geometrids is significant, too ($P < 0.05$, Table 4), geometrids being more patchily distributed than noctuids, although here the sources of variation must be exactly the same in the two groups. This difference may have something to do with the size of the species, and their mode of flight, geometrids being generally smaller and weaker fliers than noctuids. A testable corollary is that in moths spatial variation decreases with increasing size. Niemelä et al. (1981) have recently shown that in Finnish noctuids size and diet niche width are positively correlated. This fits very well with the present assumption that niche width and spatial variance are negatively correlated. The actual causal relationships need much clarification.

In Section 2 it was hypothetized that the regression coefficient increases with the degree of specialization (decreases with increasing niche width); in this section I have suggested that the level of spatial variation does the same. There is an important difference between the two hypotheses, as the level of spatial variation reflects the static result of specialization, whereas the regression coefficient has more to do with the corresponding dynamics. Combining the two hypotheses leads to the prediction that b_s is positively correlated with average spatial variation. A relative measure of variation is obviously needed here. The hypothesis is supported by the data, as the correlation coefficients are positive and significant at the 1 or 5 % level, except in the aphids, where the correlation is only indicative (Table 4). Although less than 5 % of the variation is accounted for, the result again suggests that more detailed analyses are worthwhile.

It should be noted that even in many "specialist" species, defined to show a positive residual from the interspecific regression in Table 3, the value of the regression coefficient is less than 2, and is almost always so in birds (Fig. 2). Therefore, in absolute terms, such "specialists" tend to become less patchily distributed than predicted by the null hypothesis with increasing abundance ($b_s < 2$). The interpretation that is given to the regression coefficient here — that it correlates with the degree of ecological specialization — must be considered in relative terms, and in the context of some specified environment. This is common sense, as specialization cannot be defined without defining its object. The important point is that this is a testable hypothesis.

Table 4. Means and standard deviations of the absolute spatial variation, $a+bx+(c-1)x^2$ (parameters from Table 3), and the correlation coefficient between the mean and average abundance, log m_s (r_1). The other correlation coefficient (r_2) was calculated between relative spatial variation (i.e. residuals from the regressions in Table 3; see also the text) and the intraspecific regression slope, b_s (Fig. 2).

	Absolute spatial variation		Correlation	
	Mean	*SD*	r_1	r_2
Aphids	0.31	0.30	—0.583***	0.186°
Noctuids	0.82	0.29	—0.592***	0.236**
Geometrids	0.90	0.27	—0.523***	0.209*
Birds	0.79	0.54	—0.820***	0.199*

°$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

We thus conclude that the slope of the variance to mean regression may indeed reflect the ecology of the species, though probably not in the sense suggested by Taylor & Taylor (1977). Hanski's (1980a) simulation model, which is in line with the present assumptions, demonstrated variation in the level of spatial variation, but not in the slope, simply because I did not model spatial variation due to restricted geographical ranges, variation due to habitat selection, or due to any other form of ecological specialization. I still maintain that patterns found and discussed in this paper would not have been found if all the sites were similar to each other, in which case the observed spatial variation would be pure stochastic variation. In Taylor's data, the sampling sites are more similar to each other for aphids than for moths or birds. It is encouraging, therefore, that aphids agreed most closely with the null hypothesis, $b_s = 2$, both in terms of the average and the scatter around it (Table 2). Taylor et al. (1980) did not check in how many cases the slope was significantly different from 2. Judging from their results on birds, where two regressions were available for each species and their difference was actually tested, most of the values in Fig. 2A—C do not deviate significantly from 2.

6. Spatio-temporal variation in carabid beetles

It is important to establish which, if any, of the previous results are artefacts of sampling methods.

This is particularly important since it is known that light-traps are not equally attractive to all species (e.g. Southwood 1966, Taylor 1979). Suction-traps, on the other hand, give a more reliable picture of the numbers of flying insects, and especially of the small ones, such as aphids (Taylor 1962, Taylor & Palmer 1972).

