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QUANTITATIVE EXAMINATION OF GASTROPOD AND SOIL RELATIONSHIPS IN AN OAK-HICKORY FOREST IN THE LOWER ILLINOIS VALLEY REGION

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ABSTRACT

Malacology can contribute significantly to the reconstruction of the local ecology at archaeological sites. Detailed reconstructions, however, are hampered by the paucity of molluscan ecological information, particularly at the local level.

Seven soil variables and their effects on the distribution of thirteen snail species were examined for part of a mesic oak-hickory stand in the lower Illinois Valley region. Generalized relationships between soil variables and snails were apparent. The number of species, and less so the number of specimens, tends to increase as the sample area increases. Traditional methods of graphic analysis and bivariate statistics did not provide optimal information on underlying relationships between the data sets. Few significant bivariate correlations were obtained between snail species and soil variables.

There was generally a nonlinear or negative correlation between snail species and soil pH. No significant bivariate correlations were found between snail species and organic matter, available phosphorus, acid soluble phosphorus or exchangeable magnesium. A high positive correlation existed between calcium and three of thirteen species but was significant only between *Strobilops labyrinthica* (Say) and calcium. A generally positive but not significant correlation existed between three species widely distributed over North America, and all measured soil parameters except exchangeable potassium.

Factor analysis delineated three underlying patterns in the variability and covariance of the data and provided a basis for inferring the secondary influence of soil factors on the distribution of snails. Variables which covary in each eigenvector were usually snail species rather than snail and soil variables. Habitat groups of snails were defined on the basis of species with a similar pattern of covariation.

INTRODUCTION

The environment of prehistoric village and mortuary sites has become a subject of increasingly popular interest among archeologists for several decades. This interest is warranted due to the current orientation of archeological research--an evaluation of man's interaction in an ecosystem.

Terrestrial mollusks, because of their sensitivity to local habitat conditions, are useful in the reconstruction of past environments. Interpretation of gastropod assemblages from archeological contexts rests partly on knowledge of presently living species. Analysis of archeological assemblages requires intensive and extensive sampling at the local level of the site. There are few analyses of living snails, particularly at the local level, which are sufficiently detailed to use as analogs in the explanatory and interpretative framework for assemblages from prehistoric sites.

The present study is a quantitative examination of relationships between gastropods and soil factors on the surface of a burial mound in a mesic oak-hickory forest. It deals intensively with microhabitat variation in soils and snails and quantitatively measures the covariation of each.

ACKNOWLEDGEMENTS

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DESCRIPTION OF PROJECT AREA

The Mueller-Ringhausen forest, on the property of Mr. George Mueller, is located (Fig. 1) about 2.5 miles north of the town of Hamburg, Illinois, about one mile east of the east bank of the Mississippi River (northeast corner of northeast quarter of southwest quarter of Section 14 Township 9 South, Range 3 West).

Much of the area of upland slopes of interior Calhoun County supports oak-hickory forests. The long-standing deciduous forests, in addition to climate, are primarily responsible for thick well developed Alfisol soils common in the county.

The collecting area is located on a northwest-southeast oriented ridge which drops with a gentle slope to the north. The area is adjacent to a broad plateau around which are numerous dissecting valleys. A group of four Late Woodland burial mounds is located on one of the ridges. The gastropod assemblage discussed below was recovered from the surface of Mound 2. The surface of this mound was selected for the study because of its degree of preservation and the presence of what appeared to be a nearly homogeneous microhabitat over the area of the mound. The vegetation on Mounds 3 and 4, located near a fenceline bordering an open pasture, had been greatly altered into edge area habitats and Mound 1, to the north, was the target of recent disturbances by collectors.

FORMULATION OF HYPOTHESES

The effect of soil factors on the distribution and abundance of terrestrial gastropods has been previously investigated on a regional scale in three counties in eastern Virginia (Burch 1955, 1956) Contrary to Boycott (1929) and Oughton (1948) Burch concluded that organic matter did influence the presence of land snails, thus agreeing with Shimek (1930) that organic matter as a potential food is a major limiting factor in the distribution of land snails.

Burch also investigated several other soil parameters. He concluded that pH did not affect the distribution of land snails. Research by other investigators (Strandine 1941) has not established a clear systematic relationship between this parameter and terrestrial gastropods. This variable is presently considered to be of indirect or negligible importance to the distribution of snails.

