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19. TEMPORAL AND SPATIAL VARIABILITY AS NEGLECTED ECOSYSTEM PROPERTIES: LESSONS LEARNED FROM 12 NORTH AMERICAN ECOSYSTEMS

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INTRODUCTION

Evaluating and monitoring the "health" of large-scale systems will require new and innovative approaches. One such approach is to look for ecological signals in the structure of ecological variability observed in space and time. Such variability is sometimes considered something to minimize by clever sampling design, but may in itself contain interesting ecological information (Kratz et al. 1991). In fact, much of ecology can be considered an attempt to understand the patterns of spatial and temporal variability that occur in nature and the processes that lead to these patterns. Despite widespread interest in patterns of variation there have been relatively few attempts to describe comprehensively the temporal and spatial variation exhibited by ecological parameters. As a result, we have no general laws that allow us to predict the relative magnitude of temporal and spatial variability of different types of parameters across the full diversity of ecological systems. Even within single ecosystems, understanding of the interplay

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between temporal and spatial variability is lacking. For example, Lewis (1978) noted that despite a large literature, the relation between temporal and spatial variability in plankton distribution within a lake is not well understood. Matthews (1990) makes a similar point regarding fish communities in streams.

In this paper we describe general patterns exhibited by ecological parameters across a wide variety of ecosystem types. We attempt to answer three basic questions regarding ecological variability: 1) do climatic, edaphic, and biological parameters differ systematically in variability, 2) how is variability partitioned between spatial vs temporal components, and 3) to what extent are ecological parameters spatially or temporally coherent (Magnuson et al. 1990)? By coherence we mean the tendency for different locations within a landscape to behave similarly in different years independent of the average for the locations (temporal coherence) or the tendency for locations within a landscape to be consistently different regardless of the year (spatial coherence). We use data collected at 12 diverse North American ecosystems represented in the Long Term Ecological Research (LTER) network. For each of the 12 LTER sites, data are available for several years at several locations. Therefore, we are able to analyze both the spatial and temporal aspects of variability at each site.

In addition to these general questions about patterns of variability and the effects of scale, we also used cross system comparisons of variability to test two smaller-scale ecological hypotheses: 1) that deserts are more variable than lakes temporally, but less variable spatially; and 2) that in predator-prey pairs, the smaller-shorter lived member of a pair is more temporally variable regardless of whether it is the prey or the predator. We posited that deserts are more variable among years than lakes because they are more sensitive to among year differences in weather than are physically buffered lakes. Conversely, we hypothesized that lakes would be more variable spatially because they are more isolated from one another than are areas of continuous desert. We also felt that variability in a population was more a function of its life history than its position in a food web.

Variability is highly dependent on the temporal and spatial scales of the data set and on the level of aggregation of the parameter of interest (e.g. species level vs community level) (Allen and Starr 1982, Frost et al. 1988, Frost et al. 1992, Wood et al. 1990) This scale dependence raises a complication in comparative studies, because it is possible to confound differences in patterns of variability with differences in scales of measurement at two or more systems. There are two different aspects of scale, grain and extent, and the effect of these on observations of variability need to be considered independently (Allen and Starr 1982; O'Neill et al. 1986; Turner 1989; Wiens 1989). Grain refers to the level of resolution of the study. Extent refers to the size of the study area or the duration of the study period. In this study we focus on a temporal grain of one year because a year is a physically and biologically meaningful unit of time for which data are available. The spatial grain was more difficult to fix, however, because the size of study units sampled was not standardized across LTER sites, and varied by a factor of about 64000 across the 12 LTER sites. Therefore, we were required to address two scale related questions: 1) what is the effect of sampling unit size on measured variability; 2) how sensitive is the observed variability to the temporal extent of the measurements. We also considered the degree to which observed variability is related to degree of aggregation of the parameter measured.

METHODS

The Study Sites

The 12 sites from the LTER network are listed in Table 1 and their locations are shown in Figure 1. Ecosystem types represented include desert, prairie, alpine tundra, forest, lake, estuary, and river. We intentionally chose diverse sites so that our comparison of variability would include a wide range of biotic and abiotic conditions. Descriptions of the sites are given in Van Cleve and Martin (1991).

Figure 1. Locations of 12 LTER sites participating in this study.

Table 1. Data set characteristics for each of the 12 LTER sites.

LTER Site	Abbreviation	Number of Locations	Number of Years	Size of Location (ha)	Total Number of Variables	Number of Climatic Variables	Number of Edaphic Variables	Number of Plant Variables	Number of Animal Variables
Cedar Creek Natural History Area	CDR	4-18	5-6	3	17	0	0	12	5
Hubbard Brook Experimental Forest	HBR	2-6	5-6	3.7	49	4	45	0	0
Illinois River	ILR	5	4-5	6400	19	5	6	0	8
Konza Prairie Research Natural Area	KNZ	6-9	5-7	50	52	3	0	22	27
North Inlet	NIN	3	6	880	57	6	48	3	0
Niwot Ridge	NWT	6	5	0.1	28	6	0	10	12
Northern Temperate Lakes	NTL	5-7	4-6	240	102	6	50	9	37
H. J. Andrews Experimental Forest	AND	3-9	4-17	15	33	21	9	3	0
Central Plains Experimental Range	CPR	4-9	4-6	2	13	0	0	12	1
Bonza Creek Experimental Forest	BNZ	7-14	12-14	0.1	4	3	0	1	0
Jornada	JRN	6-7	3-5	1.1	56	11	4	13	28
Coweeta Hydrologic Laboratory	CWT	3	6-17	96	18	12	6	0	0
Total					448	77	168	85	118

The Data Set

The data set, VARNAE (Variability in North American Ecosystems) was compiled in preparation for a workshop attended by representatives of each of the 12 sites (Kratz et al. 1991; Magnuson et al. 1991). The data set consists of a series of derived statistics for each of 448 parameters. For each parameter at least one LTER site had gathered data over several years (mean 5.9 years, range 3-17 years) at several locations at the site (mean = 5.8 locations, range 2-18 locations). Throughout this paper we use "location" to refer to one of several study areas within an individual LTER site, and "site" to refer to different LTER sites. Locations within an LTER site might, for example, refer to individual lakes, places along a transect, or different forest plots, whereas sites refer to Cedar Creek Natural History Area, Hubbard Brook Experimental Forest, etc. Data for each parameter were summarized to fill out a "year by location" matrix for each LTER site. Each entry in the matrix was the best estimate of the parameter for a given year at a given location, and may itself have been summarized from many individual measurements. For example, for mean summer chlorophyll *a* concentration at the North Temperate Lakes site, a five year by seven location (lake) matrix was completed, with each entry estimating the mean summer chlorophyll concentration in a particular lake at the North Temperate Lake site for a particular year. In this example, each of the 35 year-lake estimates in this matrix was derived from 14-50 individual measurements of chlorophyll.