Den Boer has trapped carabid beetles within an area of c. 200 km^2 in the Netherlands since 1959. He and his co-workers (Den Boer 1979, Baars 1979) have demonstrated that annual catches from a standard set of 3 pitfalls give a good estimate of the population size in the "interaction group" (local population), and hence such trapping should reveal true population changes. To substantiate his earlier theoretical ideas (Den Boer 1968, 1970), Den Boer (1979) has presented a well-documented report on spatial and temporal stability in 148 species of carabid beetles, recorded between 1959 and 1967. As his methods of analysis are different, I have calculated, for the present purpose, variance to mean regressions for three sites in Den Boer's material. These are a moist deciduous woodland (site B in Den Boer 1979, Appendix), heath (N), and an unstable habitat characterized by *Molinia* tussocks (M). Trapping was carried out continuously at all of the sites for 8 years.

Den Boer also collected at many other woodland and heath sites for shorter periods of time. Data from sites B, C, AK, AL, and AM, collected in 1962, were used to calculate spatial variation between woodland sites, and data from sites N, O, Z, and TG, also collected in 1962, were used to calculate variation between heath sites. Unlike the situation in previous sections, we are here dealing with spatial variation between *similar* sites situated relatively far apart from each other. Woodland sites are isolated habitat islands in the sea of cultivated countryside, while the heath sites are different parts of one extensive nature reserve (Den Boer 1979).

Table 5. Means and standard deviations of temporal (log a_t) and spatial variation (log a_s) in the frequently moving macropterous (B species) and in the brachypterous and less mobile macropterous carabid beetles (A and C species; from Den Boer 1979). This table also gives the following correlation coefficients: r_1 = between temporal and spatial variation, r_2 = between temporal variation and the size of the species, and r_3 = between spatial variation and the size of the species.

	Woodland	Heath	Unstable habitat
Temporal variation			
B species	−0.43	−0.17	−0.38
A and C species	−0.41	−0.17	−0.22
all species	−0.42±0.25[a]	−0.17±0.36[a]	−0.30±0.30
Spatial variation			
B species	−0.17±0.28[b]	−0.01±0.29	
A and C species	0.10±0.30[b]	0.10±0.23	
all species	−0.01±0.31	0.07±0.24	
r_1 : log a_t vs. log a_s	0.37	0.46[c]	
r_2 : log a_t vs. size	0.37	−0.20	−0.11
r_3 : log a_s vs. size	0.21	0.14	

a) t = 2.36, df = 37, P = < 0.025; b) t = 1.77, df = 13, P < 0.1; c) df = 23, P < 0.05.

6.1. Temporal variation

The results (Fig. 5) are in good agreement with those presented in Fig. 3 for noctuids trapped with light-traps from southern Finland. The regression slope increases with increasing mean abundance, up to a density of 3 to 10 individuals per year, beyond which $b_t = 2$ is a good approximation (Fig. 5). Because of this, a good measure of temporal variation for the abundant species, not much influenced by abundance, is:

$$\log a_t = 2 \log CV,$$

where *CV* is the coefficient of variation. This is the absolute measure of variation in the previous section.

There were differences between the habitats in the level of temporal variation, log a_t (Table 5): the most stable populations occurred in woodlands, and the least stable ones in the heath, the difference in the means being statistically significant ($P < 0.025$, Table 5). As trapping was carried out in woodland sites B and C for 8 years, one can test whether there were consistent differences between the species. A positive correlation was found ($r = 0.55$, $df = 13$, $P < 0.05$), which justifies a further analysis of correlates of temporal variation. Explanation of temporal variation in site B is attempted throughout.

Den Boer (1979) divided the species into two groups, depending on whether they fly frequently or not; the former, termed B species, are all macropterous, while the latter, A and C species, are either brachypterous or macropterous. There was no difference between the two groups in temporal variation (Table 5). One might suspect a difference between species breeding in spring and during other times of the year (mainly summer and autumn), but there was none. Neither was temporal variation related to the size of the species (Table 5), which may be related to species' reproductive capacity.