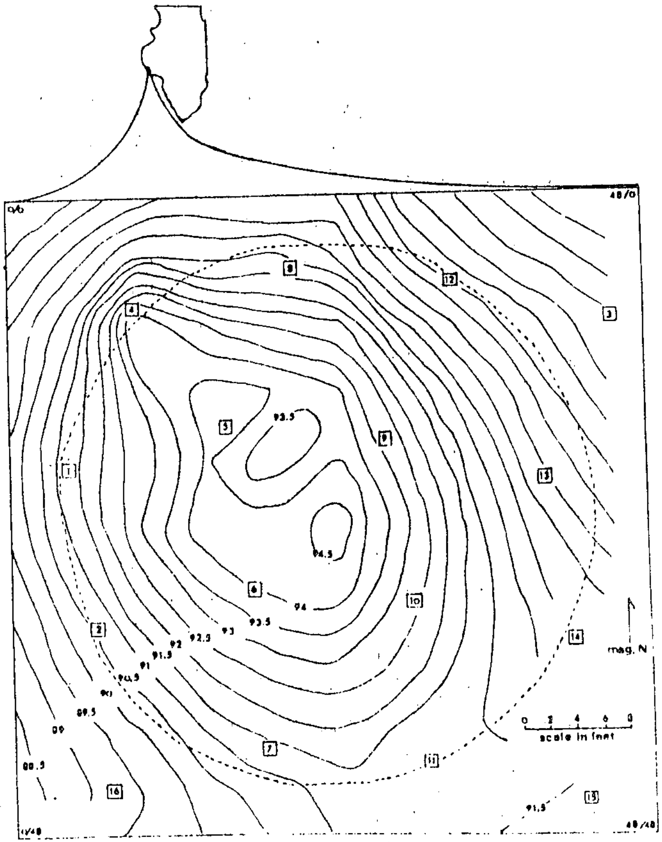

FIGURE 1. Topographic map showing position of samples of the stratified systematic unaligned sample of the surface of Mound 2 of the Mueller-Ringhausen mound group. Location of samples is approximate with respect to topography since they were obtained by measuring along ground surface. Dashed line is approximate perimeter of mound fill.

With respect to other soil factors snail frequencies were found to increase as the concentration of calcium (CaO), magnesium (MgO) and potassium(K_2O) in the soil increased. Potassium in addition to phosphorus and pH were concluded to have an indirect effect on the distribution of land snails (Burch 1955, 1956). Other investigators (e. g. Atkins 1966) demonstrated a positive relationship between an increase in calcium carbonate ($CaCO_3$) and an increase in frequency and species per unit area in alkaline soils. In all cases although the variables are quantified by the respective investigator an actual measure of correlation is not provided.

The present study attempts to determine the quantitative degree of covariance between gastropods and soil parameters similar to those used by Burch, on a local level. The soil variables investigated were organic matter content, available phosphorus, acid soluble phosphorus, exchangeable potassium, exchangeable calcium, exchangeable magnesium and soil pH. All of the soil parameters measured are interrelated, and are a product of the interactive system of soil and the non-soil environment, e. g. vegetation and climate. The latter variables are, however, important in the development of a soil but for the purposes of this analysis are treated separately.

Previous studies (cf. Burch 1955, 1956) have not included the quantitative explanation of local variability in soil parameters as they relate to gastropods, nor the investigation of alternate forms in phosphorus can be extracted. Burch's study, limited to a region of eastern Virginia, gives important clues to the ecological relationships of gastropods and soils. In each location for which soil data were measured, however, the sample area at each site was not subdivided. This produces an average of soil conditions which may or may not show the range of variability in each area. Secondly, the distribution of species may change markedly within a few feet.

Numerous investigators have contributed to a large body of literature on the occurrence and abundance of species in forests of varying vegetational composition (e. g. Van Cleave 1951; Shimek 1930). The delineation of a complex of species characteristic of forests has proceeded on a qualitative basis for many years. The composition of the habitat group should be expected to change between regions due to the effect of changes in marked interregional climatic patterns. Within the same region species comprising a habitat group likely change on a continuum responding to the primary factors of vegetation (cover) and moisture. Plant ecologists have given ample demonstration of a vegetational continuum rather than the existence of discrete vegetational units (cf. Curtis 1959). Significant positive correlation between species diversity and moisture regime and between snail diversity and the number of dominant tree species has been documented for eight habitats in the Great Smoky Mountains (Getz 1974).

Quantitative definition of habitat groups as used in this study is based on the division of an assemblage into groups of species with the greatest similarity of covariance. Within each habitat spatial variation in the distribution of species and frequencies can be used to detect minor changes in a contemporaneous population. Some of the changes can be expected to be related to the autecology of the species present in the area. By examining many sites in a given region the soil and gastropod variables which show systematic variation take on regional significance.

The present analysis examines the relationship between gastropods and soils in a part of one stand of oak-hickory forest. If the relationship between gastropods and a complex of soil variables can be quantitatively defined on a local level gastropod and soil analyses of archeological sites can be used to provide substantial reconstruction of local environmental conditions. It is clear that the soil factors (with the probable exception of calcium) affecting the spatial distribution of gastropods are minor compared to the effect of plant cover and moisture. Soil factors are interrelated and reflect plant conditions. Some soil parameters change markedly during the depositional history of an archeological site. Therefore it is important to focus on the more stable variables of soil which undergo minor changes through time; e. g., phosphorus, and bulk density. Due to nutrient pumping by plants (Odum 1971) even these variables may change radically unless deposition on the surface is rapid. If gastropod distribution was affected directly by soil factors interpretation of archeological assemblages would be inextricably complex due to the nearly constant change in the soil environment.