This compilation resulted in 448 "year by location" matrices for the 12 LTER sites in total. For each of these matrices we used a two way analysis of variance framework to compute the variance associated with year and with location. The remaining variance is attributable to a combination of year-by-location interaction and error. Because our matrices had no replication in each of the cells, we could not separate error from interaction. Up to this point this is the same analytic framework used by Lewis (1978) and Matthews (1990) albeit at a different time and space scale. However, because we wanted to compare the variabilities of parameters measured in different units, before we computed the analysis of variance we relativized each matrix by dividing each element in the matrix by the grand mean of that matrix. The resulting "relative variances" are equivalent to the square of the coefficient of variation. The advantages of using relative measures of variation in ecological analyses have been reported by Kratz et al. (1987, 1991) and Rothschild and DiNardo (1987). None of the matrices had any missing data. The relative variances were computed using the following formulas:

$$V_L = (MS_L - MS_{YxL})/N_Y$$
$$V_Y = (MS_Y - MS_{YxL})/N_L$$
$$V_{YxL} = MS_{YxL}$$
$$V_T = V_L + V_Y + V_{YxL}$$

where, V refers to variance, MS refers to mean square, and L, Y, YxL, and T refer to location, year, interaction plus error, and total, respectively, from the two way analysis of variance; N_Y is the number of years in the matrix; and N_L is the number of locations in the matrix. Corresponding CV's are:

$$CV_L = \mathrm{sqrt}(V_L)/\mu$$
$$CV_Y = \mathrm{sqrt}(V_Y)/\mu$$
$$CV_{YxL} = \mathrm{sqrt}(V_{YxL})/\mu$$
$$CV_T = \mathrm{sqrt}(V_L + V_Y + V_{YxL})/\mu$$

where CV is coefficient of variance, μ is the grand mean of the matrix, and other terms are as defined above. V_Y is a measure of the variability that is due to the tendency for all locations to behave similarly in different years independent of the average for the locations. As an example, consider again chlorophyll concentrations at the Northern Temperate Lakes site. If in certain years (perhaps years of lower that average precipitation leading to lower than average nutrient loading) each lake had chlorophyll concentrations lower than the lake's average, and in years of plentiful rain each had values higher than the location's average, V_Y would be relatively large. On the other hand, if some lakes responded to drought years by having lower than normal values, while other lakes responded by having higher than average values, V_Y would be relatively low. Therefore, V_Y measures the degree to which a parameter is "coherent" in time (Magnuson et al. 1990). Similarly, V_L measures the degree to which a parameter is "coherent" in space, i.e. the degree to which difference in locations occurs independent of the year.

The interaction term is a measure of additional variability that is not associated with a fixed location effect nor a fixed year effect. This variance has been termed "ephemeral" because it is a measure of patchiness that differs on different dates (Platt and Fillion 1973, Lewis 1978). However, because the interaction term is not associated with fixed effects of location or years, it is also possible to interpret it as an additional amount of variability that is "incoherent" with respect to location or year. Therefore, it represents an additional amount of temporal variability, and symmetrically, an additional amount of spatial variance. We interpret the sum of the fixed year effect and interaction variabilities as total year variability, and similarly, the sum of the fixed location variability and interaction variability as the total location variability. These two terms are computed as follows:

$$V_{TY} = V_Y + V_{YxL}$$
$$V_{TL} = V_L + V_{YxL}$$

where V_{TY} is total year variability and V_{TL} is total location variability. In fewer than 5% of the parameters one of the computed variance terms was negative, and these negative values were set to zero.

For each of the 448 parameters we computed these six measures of relative variation: coherent year, coherent location, incoherent, total year, total location and total. Incoherent, total year, and total location are somewhat biased because they each contain the interaction term and we were unable to separate measurement error from the interaction term. Therefore, we overestimate each of these three terms. The effect of this bias is less important in our estimates of total year and total location variability because both terms contain the same bias and comparisons of the two terms will be valid, if not numerically exact.

We classified each of the 448 parameters into one of four categories: climatic, edaphic, plant related, or animal related. This grouping was necessary because, although each of the sites has similar long-term goals, the sites differ so much from each other that no single parameter was measured at all sites. The number of parameters available for this study in each of these categories at each LTER site is given in Table 1. An indication of the types of parameters grouped into the four categories for each site is given in Table 2.

Sensitivity to scale

Temporal Scale - Three of the LTER sites had data sets spanning at least 14 years. These longer data sets allowed us to test the sensitivity of our estimates of variability to the number of years in the data string. We tested the sensitivity by computing the average for each of the six variance estimates using all combinations of two consecutive years, three consecutive years, etc. For a 14 year data set, for example, there were 13 combinations of 2 consecutive years, 12 combinations of 3 consecutive years, 11 of 4..., 2 of 13. Finally, of course, there is just one combination of 14 consecutive years. We performed the sensitivity analysis for five parameters: two climatic (maximum and minimum streamflow from Coweeta), two edaphic (total N and Ca from H. J. Andrews), and one biological (basal area increments of trees from Bonanza Creek).