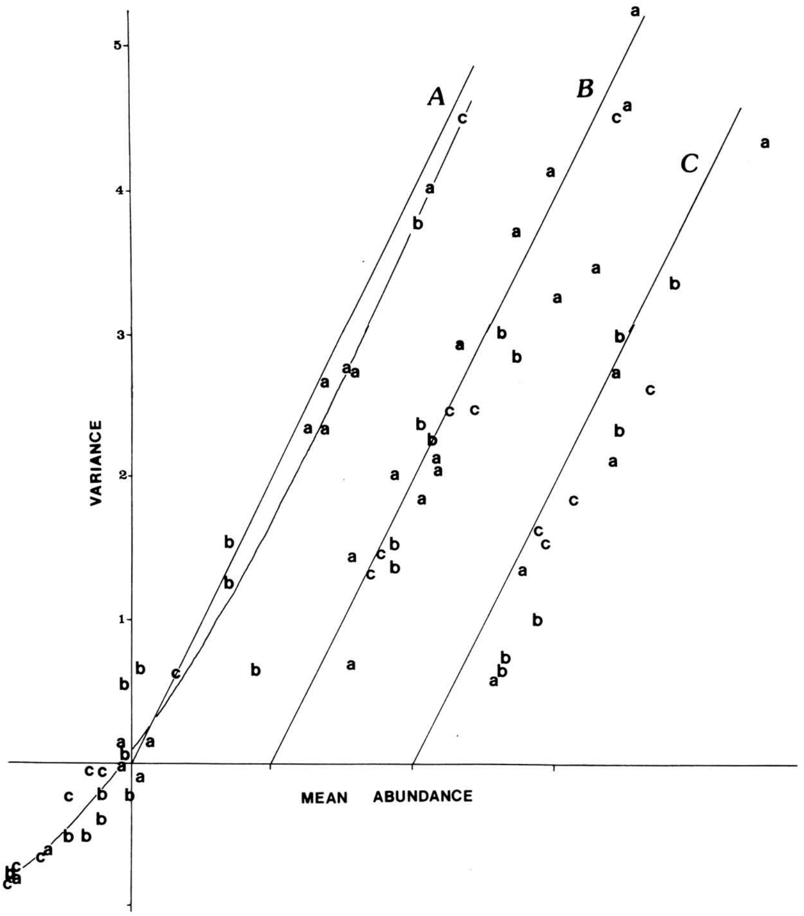

Fig. 5. Regression between (log) temporal variance and (log) mean abundance in carabid beetles from the Netherlands. Data are from Den Boer (1979). Three sets of data are included: A = an unstable habitat, B = heath, and C = woodland. The species have been divided into 3 groups (by Den Boer), denoted by a, b, and c, the main difference between them being that b species are more mobile at the between-site scale than a or c species. The line log $V = \log m^2$ is drawn for each set of species (x-axis positions of the heath and woodland species have been deplaced to improve clarity). In A, all the species have been included, while in the other sets of data only the relatively abundant species are shown (log $m > 0.5$). The regression line in A is log $V = 0.10 + 1.34 \log m + 0.24 \log m^2$.

6.2. Spatial variation

Results on spatial variation confirm the null hypothesis, $b_s = 2$, for similar sites situated far apart (Fig. 6; though note that there are many, not just one species). There is no significance in the fact that log a_s happens to be close to zero.

There was no difference in spatial variation between populations from woodlands and from heath, but the frequently flying macropterous species tend to be less patchily distributed than the others (Table 5). This is what one should expect: more movements decrease abundance differences between sites, though only if the movements do not deviate too much from a random pattern (Hanski 1980a, see Section 7). This result does not support Taylor's model of movements always tracking resources. There was no relationship between spatial variation and the size of the species (Table 5).

6.3. Spatio-temporal variation

The parameters log a_t and log a_s are positively correlated, though the correlation was not significant in the woodland sites (Table 5, Fig. 7). One of the B species, *Pterostichus diligens* Sturm (no. 133 in Fig. 7), was probably an intermediate case between Den Boer's classes, as only 4 % of the individuals were macropterous, and hence able to fly (Den Boer 1979: Table 3). Correlation between the remaining "good" B species was really very good (Fig. 7), though one cannot conclude much on the basis of 5 species. Nevertheless, this suggests that correlation between temporal and spatial variation is especially good in species that move a great deal. In agreement with this, the correlation was better in heath, where Den Boer (1979: Table 3 and p. 83) observed more flying, than in woodlands. Between-site movements are possible by walking in heath but not between the isolated patches of woodland.