Burial mounds provide a situation where buried humus zones are frequently encountered. Rapid addition of fill above humus layers effectively seals off the underlying strata and their contained flora and fauna. Alkaline soil environments are favorable for the preservation of gastropod shells and in some cases the spatial relationships of the assemblage may be preserved (death assemblage) with minor modifications. In such cases comparison of the archeological assemblage with assemblages recovered from known ecological situations may reveal evidence of spatial distribution of habitats over the area of the buried surface of the mound, or the original surface on which the mound was erected. These data can reveal the record of short term shifts in ecotones provided the mounds are sufficiently dense over an area and can be arranged chronologically.

SUMMARY OF HYPOTHESES

The surface gastropod assemblage of a part of the Mueller-Ringhausen forest was used to evaluate the following hypotheses:

1. The habitat group characteristic of the part of the oak-hickory forest sampled would be similar to the complex of species most common in other areas of oak-hickory forest. In this case however the delineation of the habitat group is largely quantitative. Due to its vegetational structure this stand may be expected to contain the species common in a qualitatively defined habitat group but in different proportions in response to local conditions.
2. The spatial relationships of gastropod species can be expressed quantitatively by analysis of their frequencies per unit area and summarized by their patterns of covariance. Generally the greater the frequency and relative diversity per unit area the greater will be the amount of contained information.
3. Minor changes or variation in the distribution of snails and associated soil data reveal minor changes in a relatively homogeneous macrohabitat.
4. Soil pH should have little effect on the distribution of snails in this particular macrohabitat. Organic matter, and secondarily calcium, magnesium, and potassium should generally increase as snail frequencies increase.

Each of these variables should covary with gastropod species which show positive response to increases in snail parameters.

FIELD AND LABORATORY METHODS AND MATERIALS

The strategy employed during the design of a sampling program for the surface of Mound 2 was to obtain samples from points over the entire extent of the mound surface. This necessitated a design which would insure obtaining samples from the highest point of the mound where vegetation was less dense, as well as on the slopes and edge of the mound which supported a thick layer of decomposing litter. The final choice of a design was the stratified systematic unaligned sample (Haggett 1965). The procedure offers the advantages of randomization, stratification and systematic sampling and avoids the alignment of sample points and thus the possibility of error due to periodicities in the phenomena being sampled (Hagget 1965: 196).

The position of samples over the surface of the mound is indicated in Figure 1. A 48-foot square was sufficient to cover the mound and some overlap in the corners off the circular mound was thus obtained. The square was divided into four quadrants and four samples were selected at random in each 24-foot square quadrant. In the field the samples were obtained by establishing a temporary datum point on the highest part of the approximate center of the mound. The sampling grid was oriented toward magnetic north. Tapes were then used to measure along ground distance along the four coordinate lines and out to a sample point at right angles to the coordinate lines. The measurements were taken along ground distance to the northwest corner of the one-foot square sample. Although the slope is relatively constant the snail sampling grid is not precisely related to the archeological grid by which the mound was subsequently excavated.

By shifting the points of origin of the X and Y axes of the sampling grid (cf. Haggett 1965: 196) five series of random samples were established. The first series contained 16 samples; the remaining four contained nine samples each. All but the fifth series of samples were collected. The first series, i.e. 16 samples, is reported in the present study.

Each sample consisted of two parts. All of the surface litter in one square foot down to the interface of the O2 and A1 soil horizons was placed in a plastic bag. A soil sample one inch deep and one foot square was placed in a separate plastic bag. The litter samples were subsequently soaked in a solution of sodium bicarbonate and water in screen-covered buckets before being washed in number 40-mesh screens and air-dried, followed by sorting. Sample processing and shell identification methods are discussed at length elsewhere (Riggle 1975; Jaehnig 1971).

The soil samples initially included all soil in one square foot for a depth of one inch below the surface litter. Subsequently each soil sample was thoroughly mixed and approximately 300 mililiters was placed into heavy polyethylene bags and forwarded for analysis to Dr. Theodore R. Peck (Department of Agronomy, University of Illinois, Urbana).

Soil pH was determined by the paste method utilizing distilled water and a one-half hour equilibrium interval before the reading was obtained with a Beckman Zeromatic pH meter.

Organic matter was determined by the Walkly-Black procedure (Black 1965: 1372) and the results read colorimetrically.

Bray's P1 (Bray and Kurtz 1945) method was used to measure available phosphorus. Results were read colorimetrically. The extractant used was 0.03 normal ammonium fluoride (NH_4F) in 0.025 normal HCl. Acid soluble phosphorus was determined by Bray's P2 method using 0.03 normal NH_4F in 0.1 normal HCl as the extractant. The P1 method extracts phosphorus associated primarily with aluminum. Aluminum, in addition to some calcium phosphate, is extracted by the P2 method. The ratio of acid soluble to available phosphorus should be low in acid soils such as those present in the Mueller-Ringhausen forest.