Spatial Scale - To understand the influence of spatial grain on variability we correlated the variability exhibited at each site with the size of the sampling unit. Determining the size of the sampling unit was problematic. The approach we took was to use the size of the location thought to be represented by the measurement. This size was determined using expert judgment by representatives from each site. For example, at the NTL site the samples are often taken at a central location in a lake. But because the lakes are generally well mixed horizontally the sample represents the entire lake. Therefore, the average location size for NTL was the mean area of the seven lakes. Measures of variability included in the analysis were coherent year, coherent location, incoherent, and total for each of climatic, edaphic, plant, and animal data, yielding a total of 16 measures of variance.

Aggregation Scale - We tested the relationship between observed variability and level of aggregation for edaphic, plant, and animal parameters. Edaphic parameters were grouped into three aggregation levels, and plant and animal parameters were grouped into four levels. Aggregation level was not a meaningful concept for the climatic data used in the study. For edaphic data, the finest level included parameters like ammonia or

Table 2. General description of the parameters by site and type. CPUE is catch per unit effort.

LTER Site	Climatic	Edaphic	Plant	Animal
Cedar Creek	-	-	Biomass of functional groups	CPUE of small mammals
Hubbard Brook	air temperature	major ions, nutrients, DOC, Al	-	-
Illinois River	water temperature and level	turbidity, pH, solids, conductance	-	CPUE of fish
Konza	soil moisture	-	% cover and diversity	relative abundance of grasshoppers and small mammals; diversity of small mammals
North Inlet	water temperature	nutrients, DOC, salinity, sediment characteristics	chlorophyll	-
Niwot Ridge	air temperature, precipitation, growing season length	-	biomass of species and groups	biomass and density of small mammals
Northern Temperate Lakes	water temperature	ions, nutrients, dissolved oxygen	chlorophyll	CPUE of fish, density of zooplankton
H.J. Andrews	streamflow, precipitation, air temperature, soil temperature	ions, nutrients in streams	litterfall	-
CPER	-	-	frequency, production	cattle weight gain
Bonanza Creek	air temperature, precipitation	-	basal increments of trees	-
Jornada	soil moisture, water input	soil nitrogen	cover and diversity of functional groups	density and diversity of small mammals and ant colonies
Coweeta	precipitation, streamflow	calcium, chloride	-	-

nitrate, the next level contained parameters such as total N. Finally, the coarsest level contained parameters such as total conductivity or total base cations. For the biological parameters the finest level contained species level information, the next contained guild level data such as C_3 grasses or zooplanktivorous fishes, the next coarsest included major groups such as all grasses or all fishes, and the coarsest level data included total animal or plant data such as total biomass of plants. To test for a relationship between variability and level of aggregation we computed the median of the total variability for each level and examined the relationship between variability and aggregation level for edaphic, plant, and animal data.

RESULTS

Sensitivity to Scale and Data Aggregation

Estimates of variability were relatively insensitive to the number of years in the data set when four or more years of data are included, at least to a maximum of 16 years (Figure 2). Estimates based on less than four years of data tended to be larger than those based on longer durations, for example, at Andrews for N and Ca. One possible exception to this general pattern in the data sets we analyzed was total nitrogen at Andrews which exhibited a slight decreasing trend for coherent location variance and a slight increasing trend for incoherent variance as more years were added. We conclude that 5 years of annual data for the 448 parameters we analyzed were adequate to estimate variability and that differences in the number of years available above 5 years did not bias the overall analyses.

We found little evidence for a relationship between spatial grain and variability. Of the sixteen possible correlations between variability and size of sampling unit, none had a correlation coefficient above 0.5 (in absolute value) and none were significant. However, 14 of the 16 correlation coefficients were negative, indicating that samples representing larger areas tended to be less variable spatially and temporally. We had difficulty assigning sizes to sampling units, and it is possible that we did not find a relationship between variability and size of sampling unit because of our definition of sampling unit. We concluded that differences in the size of sampling units among LTER sites should not proscribe further analyses, but that interpretation of differences in variability among sites may be biased.

There was a strong relationship between total variability and level of aggregation for biological parameters, but not for edaphic parameters (Figure 3). For edaphic parameters there was no statistical difference in variability of parameters at species, group, or major group levels of aggregation ($p > 0.1$, this and subsequent p values in this paragraph are based on Mann-Whitney tests). For plant parameters, species-level data were not more variable than guild-level data ($p = 0.745$), however, both species level data and guild level data were significantly more variable than group data ($p = 0.003$; $p = 0.004$, respectively). For animal parameters species-level data were more