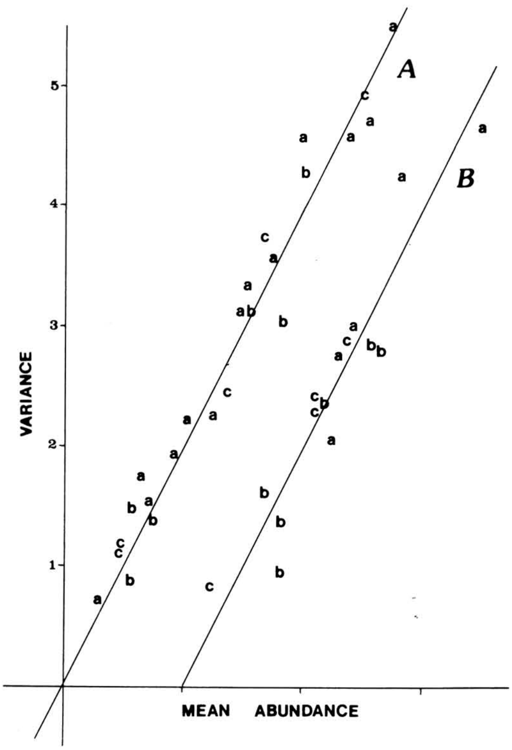

Fig. 6. Regression between (log) spatial variance and (log) mean abundance in carabid beetles from A) heath and B) woodland sites. For further explanations see Fig. 5.

7. Discussion

The most evident difference between birds and insects was the distinctly smaller average value of b_s in birds. This means, in biological terms, that in comparison with insects, birds tend to become relatively less patchily distributed amongst the sampling sites with increasing abundance. Clearly, this would happen if the "best" habitats are/become saturated with avian individuals but not with insect individuals; remaining birds must go somewhere else. In this way I reach a very different conclusion from the one expressed by Taylor et al. (1980: 841): "The linearity of the regressions showed that no species in these samples reached a saturation density that might impose a restraint on spatial variability. Even at high density in woodlands birds retained their characteristic species variance. This is not easily equated with population control by extrinsic factors." The linearity of the regression is one thing, the value of the regression coefficient is another. It appears that the relevant comparison here is in the latter.

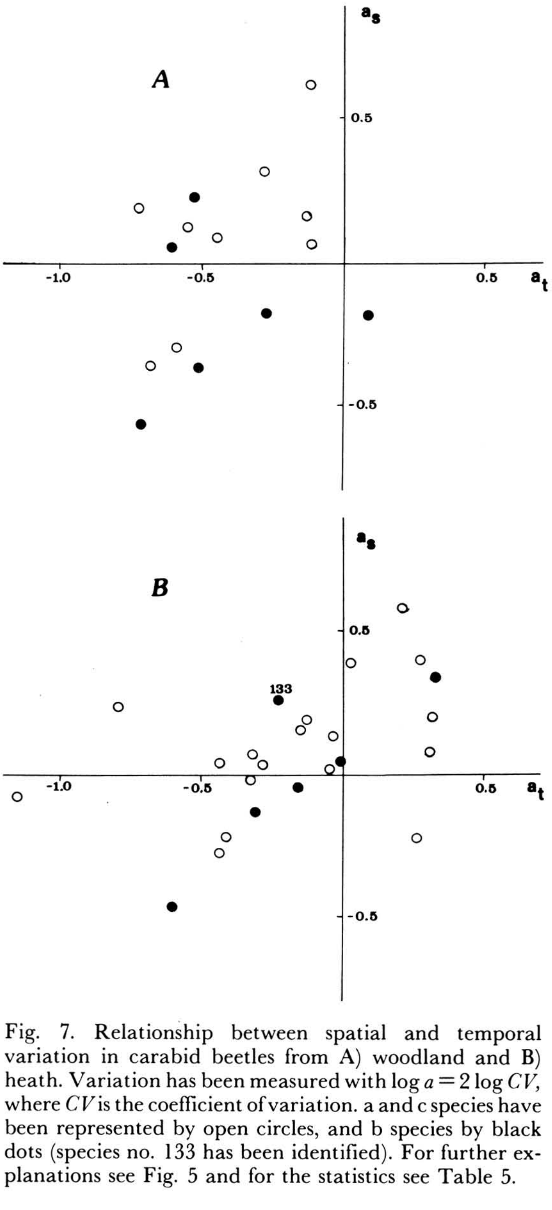

Fig. 7. Relationship between spatial and temporal variation in carabid beetles from A) woodland and B) heath. Variation has been measured with $\log a = 2 \log CV$, where CV is the coefficient of variation. a and c species have been represented by open circles, and b species by black dots (species no. 133 has been identified). For further explanations see Fig. 5 and for the statistics see Table 5.