Exchangeable potassium was extracted with 1 normal ammonium acetate at pH 7.0 and the result determined by flame photometry from a one to ten ratio of soil to extractant.

Exchangeable calcium and exchangeable magnesium were extracted using the method applied to the samples for extracting exchangeable potassium but a one to twenty ratio of soil to extractant was employed. The results were determined with atomic absorption spectrophotometry.

Botanical data collected during the field work were used to evaluate the relative amount each tree species contributed to the vegetation in the sample area. Although more rigorous procedures of establishing the characteristics of a stand are available (e. g. Curtis 1959) time did not permit exhaustive study of the vegetation.

Trees over three inches in diameter breast high were identified and counted. The trees on the surface of Mound 2 were predominantly white oak *(Quercus alba)*, shagbark hickory *(Carya ovata)* and flowering dogwood *(Cornus florida)*. Flowering dogwood and white oak trees were most common on the toe of the side slopes of the mound. One flowering dogwood and two white oak trees were located on the summit of the mound. Redbud *(Cercis canadensis)*, dogwood *(Cornus* sp.) and white oak dominate the trees around the mound. Redbud and dogwod saplings (less than one-half inch in diameter) were sparsely distributed over the surface of the mound.

ANALYSIS AND DISCUSSION

Phenology and Taxonomy

Two problems which may have had some small effect on the quantitative analysis of the assemblage which follows this section are the phenology of certain snail species and the taxonomic assessment of one of the species.

The acidity of the soil samples obviates the possibility that the shells recovered represent a long-term accumulation. Since the calcareous shells dissolve in an acidic pH environment in less than two years (cf. Evans 1972) the sample population studied at present very likely includes only specimens born and partly maturing during the several months preceding collection. Having collected the samples in June many of the shells from the previous summer and winter were probably decomposed. Since the samples were collected in early summer there may be some effect on the percentage of juveniles since not all of the species mature at the same time nor at the same rate.

Nearly 65 percent of the identifiable shells were classified as juveniles. Many of the juvenile shells are small *Punctum minutissimum*. If there is a phenological effect on the assemblage this species may be inferred to mature during late June and July although an unknown number of these shells may have died just prior to collection.

Seasonal periodicities are 'nearly universal in communities and often result in almost complete change in community structure during the annual cycle' (Odum 1971: 157). Seasonal changes in abundance of aquatic snails and in the variance of their species abundance distributions were documented for five watercourses in Egypt (Hairston 1964). Critical periods of environmental stress caused the frequency of the most abundant species to decrease drastically; less abundant species underwent a period of increase in many cases at the same time. Strandine (1941) found that fluctuations in a population of *Succinea ovalis* Say coincided with seasonal fluctuations in soil moisture, organic matter and pH.

An alternative conclusion is also possible with respect to phenological variation. Late spring conditions during 1972 may have been deleterious to *Punctum minutissimum*, many of them having succumbed before maturity (cf. Douglas 1963). This can be tested in the future by analyzing additional assemblages under similar conditions and at different times of the year.

The second problem is the taxonomic assignment of *Strobilops labyrinthica*. Identification of species in the genus *Strobilops* are based on shell morphology and, more importantly internal soft part anatomy. *Strobilops labyrinthica*, *S. affinis*, and *S. aenea* are highly variable with respect to shell morphology particularly the number and size of basal folds and lamellae as seen through the base of the shell (Pilsbry 1948).

All of the complete mature specimens from the assemblage thought to be one or the other of these species were measured. None of the specimens was larger than 2.7 mm, which is the minimum diameter of *S. affinis* (Pilsbry 1948). However, none of the 44 specimens was less than 2.5 mm, the maximum size of *S. labyrinthica (Ibid.)*

In addition the shell morphology, other than diameter, suggests that none of the specimens are *S. aenea*; e.g. the lack of an angular periphery characteristic of the latter, which Pilsbry (1948: 862) emphasizes is, 'distinctly but bluntly angular.' The diameter of this species varies from 2.4 to 2.8 mm and thus overlaps the upper limit of *S. labyrinthica* and the lower limit of *S. affinis*.'

It thus appears that the specimens of *Strobilops* from this particular assemblage are large examples of *S. labyrinthica* since only one is near the lower limit of *S. affinis* and since all lack the distinguishing morphological characteristics of *S. aenea*.

Analysis of living material of the family Strobilopsidae would provide a more solid basis for specific identification than presently exists on the basis of shell morphology (van der Schalie, personal communication, November 1975).

DESCRIPTIVE STATISTICS

Assessment of variability

The raw frequency data for the gastropod assemblage represented by the first series of 16 samples are summarized in Table 1. Seventeen species of terrestrial gastropods representing thirteen genera and 1,544 identified individuals were recovered. Of these 1,051 were classified as identifiable juveniles (65.1 percent). Juvenile shells of *Punctum minutissimum* contribute in large part to the high percentage of identifiable shells.