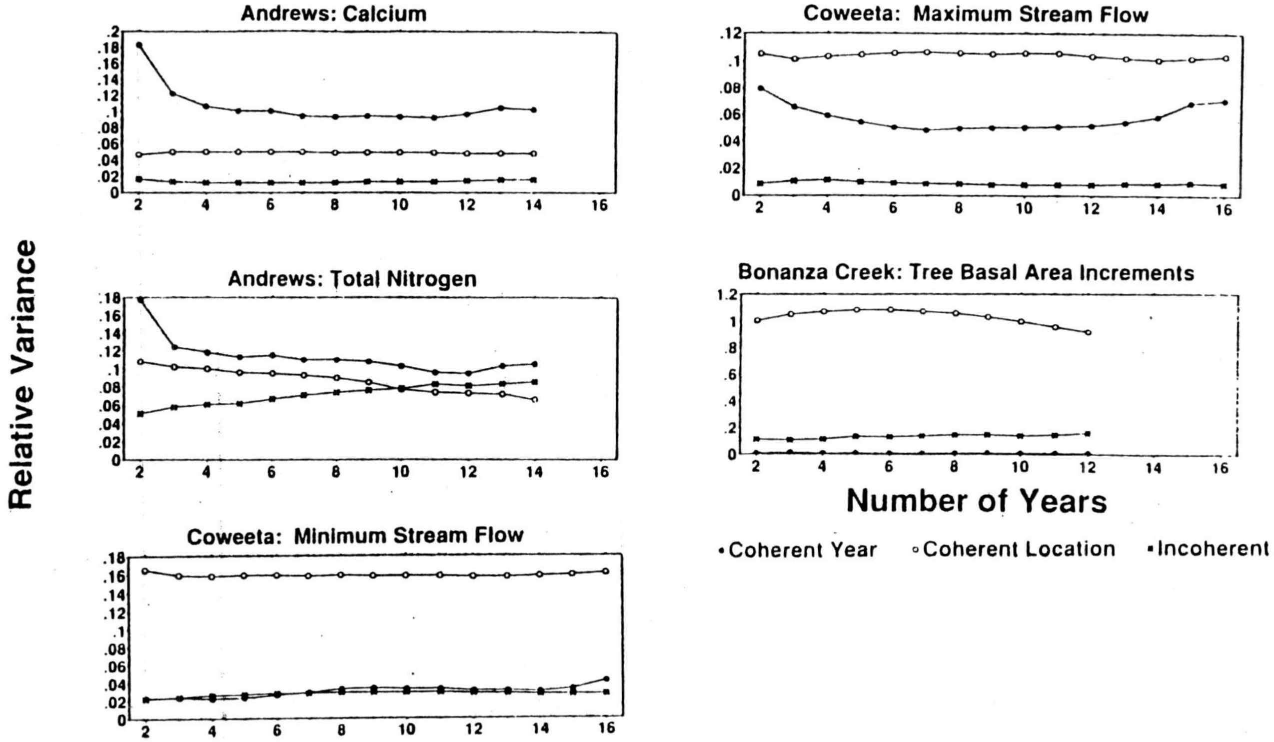

Figure 2. Sensitivity of coherent year, coherent location, and incoherent variance to number of consecutive years of data used for calculation.

variable than guild-level data ($p < 0.0001$) and group data ($p < 0.0001$); and guild-level data were more variable than group-level data ($p = 0.03$). We concluded that differences in level of biological aggregation could significantly bias our analyses and that comparisons should be made at the same level of biological aggregation.

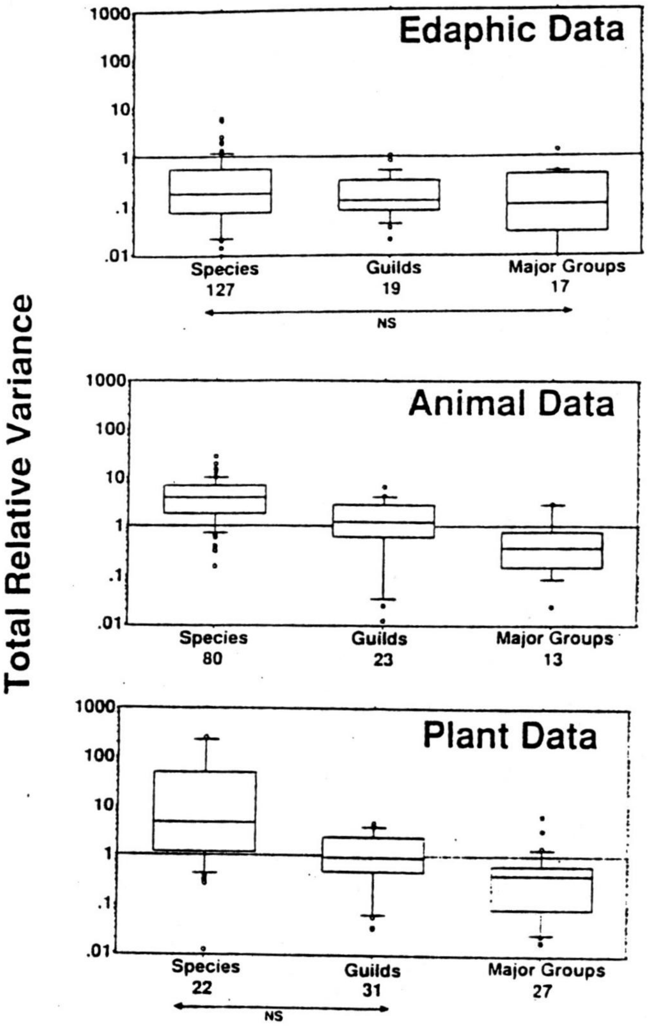

Figure 3. Relationship between total relative variance and aggregation level of data for edaphic, animal, and plant data. Numbers under group identifiers indicate sample sizes. Lines under plots for edaphic and plant data indicate groups that do not differ significantly at the P=0.05 level.

Overall Patterns of Variability

We compared the total relative variability of climatic, edaphic, plant, and animal data (Figure 4; Table 3). Because level of aggregation is an important determinant of variability in biological data, we used only species level data for plant and animal variables. Climatic data were all at the same level of aggregation and edaphic data showed no pattern with aggregation, so we used all climatic and edaphic data. We made pairwise comparisons for each of the four variable types.

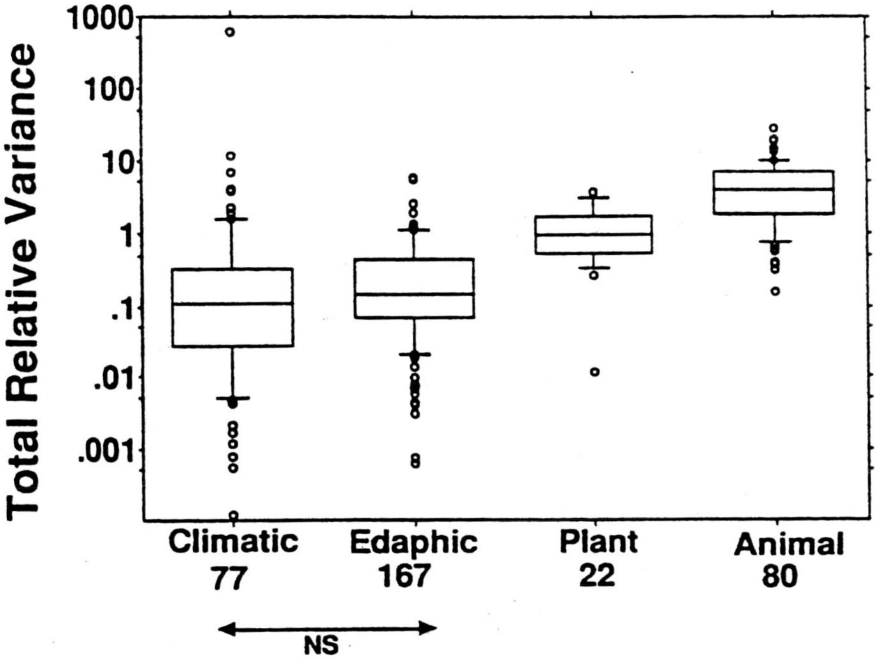

Figure 4. Total relative variance of parameters classified into climatic, edaphic, plant, and animal groupings. Numbers under parameter type indicate sample size. For plant and animal categories, only species-level data were used. Climatic and edaphic data did not differ significantly with respect to total relative variance.