There are, in actual fact, theories in bird ecology which predict this result. Svärdson (1949) suggested that habitat selection is controlled by the opposing forces of intraspecific and interspecific competition, increasing abundance widening species' habitat spectrum. Fretwell and Lucas (1970) proposed, reasonably enough, that habitats are filled starting from the most suitable ones. The fact that even in birds the regression coefficients are nevertheless around 1.5 proves that variance still increases with mean abundance, either because the "best" habitats are not always saturated, or because "carrying capacities" are not constant but vary with time.

Carabid data confirmed another hypothesis about spatial variation: between-site movements tend to decrease the level of variation. In a study of between-pasture variance in the numbers of dung beetles (Hanski 1980a), I found the same, both in a group of similar species *(Aphodius)*, differing in the intensity of long-distance movements, and within species, spatial variation decreasing during the flight season, apparently due to accumulated movements. On this basis one would expect that in the moths in Britain, the level of spatial variation is negatively correlated with the intensity of movements. Unfortunately, I do not possess data to test this hypothesis.

The function of movements is undoubtedly connected with changing environment (Southwood 1962, 1977, Den Boer 1968, 1979, Vepsäläinen 1979, and many others), though there are theoretical reasons to expect movements to occur in stable habitats, too (Hamilton & May 1977, Comins et al. 1980). Woodlands in Den Boer's (1979) study were relatively stable for carabid beetles, yet movements were observed. Does it follow from the general significance of movements that aphids and other insects maximize some function of dispersal by sophisticated movement behaviour, as has been suggested by Taylor?

Undoubtedly, natural selection will mould the decision patterns of whether to move or not to move, and for how long to move if movement is made. To this extent, movements are certainly non-random. However, if the changing environment is the main cause of between-site movements, a changing environment in itself makes it practically impossible for insects to know exactly where to go. To this extent, movements may well be random, i.e. random with respect to orientation or habitat quality. The fact that an increase in the intensity of movements tends to decrease spatial variance corroborates this hypothesis, but does not support Taylor's Δ-model.

Taylor's scepticism about "population control by extrinsic factors", or habitats being saturated with insect individuals, seems better justified. Indeed, the patterns observed, average b_s close to 2, do not lend much direct support to such theories. The analysis of temporal variation in the Finnish moth community proved that even the most abundant species do not deviate from the common trend of increasing variance with mean abundance. Notably, the simplest possible model, rounding of abundances to integers, explained deviations of the rarest species from the null hypothesis, and it was not necessary to invoke other kinds of demographic stochasticity. A partial explanation of this may be, however, that moth species caught in small numbers from light-traps are vagrants from other habitats rather than members of very small local populations (K. Mikkola unpubl.). There is much scope for experimental field work here.

Do the patterns observed, then, give no hint of density-dependence in the population dynamics of insects? There is one result which does.

The intraspecific b_t values that were reported by Taylor & Woiwod (1980) for noctuids from Britain are mostly smaller than the interspecific b_t calculated for moth communities from southern Finland (this study) and from Britain (Kempton & Taylor 1979) and, in the case of abundant species, smaller than the interspecific regression calculated from the British data presented by Taylor & Woiwod (1980). This result suggests density-dependence in the abundant species.

It is important to note that two kinds of interspecific regressions have been used here, based on either average means and variances of the species from many sites (British data given by Taylor & Woiwod 1980) or on the mean and the average from one site (Finnish data and Kempton & Taylor 1979). The question why the two results differed in the rare species (Fig. 1A) remains unanswered. In the abundant species the results are clear-cut, however, which justifies the tentative conclusion that temporal variation in abundant (but probably not in rare) moths is density dependent if the whole range of variation in abundance is considered; but at any one site, density dependence is usually non-existent or impossible to detect.

The averabe b_t of aphids was close to 2 in abundant and relatively abundant species, which suggests that there is no density dependence in them. Interestingly enough, the b_s values of aphids, unlike those of other groups studied (Fig. 2), show a tendency towards lower values in low abundance. This has a natural explanation in the similarity of the aphid sampling sites, and in the wide geographical distribution of most aphid species; spatial variation is then fundamentally similar to temporal variation, and the model developed in Section 4 to include Poisson variance in the rare species is applicable.