There is an apparent high degree of variation in the number of specimens between species; ranging from one specimen of *Gastrocopta corticaria* to 459 specimens of *Punctum minutissimum*. The number of shells recovered from specific samples is also highly variable; ranging from 13 individuals in samples 5 and 6, to 281 individuals in sample 3.

The random manner in which the samples were collected and the size of the assemblage preclude a cursory examination of the raw frequency data in order to assess the major source of variability. The analysis of variance for a randomized complete-block design (Steel and Torrie 1960: 134) was used to determine if arithmetic means of species between samples differed significantly, and thus to determine the major source of variation. Due to the apparent lack of a normal distribution of species within or between samples, and to the presence of numerous raw frequencies of less than ten, a transformation of the raw data by the $\sqrt{x+1}$ was used prior to the wnalysis of variance (Steel and Torrie 1960: 157).

The analysis of variance for the transformed data matrix (Table 2) is summarized in Table 3. The very highly significant ($P > .01$) F ratio for samples (blocks) and species (treatments) indicates, 1) the presence of significant differences of means of spe-

Table 1. Raw frequency of gastropods for each sample. Grid location numbers may be used to locate sample in Figure 1.

Grid Location	4R20	6R32	45R9	9R8	16R17	18R29	19R41	21R5	28R18	30R30	31R42	33R6	40R21	42R33	43R45	7R44	Total
Sample No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Anguispira alternata	2	2	3	4	1	-	3	6	1	-	-	5	3	3	1	-	34
Euconulus fulvus	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	3
Gastrocopta armifera	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	3
G. contracta	2	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	5
G. corticaria	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
G. pentodon	6	6	29	-	2	1	2	27	1	4	6	13	22	35	35	20	209
Hawaiia minuscula	19	8	29	4	1	10	13	8	15	17	7	16	34	32	24	19	256
Helicodiscus parallelus	16	7	90	1	2	1	4	43	7	-	2	11	20	35	7	22	268
H. singleyanus	1	6	10	-	4	-	-	32	-	1	-	-	-	9	8	4	75
Mesodon thyroidus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mesomphix friabilis	-	-	-	-	-	-	-	1	-	-	-	-	5	-	-	1	7
Punctum minutissimum	10	21	53	1	-	-	4	5	-	11	4	15	110	108	42	75	459
Pupoides albilabris	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Retinella indentata	1	3	18	2	-	-	1	3	-	-	-	5	11	20	5	8	77
Strobilops labyrinthica	3	9	24	4	-	1	4	14	1	3	4	13	13	14	7	21	135
Succinea sp.	-	-	3	2	-	-	1	1	-	-	-	-	-	-	-	-	7
Vallonia perspectiva	-	-	-	-	1	-	1	-	-	-	-	-	-	1	-	-	3
TOT. IDENT. IND.	60	62	262	18	11	13	34	143	25	36	23	78	222	258	129	170	1544
Unident. juv.	1	5	7	-	2	-	1	2	2	-	-	3	7	7	7	3	47
Unident. Fragments	2	2	12	1	-	-	1	9	2	-	-	8	18	-	3	8	66
TOT. INDIVID. REC.	63	69	281	19	13	13	36	154	29	36	23	89	247	265	139	181	1657
% Ident. Juv.	63.3	72.6	73.3	66.7	72.7	30.8	67.6	68.5	72.0	55.6	39.1	43.6	65.3	72.1	69.0	76.5	65.1
No. Ident. Juv.	38	45	192•	12	8	4	23	98	18	20	9	34	145	186	89	130	1051
No. of Species	9	8	11	7	6	4	10	10	5	5	5	7	11	10	8	8	

Table 2. Raw frequency data of Table 1 transformed by $\sqrt{x+1}$.

Sample No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Anguispira alternata	1.73	1.73	2.00	2.24	1.41	1.00	2.00	2.65	1.41	1.00	1.00	2.45	2.00	2.00	1.41	1.00
Euconulus fulvus	1.00	1.00	1.73	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00	1.00
Gastrocopta armifera	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
G. contracta	1.73	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00	1.00	1.73	1.41	1.00	1.00
G. corticaria	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
G. pentodon	2.65	2.65	5.48	1.00	1.73	1.41	1.73	5.29	1.00	2.24	2.65	3.74	4.80	6.00	6.00	4.58
Hawaiia minuscula	4.47	3.00	5.58	2.24	1.41	3.32	3.74	3.00	4.00	4.24	2.83	4.12	5.92	5.74	5.00	4.47
Helicodiscus parallelus	4.12	2.83	9.54	1.41	1.73	1.41	2.24	6.63	2.83	1.00	1.73	3.46	4.58	6.00	2.83	4.80
H. singleyanus	1.41	2.65	3.32	1.00	2.24	1.00	1.00	5.74	1.00	1.41	1.00	1.00	1.00	3.16	3.00	2.24
Mesodon thyroidus	1.00	1.00	1.41	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mesomphix friabilis	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00	1.00	1.00	2.45	1.00	1.00	1.41
Punctum minutissimum	3.32	4.69	7.35	1.41	1.00	1.00	2.24	2.45	1.00	3.46	2.24	4.00	10.54	10.44	6.56	8.72
Pupoides albilabris	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00	1.00
Retinella indentata	1.41	2.00	4.36	1.73	1.00	1.00	1.41	2.00	1.00	1.00	1.00	2.45	3.46	4.58	2.45	3.00
Strobilops labyrinthica	2.00	3.16	5.00	2.24	1.00	1.41	2.24	3.87	1.41	2.00	2.24	3.74	3.74	3.87	2.83	4.69
Succinea sp.	1.00	1.00	2.00	1.73	1.00	1.00	1.41	1.41	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Vallonia perspectiva	1.00	1.00	1.00	1.00	1.41	1.00	1.41	1.00	1.00	1.00	1.00	1.00	1.00	1.41	1.00	1.00