Table 3. Comparison of variability of climatic, edaphic, plant, and animal data. Group with greater variability is indicated; numbers are p-values for Mann-Whitney test. Bold-faced indicates p-values less than 0.05.

Comparison	**Coherent Location**	**Coherent Year**	**Incoherent**	**Total Location**	**Total Year**	**Total**
Climatic vs Edaphic	**Edaphic** **0.012**	Climatic 0.064	Edaphic 0.164	**Edaphic** **0.025**	Climate 0.91	Edaphic 0.128
Climatic vs Plant	**Plant** **0.0001**	Climatic 0.40	**Plant** **0.0001**	**Plant** **0.0001**	**Plant** **0.001**	**Plant** **0.0001**
Climatic vs Animal	**Animal** **0.0001**	Animal 0.50	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**
Edaphic vs Plant	**Plant** **0.0001**	Plant 0.70	**Plant** **0.0001**	**Plant** **0.0001**	**Plant** **0.0012**	**Plant** **0.0001**
Edaphic vs Animal	**Animal** **0.0001**	**Animal** **0.012**	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**
Plant vs Animal	Animal 0.056	Plant 0.27	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**	**Animal** **0.0001**

For total variance, biological parameters were significantly more variable than nonbiological parameters. Climatic and edaphic parameters did not differ significantly in variability. However, both climatic and edaphic parameters were significantly less variable than either plant or animal data. Plant data were also significantly less variable than animal data. This general pattern also held for the other variability types, except for coherent year variability, where the only significant difference in variability was that animal parameters were more variable than edaphic parameters.

We also tested for differences among coherent year, coherent location, and incoherent variability (Figure 5). For these tests we stratified the data by climatic, edaphic, plant, and animal. The general pattern that emerged was that variability was ranked in the following order:

coherent location > incoherent > coherent year

This pattern held for edaphic and plant data. For animal data this pattern also held with the exception that there was no difference between coherent location and incoherent variability. Interestingly, for climatic data there was no significant difference among any of these three variability types. Total coherent variability (i.e. the sum of coherent year and coherent location variability) was larger than incoherent variability for climatic, edaphic and plant data, but there was no difference for animal data.

Desert vs Lakes

Deserts are exposed ecosystems with a highly variable, severe environment where variation in precipitation is critical. In contrast, a lake can be considered as a more constant environment, well buffered from thermal change by the mass and heat capacity of water and, depending on the organism, from biological invasions owing to isolation. To evaluate the prediction that deserts are more variable than lakes, we made a detailed comparison of the variabilities exhibited by the Jornada desert and the North Temperate Lakes sites. For these comparisons we stratified the data into the following, non-mutually exclusive groups: all data, abiotic, climatic, edaphic, and animal. Because of the relationship between aggregation level and variability in biotic data, we used species level data only, which meant that no comparisons for plant data could be made. For year-coherent variability, the desert site was significantly more variable than the lake site for all data considered together, climatic data and abiotic data (Table 4).

For location coherent variability, lakes were significantly more variable for abiotic data, but the two sites did not differ with respect to the other data groups. For incoherent variability, the lake site was more variable for animal data, whereas the desert was more variable for abiotic data. Finally, for total variance the desert was significantly more variable for the categories of all data, abiotic data, and climatic data.

Predator vs Prey

How variable in time are prey populations relative to those of their predators? One hypothesis, consistent with many ecological models, is that the species which is smaller-bodied, shorter-lived, and (or) has a faster turnover rate should respond most intensely to environmental variations and therefore be most variable. In contrast, larger-bodied, longer-lived, species with slower turnover rates should persist through short-term environmental fluctuations and therefore be less variable. We tested this hypothesis using annual variances of co-occurring predator-prey pairs.

Table 4. Comparison of variability between Jornada Desert and North Temperate Lake sites. Results of Mann-Whitney U test are shown. Site that is more variable is indicated. NS indicates p-value > 0.05. For significant differences p-value is given.

Variable	Location Coherent	Year Coherent	Incoherent	Total
All Data	NS	Desert 0.0001	Desert 0.0007	Desert 0.0018
Climatic	NS	Desert 0.0012	Desert 0.0009	Desert 0.0009
Edaphic	NS	NS	Desert 0.0075	NS
Animal	NS	NS	Lake 0.0208	NS
Abiotic	Lake 0.0058	Desert 0.0006	Desert 0.0001	Desert 0.0009

All species level data were examined to select predator-prey pairs. We required that (1) neither species be rare, (2) the prey be a major diet item for the predator, and (3) the predator be among the major causes of mortality for the prey. Fourteen pairs of predator and prey met these criteria. The pairs include 10 terrestrial plant-herbivore pairs, and 4 aquatic carnivore-carnivore pairs (Table 5).

Predator-prey pairs were evenly divided with regard to whether prey (7) or predator (7) was smaller and shorter-lived. With regard to which member had highest annual variance, the division was nearly even. In 6 pairs the prey was more variable; in 8 pairs the predator was more variable.

However, cross-classification of the predator-prey pairs showed that the smaller, shorter-lived species had higher annual variance regardless of whether it was predator or prey (Table 5). The null hypothesis that the probability of a species being shorter-lived is independent of its probability of having higher annual variance was tested using Fisher's exact test (Sokal and Rohlf 1981). The p value of 0.05 supports the inference that shorter-lived members of predator-prey pairs tend to have higher annual variance.