It must be emphasized in this context that density dependence is observed here if $V_2 < a^2 V_1$ when $x_2 = ax_1$, where 1 and 2 denote two samples, and x and V are mean and variance, respectively. Why the variance is V_1 when the mean is x_1 is an open question in this model, though the influence of some factors was identified. Another open question is whether such density-dependent processes exist in nature that $V_2 \sim a^2 V_1$ when $x_2 = ax_1$.

It is not contradictory that moths show signs of density dependence in temporal but not in spatial variation. These results suggest that local moth communities have relatively independent dynamics. On the other hand, the results on spatial variation indicate that local dynamics in local bird communities are more interdependent, which is intuitively obvious in northern European bird communities.

It is significant that spatial and temporal analyses revealed precisely opposite trends in the deviation of intraspecific values of b from the interspecific slope. In temporal variation these deviations reflect the ecology of the species. In spatial variation, the corresponding deviations demonstrate qualitative differences between the species, i.e. their evolution, and specifically the correlation between niche width and abundance.

The role of the environment in determining temporal variation is underlined by the carabid data; unlike any characteristic of the species, the environment affected temporal variation in these insects. Presumably, environmental stochasticity was greater in heath than in woodlands, perhaps because of the openness of the former habitat. Comparison of temporal variation in moth communities from southern Finland (Fig. 3) and from Lapland gave no difference, however, although one would expect environmental stochasticity to be greater in Lapland. Linnaluoto and Koponen (1980) trapped moths with light-traps in northeast Lapland for 8 years. Geometrids were caught in light-traps more frequently than noctuids, a total of 27 species being trapped in 8 years. Six of these were abundant (log $m_t > 0.5$), and their average temporal variation was log $a_t = 0.01$, i.e. the same as for the abundant species in southern Finland (Fig. 3). These two examples underline the difficulty of deducing any general laws about population stability in nature.

In Den Boer's study, populations from the more species-rich habitat (heath) were less stable than populations from woodlands, where species diversity was lower. Kempton & Taylor (1979) found, on the other hand, an indication of positive correlation between diversity and stability in the species composition in the above-mentioned 14 British moth communities. The latter result is expected, other things being equal, as instability promotes local extinctions, which lower species diversity.

8. Concluding remarks

Two conclusions of wider interest are that density dependence in the dynamics of abundant moths was detected only when the whole range of variation in abundance from many sites was considered; and that environmental stochasticity is the likely determinant of these patterns. The latter point was corroborated by the difference observed in average temporal variation in carabid beetles from two different environments.

No support is found for the recent suggestions that apparently chaotic fluctuations in abundance are caused by deterministic population dynamics in the discrete-time context (Beddington et al. 1975, May 1975a). If the level of temporal variation were determined by such "intrinsic factors", a very good correlation between temporal variance and mean abundance would be unlikely, though admittedly nobody appears to have studied which kind of multispecies patterns one should expect. Roughgarden (1979: 345) also observes that no examples of "deterministic chaos" are known from nature. Smith & Mead (1980) make the interesting point that stochasticity tends to reduce the deterministic chaos into simple limit cycles.

The question of density dependence in temporal population dynamics is a difficult one; theoretically, some density dependence is more than likely to occur, but in practice its demonstration frequently fails — and much controversy has arisen. The present results — though far from sufficiently complete to provide a solution — suggest one major reason for the difficulties in demonstrating density dependence in natural populations. In any one community, populations may vary without any or much sign of density dependence; this was found in the Finnish moth community in this paper and by Kempton & Taylor (1979) for British moth communities. Density dependence became apparent here in the abundant moths only when the whole range of variation in abundance from many sites was analysed. The implication therefore is that most of the time most of the populations may vary independently of density, and only seldom are the mechanisms of density dependence, whatever they are, effective. In the rarest species, even this was not detected. The practical conclusion that studies on only one population may lead to inconclusive results is not surprising, though it is frequently ignored. Crude as the present approach may be, it has the distinct advantage of including, within the same frame of analysis, a whole ecological community.

A sceptical view (Miller 1971) about the variance to mean regressions is that they are unable to reveal anything interesting about population dynamics, in the same sense that the lognormal abundance distribution is (said to be almost) uninteresting ecologically (e.g. May 1975; but see Sugihara 1980). This may or may not be true, and only empirical studies can settle the issue. What is needed are testable hypotheses relating variance to mean plots to the established ecological theories. It is in this spirit that the present study was undertaken.

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