Table 3. Analysis of Variance for data of Table 2.

Source of Variation	df	SS	MS	F
Blocks (samples)	r - 1 = 15	699.986	46.666	-8.006***
Treatments (species)	t - 1 = 16	1451.982	90.982	-15.568***
Error	(r - 1)(t - 1) = 240	-1398.980	-5.829	
Total	rt - 1 = 271			

*** very highly significant P > .05.

Table 4. Descriptive statistics of soil data.

Soil Sample Number	pH	Organic matter %	Avail. P (ppm)	Acid Sol. P. (ppm)	Exch. K (ppm)	Exch. Ca. (me/100g)	Exch. Mg. (me/100g)
1	6.1	3.6	39.0	54.0	132	10.31	1.37
2	6.2	6.7	45.0	66.7	182*3	13.44	2.08
3	5.6	4.7	43.5	68.3	147	13.75	2.47
4	6.4	5.9	34.1	52.9	219	16.25	2.15
5	5.7	2.3	12.7	24.5	125	5.94	1.24
6	6.0	3.7	20.5	31.5	150	8.75	1.56
7	5.5	4.7	37.1*1	55.3*2	178	7.03	1.37
8	6.6	5.7	34.4	58.3	171	15.63	2.47
9	6.6	3.5	44.0	60.0	418	7.81	1.86
10	6.2	3.9	43.7	63.2	166	11.88	1.37
11	5.5	7.3	55.0	71.2	185	15.63	3.52
12	6.0	5.0	32.8	50.0	122	12.22	2.47
13	6.8	6.7	26.5	43.5	174	20.63	3.45
14	5.2	5.3	43.3	55.0	231	8.13	2.08
15	5.9	6.7	42.5	65.5	150	15.16	2.96
16	7.0	5.3	38.9	65.0	164	16.88	2.67
n	16	16	16	16	16	16	16
X	97.30	81.00	593.00	884.90	2914	199.44	35.09
SS	595.61	440.02	23585.50	51473.85	603590	2747.83	84.82
x	6.08	5.06	37.06	55.31	182.13	12.47	2.19
s^2	.2603	1.9972	107.1626	168.89	4858.5167	17.4539	.5244
s	.5102	1.4132	10.3519	12.9958	69.7031	4.1778	.7242
s_x	.1275	.3533	2.5880	3.2489	17.4258	1.0444	.1810
C.V.	.0839	.2792	.2793	.2350	.3827	.3352	.3302
CL*4 L_1	5.81	4.31	31.55	48.39	145.00	10.24	1.80
L_2	6.35	5.81	42.58	62.23	219.26	14.70	2.58

* The value shown is the x of the remaining 15 values. These values were originally out of agreement with the remaining values.

*1 Original value = 91.1

*2 Original value = 136.1

*3 Original value = 900

*4 CL$(\bar{x} \pm t_{.05} s_{\bar{x}})$

cies between samples; and, 2) that the precision of the sampling design was greatly increased relative to what could have been expected from a completely random design (cf. Steel and Torrie 1960:136).

Data for the seven soil variables analyzed are summarized in Table 4, which also summarizes the descriptive statistics for each soil variable. The variance (s^2), standard deviation (s) and standard error of the mean ($s_{\bar{x}}$) differ markedly between variables. The least variable of the parameters is pH (coefficient of variation - C.V. - of 8.39 percent). Considering the apparent variability between samples and among species (Table 3) high positive correlation between a group of gastropod species and pH in this kind of macrohabitat seems unlikely.

The variability of the remaining six parameters approximates two clusters. The first group includes organic matter, available phosphorus and acid soluble phosphorus. The second group includes exchangeable potassium, exchangeable magnesium and exchangeable calcium. The presence of two groups of soil variables with internally similar coefficients of variation suggests the possibility that a complex of species might covary with one or the other of the groups but that no species by itself would covary strongly with only a single soil variable.