Table 5. Analysis of variability of predator vs prey as a function of life span. For each predator-prey pair, organisms with shorter lifespans are underlined and those that exhibited more variability are in bold.

Site	**Predator**	**Prey**
Konza	mouse	**annual grass**
Konza	**grasshoppers**	forbs
Konza	**insects**	grasses
Konza	**mouse**	*Poa*
Konza	**mouse**	C_3 grass
Northern Temperate Lakes	**northern pike**	yellow perch
Northern Temperate Lakes	muskellunge	**yellow perch**
Northern Temperate Lakes	yellow perch	***Leptodora***
Northern Temperate Lakes	**yellow perch**	Chaoborus
Jornada	mouse	**annual C_3 forbs**
Jornada	mouse	**annual C_4**
Jornada	**ants**	**perennial C_4 grass**
Cedar Creek	**mouse**	grasses
Cedar Creek	**mouse**	forbs

DISCUSSION

An important result of this work is the observation that, for biological data, level of aggregation (e.g., species, guild, major group) had greater effect on observed variability than did spatial or temporal extent of the data set. The level of aggregation at which data are collected is a neglected aspect of effects of scale in ecology (Frost et al. 1988; Rahel 1990). The level is often dictated by logistical rather than ecological reasons, even though the choice of aggregation level may be one of the most important determinants of a study's conclusions. For edaphic data, we observed no effect of aggregation on the relative variability. But for biological data the more aggregated the parameter, the lower the variability of the parameter relative to its mean. This difference in response to aggregation between biological and edaphic data could result from compensatory species interactions such as predation and competition. Increases or decreases in one species can be compensated for by the numerical response of another affected species. Such mechanisms, for example, result in density compensation in the abundance of species on islands (Wright 1980) and in lakes (Tonn 1985).

The effect of aggregation on observed variability has an important implication for detection of long-term trends or patterns. To detect trends and patterns it is necessary to monitor parameters that have two, potentially conflicting characteristics. Parameters must be sufficiently sensitive to environmental conditions to indicate changes that occur. But they also must not exhibit so much natural variability as to mask detection of changes in environmental conditions. Biological parameters which have a low degree of aggregation, such as species abundances, are sensitive indicators of environmental change (Schindler 1987), but exhibit so much variability that assessing the cause of change can be difficult. On the other extreme, parameters such as total plant biomass, having a high degree of aggregation, tend to be stable over time or space, and may not be sensitive of subtle environmental changes. Thus, understanding the relative variability and sensitivity of parameters as a function of aggregation level, become important in choosing optimal parameters for a monitoring program.

An important lesson for long-term ecological research is that spatial variability exceeds year-to-year variability. This robust result appears in the dominance of coherent location and incoherent variation over year coherent variation for all data groups except climatic data (Figures 5a and c) and by the dominance of coherent location variability over incoherent variability for edaphic and plant data (Figure 5b). Clearly, a single location within a landscape is insufficient to describe the full range of behaviours of systems within the landscape. One way to circumvent this problem is to assess the degree of variability among locations in a landscape for a limited period of time and then monitor a single location over the long term. This strategy would allow placement of the long-term measurement site within the context of the spatial variability exhibited by sites across the landscape. However, improvement of the long-term sampling is not likely to be this simple because incoherent variation is also large. Incoherent variation includes both error variability and variability owing to year by location interaction. Within our data framework these cannot be separated. If we assume that some percentage of the

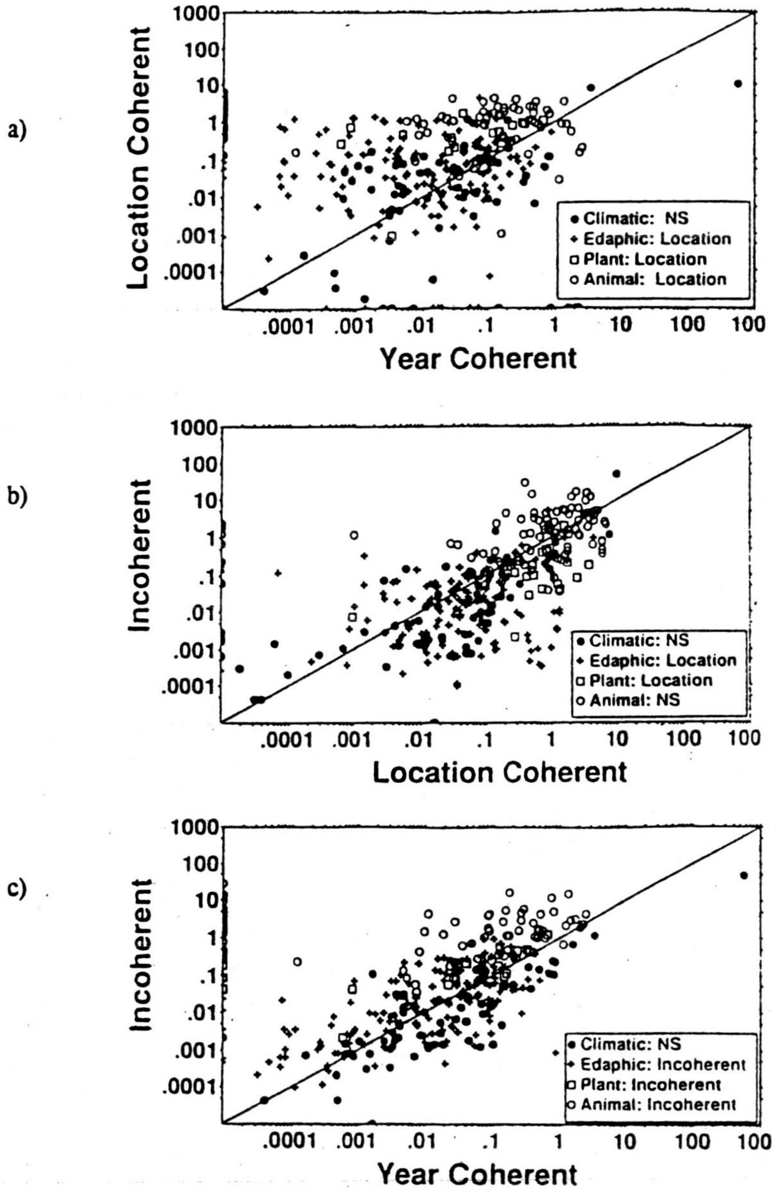

Figure 5. Relationships among year coherent, location coherent, and incoherent variability. Legend for each figure indicates for each variable type (climatic, edaphic, plant, or animal) which type of variance was significantly larger. (NS = no significant difference). All climatic and edaphic data were used, but only species-level biological data were used.

incoherent variation is from interaction, then it will be necessary to gather long-term data on a set of locations within a landscape to understand the dynamics of the spatial distribution of ecosystem properties among years.

An intriguing result of our study is that biotic data exhibit more variability than abiotic data both for animal and plant data in comparison with either climatic or edaphic data. The only exceptions to the twenty-four comparisons made in Table 3 are for the coherent year variation of climate versus plant or animal data, and the coherent year variation of edaphic data versus plant data. Variations in climatic and edaphic properties are magnified by the responses of organism to variation in physical-chemical factors among locations and owing to interaction between year and locations. An alternative explanation that measurement error is greater for biotic than abiotic data could be raised to explain the higher level of incoherent variation, but this would not be consistent with the greater location variation. Thus, at least some of these differences are generated from the behaviour of the ecological systems observed. The ability of organisms to exhibit exponential responses in growth and reproduction to incremental changes in physical and chemical factors is consistent with our result and provides one rationale. Growth and reproduction are often exponentially related to certain environmental variables. Responses to temperature provide a clear example for rate processes with ectothermic living systems (Regier et al. 1990). The vagility of animals and to some extent even plants to move among locations in a set of optimization responses also could contribute to the observation.

Within the abiotic data, the edaphic data are more variable among locations than are climatic data. Apparently, the common weather flowing across each landscape homogenizes some of the potential differences that can develop in microclimate. In contrast, the more stationary soil maintains edaphic differences in microhabitats associated with differences in morphology, hydrology, deposition or erosion, and elevation among locations.

Within the biological data, the animal data are more variable than plant data in terms of incoherent variability. Both explanations we present below rely on the greater vagility of animals compared with plants. The greater variability in animal data versus plant data could result from the greater mobility of animals that can respond quickly to spatial and temporal differences in the environment. This idea is supported by the fact that it is the incoherent variability rather than the coherent variability that is greater for animals than plants. Animals would have a greater possibility of altering their spatial distribution from year to year owing to their mobility than would the more slowly responding plants. Alternatively, we cannot eliminate the possibility that the greater incoherent variability for animals over plants results from greater sampling error with animals than with plants. The vagility of animals and their ability to hide from observers or to avoid and escape sampling devices could produce greater sampling variation than would be expected with plants that are essentially sessile by comparison. Both arguments are rational and we do not know which is more important in determining the greater incoherent variability of animal over plant data.

Comparisons Among Ecosystems

We had initially hoped to compare and contrast the properties of variability among each of the LTER sites included in this paper. We thought that some sites might be more dominated by location coherent variation, others by year coherent variation or by incoherent variation and that these again might differ in interesting ways for climatic, edaphic, plant and animal parameters. Only two sites had a rich enough array of biologic and abiotic parameters at the species level to make such a comparison with a relatively complete design. Fortunately, the two sites, deserts and lakes, differed dramatically enough in setting to make the comparison a challenge. The view that deserts and lakes are like the proverbial "apples and oranges" would discourage most conventional comparisons. Thus, the use of these dimensionless metrics of variation that are neither ecosystem nor parameter dependent were thought to have some promise. The concern that the differences in scale of spatial measurement were sufficient to bias any comparison of variation have been set aside for the one exploratory analysis on deserts versus lakes.

Desert vs Lakes

Deserts are exposed ecosystems with a highly variable, severe environment where year to year variation in precipitation is critical. In contrast, lakes are more constant environments, well buffered from thermal change by the mass and heat capacity of water, from certain chemical changes by bicarbonate buffering of pH, and from biological invasions owing to physical isolation. In terms of spatial connectivity locations along a desert catina appears more open to movement and connected than individual lakes in a lake district which are island-like and isolated from each other by land barriers and can take on their own unique behaviours. From such considerations we hypothesized that deserts would be more variable than lakes among years but that lakes would be more variable than deserts among locations. The locations were those along a catina at the Jornada Desert site and among lakes at the North Temperate Lakes site.

Our data generally supported the hypothesis that deserts are more variable than lakes among years and lakes more variable than deserts among locations (Table 4). The year coherent variability that determines the general conclusion is for the climatic data; thus, as expected, deserts are less buffered from year to year differences in climate than are lakes. The location coherent data that determines the general conclusion are for the abiotic data; thus a suite of isolated lakes differ more in physical-chemical properties than do locations along a catina.

With the exception of animal data, incoherent variability also was greater for deserts than lakes. Thus the interaction between year and location for physical-chemical factors appears to be greater in deserts while the same interaction for animals appears greater for lakes. The alternative explanation that physical-chemical variables are measured with more error in deserts than lakes and animals with more error in lakes could be possible; lakes are mixed by wind and buffered from short term change; thus the measurements could be more integrative for lakes than deserts. We see no inherent reason why sampling error for animals should be greater for lakes than for deserts. One explanation for a large incoherent variation for animals in lakes is that year to year variation in fish recruitment (reproduction) is notoriously high (Wootton 1990) and is not coherent among lakes (Magnuson et al. 1990). For example, yellow perch, *Perca flavescens*, at the North Temperate Lakes Site exhibit strong year classes every few years, but populations are not synchronous in the timing of the strong year classes in the different lakes.

This analysis points out that hypothesized differences between radically different ecosystem types can be tested by comparison of variability metrics. The analysis was consistent and to some extent explainable even though we were concerned by absence of certain types of variables, by poor representation of some variable types, and by differences in the spatial scale of measurements. Our suggestions for further work include using variables that can be measured at the same spatial scales in a wide variety of ecosystems, designing a measurement system that would allow separation of interaction from sampling error included in the incoherent variation and designing studies with a higher overlap in parameter types.