Simple correlation of snails and soils

The major purpose of the present study was to determine the relationship of gastropods to the measured soil variables in a quantitative manner. Correlation coefficients, which measure the relationship between two variables on a -1 to +1 scale, satisfy part of this goal. Such correlation coefficients are independent of the scale of measurement; e.g. soil organic matter can be compared with snail species.

One of the several options of the computer program used for the factor which follows this discussion computes correlation coefficients between variables. Due to the non-normal distribution the raw frequency data for gastropods was transformed by the $\sqrt{x+1}$. *Gastrocopta armifera*, *G. corticaria* *Mesodon thyroidus*, and *Pupoides albilabris* were eliminated from the factor analysis due to their rare occurrence. Transformation of the data for these species results in a lack of arithmetical information. Soil data were not transformed since they have a nearly normal distribution. All data were subsequently normalized for the computation of factors. This results in a new data matrix with a mean of zero and a standard deviation of one.

Correlation coefficients between variables are

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 Anguispira alternata	1.000																			
2 Euconulus fulvus	.216	1.000																		
3 Gastrocopta contracta	.125	.167	1.000																	
4 G. pentodon	.299	.399	.105	1.000																
5 Hawaiia minuscula	.087	.502	.511	.666	1.000															
6 Helicodiscus parallelus	.472	.678	.197	.744	.563	1.000														
7 H. singleyanus	.374	.134	-.210	.654	.059	.639	1.000													
8 Mesomphix friabilis	.186	.378	.487	.344	.380	.248	.021	1.000												
9 Punctum minutissimum	.111	.461	.358	.802	.812	.586	.239	.528	1.000											
10 Retinella indentata	.394	.602	.213	.817	.725	.797	.398	.337	.887	1.000										
11 Strobilops labyrinthica	.414	.528	-.025	.808	.583	.809	.498	.365	.763	.855	1.000									
12 Succinea sp.	.490	.576	-.299	.077	-.027	.472	.272	-.110	-.059	.291	.335	1.000								
13 Vallonia perspectiva	.105	-.174	-.011	-.043	-.120	-.053	.046	-.187	.024	.089	-.193	-.036	1.000							
14 pH	-.002	-.036	.190	-.055	-.009	-.009	.001	.568	.061	-.099	.148	-.115	-.598	1.000						
15 % Organic matter	.191	-.094	-.073	.447	.209	.119	.159	.343	.422	.339	.481	.055	-.338	.089	1.000					
16 Available phosphorus	-.118	-.012	-.022	.215	.314	.169	.075	-.268	.190	.147	.280	.066	-.289	-.150	.496	1.000				
17 Acid soluble phosphorus	-.038	.117	-.149	.330	.319	.290	.230	-.163	.254	.224	.456	.205	-.396	.030	.553	.944	1.000			
18 Exchangeable potassium	-.062	-.136	.265	-.285	.042	-.079	-.154	-.061	-.143	-.112	-.225	-.044	-.029	.211	-.058	.327	.216	1.000		
19 Exchangeable calcium	.188	.324	.025	.444	.255	.238	.118	.620	.446	.343	.582	.142	-.656	.530	.755	.207	.379	-.216	1.000	
20 Exchangeable magnesium	.087	.325	.046	.562	.330	.293	.125	.522	.502	.428	.551	.006	-.432	.198	.826	.340	.411	-.029	.820	1.000

Table 5. Covariances between variables; includes gastropod and soil variables. Correlation coefficients of snail species are based on all frequencies of each variable transformed by $\sqrt{x+1}$. Coefficients for soil variables are based on raw data of all soil parameters.

summarized in Table 5. The coefficients are significant at the five percent level if they equal or exceed .497 (on n–2 degrees of freedom; Freese 1967: 87). A coefficient equal to or exceeding .623 is significant at the one percent level.

Examination of the correlation coefficients permits the delineation of two groups of gastropod species. The members of each group form a complex of species with relatively similar correlation coefficients; those species which significantly correlate at the five percent level and those which show significant correlation at the one percent level. The correlation coefficients are based on comparisons between two variables at one time and depend on the direction (increase or decrease) of frequencies relative to each other. Quantitative definition of groups of correlated species is difficult on this basis since only two variables are being compared.

Very few significant correlations were obtained between snail species and soil variables. *Vallonia perspectiva* is negatively correlated with soil pH. A negative correlation was not anticipaced since *V. perspectiva* is most common in more open calcareous environments (Grimm 1959:22) and would be expected, in this case to increase as pH increased. The very low frequency of *V. perspectiva* precludes a definite conclusion about the relationship of this species to soil parameters. It should also be noted that this species is significantly negatively correlated with calcium. The calcium values of some samples are very low although available phosphorus levels are quite high (Dr. Theodore Peck, personal communication).