For example, Kratz et al. (1991) compared the variability of limnological parameters across a gradient of lakes ranging from high to low in landscape position. By comparing the same parameters measured at the same spatial and temporal scales they were able to show that lakes higher in the landscape of the Northern Highland Lake District of northern Wisconsin were more variable than those lower in the landscape (Figure 6). By analyzing the variability patterns of over 60 parameters they were also able to infer mechanisms that might lead to such a gradient in variability.

Predator Prey

Despite the small sample size, the analysis of predator-prey variability relationships suggests a significant pattern. There is no evidence that the relative variability of predator-prey pairs can be explained by trophic position. Rather, the smaller, shorter-lived species tends to have higher interannual variance, regardless of whether it is predator or prey.

The "shorter-lived, higher-variance" rule merits further investigation using a larger data set that includes a wider range of trophic levels from both terrestrial and aquatic systems. Several intriguing questions remain unanswered. How general is the rule? In view of the fact that estimates of population variance increase with the duration of the data set (Pimm and Redfearn 1988), will the rule hold at even longer time scales than those examined here? If the rule is general, then what causes exceptions? Are exceptions to the rule indicative of strong regulation of one population by the other? Do exceptions occur at regular levels of the trophic hierarchy, indicating alternate control by competition and predation (Hairston et al. 1960; Oksanen et al. 1981; Persson et al. 1988)?

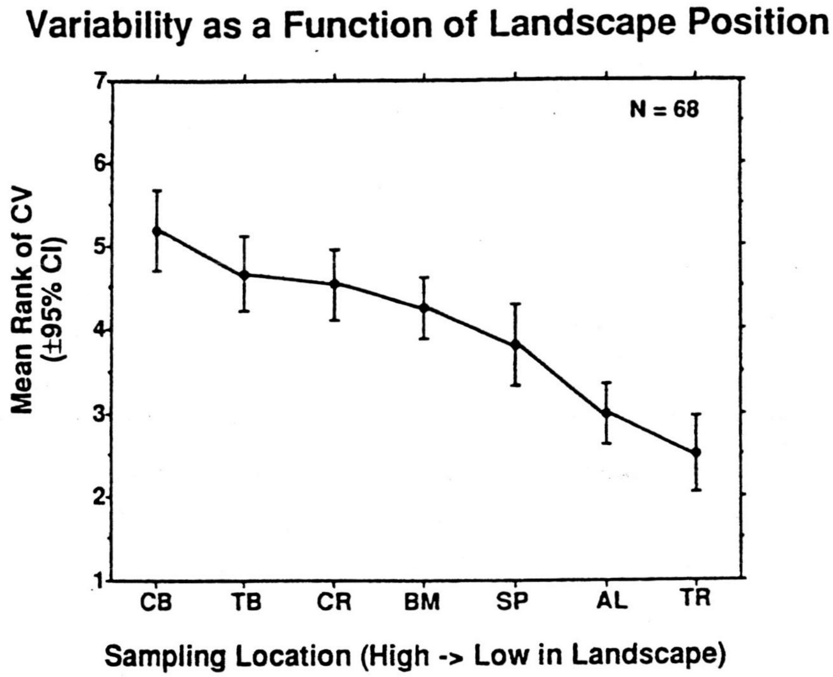

Figure 6. Average ranks of coefficients of variation (CV) as a function of landscape position for seven lakes in the Northern Higland Lake District of northern Wisconsin (adapted from Kratz et al. 1991).

IMPLICATIONS

Comparative studies in ecology vary in scale from how a single organism lives under a variety of different environments to how abstract, system-level properties vary in different system types. This study is an example of the latter scale. We found that there were few precedents to act as guideposts in conducting comparative ecology at such a general scale, yet we believe that powerful understanding can derive from comparison at the most general levels. Here we list what we consider to be some of the broader implications of our study:

1) The wide range of ecological systems on earth should not act as a deterrent to cross-system comparisons. However, the greater the variety of systems

considered, the more general the metric of comparison must be. In our study, for example, there was no single parameter, even for climate, that was measured identically at all 12 sites, so it was not possible to compare the behaviour of any single parameter across the sites. However, by grouping parameters into classes, we were able to make comparisons at a more general level. Comparative ecology requires standardized parameters, but these parameters may be at more general levels than the original data. The emphasis should be on comparable measurements in a broad sense, not simply comparable methods.

2) Even though common sets of parameters are not necessarily a prerequisite for useful cross-system comparisons, it is important to try to make measurements at similar temporal, spatial, and aggregation scales. We were able to show a strong dependence of variability on the level of aggregation of the data. However, we were limited in our study by the lack of control over spatial scale of measurement. One way to enhance control over spatial scale for some parameters would be to use remotely sensed data which are taken at clearly defined spatial resolutions and extents. Clearly, the limitations that scale dependency puts on comparative studies is not a function of the diverse array of systems, but of how they are studied.

3) The richest comparisons are made when sites to be compared have multi-level hierarchical data. In our study, data on all four major groups of parameters (climatic, edaphic, plant, and animal) were available to us only for two sites, the Jornada desert and Northern Temperate Lakes. Even then, species level plant data could not be compared between lakes and deserts because the lake site had not enumerated phytoplankton at the species level.

4) Long-term research must deal explicitly with spatial heterogeneity of ecosystems. Location coherent variation and incoherent variation is, in general, large relative to temporally coherent variation. Long-term, landscape-level studies must fully incorporate this strong spatial variation and the interaction between spatial and temporal variation in order to understand ecological processes operating at these larger spatial and temporal scales.

5) Finally, we found variability to be an interesting and informative system property that could be used to make meaningful comparisons across a wide range of ecosystems. It is likely that there are other relatively simple, but general, properties of systems that also could be used for comparisons. Some of broadest generalizations in ecology will come from including in our comparisons the full range of systems available, rather than just lakes or just deserts, or just animals or just plants, for examples.

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