The ratio of available phosphorus to acid soluble phosphorus levels is normally low in acid soils due to the insolubility of calcium phosphates in acid environments (Thompson and Troeh 1973: 269). A correlation coefficient of .944 between these two variables was obtained in this analysis. Most of the available phosphorus in acid soils is complexed with aluminum. The low frequency of *Vallonia perspectiva* in this situation is likely due to the lack of calcium which would be in the exchangeable form in calcareous environments in open areas where this species is often abundant.

Calcium and magnesium behave similarly in the soil system (Thompson and Troeh 1973: 316); a correlation of .820 was obtained in the present study. It may be expected then that gastropod species should correlate with magnesium and calcium levels in a similar manner. For example in addition to the negative correlation between *Vallonia perspectiva* and calcium this species is also negatively correlated with magnesium, although the correlation coefficient is not significant.

Mesomphix friabilis on the other hand has a significant positive correlation with pH, calcium and magnesium (.568, .620, and .522 respectively). Unfortunately this species occurred in such low frequencies that additional testing is necessary before its relationship to pH can be adequately assessed. One, five and one specimen of *M. friabilis* were recovered from samples 8, 13 and 16 respectively. The pH values for these samples are 6.6, 6.8 and 7.0 respectively. It can be tentatively concluded on this basis that *M. friabilis* is a sensitive indicator of pH ranging from 6.6 to 7.0 in addition to the presence of moist conditions (F.C. Baker 1939: 67). The shell thickness of this species decreases in lime deficient areas (Pilsbry 1946: 330). The soils of Mound 2, with low values of calcium and acidic pH indicate the lack of free carbonates in solution. The high correlation between this species and exchangeable calcium (.620) and magnesium (.522) suggests that it is existing in a less than optimal environment with a low calcium supply. These data clearly support the conclusions of F.C. Baker and Pilsbry.

Other species have high correlations with magnesium; *Gastrocopta pentodon, Punctum minutissimum,* and *Strobilops labyrinthica*. Although correlation coefficients between these species and calcium are positive the only apparently significant correlation is between *Strobilops labyrinthica* and calcium (.582). These three species, in addition to *Mesomphix friabilis,* form a group which is closely related to the supply of calcium and magnesium.

No significant correlations were obtained between the 13 snail species and the soil variables of organic matter, available phosphorus, acid soluble phosphorus and exchangeable magnesium.

A few species are correlated with increases in organic matter but not significantly; *Gastrocopta pentodon, Punctum minutissimum,* and *Strobilops labyrinthica*. The correlation between the latter species and acid soluble phosphorus (.456) although not significant is positive.

With the exceptions of *Mesomphix friabilis* and *Vallonia perspective* there is generally a nonlinear or slightly negative correlation between snail species and pH.

The use of correlation coefficients as a basis for studying the relationship of gastropods and soil variables substantiates some conclusions reached by previous investigators. The use of this bivariate statistical approach is perhaps most appropriate when dealing with species which may inhabit such macrohabitats as were studied in this case but which are most common in other environments. The data of the present analysis indicate that *Vallonia perspectiva* and *Mesomphix friabilis,* which are most common in other situations, are not common in this particular habitat because their environmental tolerances have been very nearly exceeded. The results give some insight into the environmental requirements of these species and a more detailed understanding of why they are common in their optimal habitats.

Other species, such as *Hawaiia minuscula, Helicodiscus parallelus* and *H. singleyanus,* occur in a very wide range of habitats and are common in the assemblage presently under study. In the present analysis these species show a generally positive correlation with all of the measured soil parameters except exchangeable potassium with which they show a negative correlation.

The soil variables analyzed in the present analysis are the same as those examined by Burch (1955) with the addition of acid soluble phosphorus data. For purposes of comparison the values of phosphorus and potassium are expressed in percentages by multiplying parts per million by 10^{-4}. Calcium and magnesium values are expressed in milliequivalents per 100 grams. These may be converted to parts per million by multiplying the calcium values by 200 and the magnesium values by 120, and expressed in percentages by multiplying the parts per million value by 10^{-4}. It is not necessary to relate all variables to one standard since the variance ratios between variables will remain nearly the same irrespective of the standard.

In contrast to Burch's data exchangeable potassium values are usually higher, and, like the organic matter and exchangeable calcium values, the lower end of the ranges overlaps the upper range of Burch's values. Magnesium values are higher and available phosphorus values are lower than those obtained by Burch. Soil pH values are comparable between the two data sets.

One source of variation in the two data sets is the analytical precision of the various soil testing techniques. A second possible reason for the differences between several of the soil variables is the variation in climate between the two regions, in addition to other soil factors specifically parent material and time. A third important source of variation is the difference in sample size. Burch utilized a regional approach obtaining soil data from 41 stations, encompassing two physiographic regions, the Coastal Plain and Piedmont Plateau. All of these differences preclude a direct comparison between the two data sets, although it is tempting to use the values obtained in this study to suggest the possible relationship between snails and some soil parameters, for example, at higher levels of organic matter content.

Burch plotted soil parameters against the number of species and secondly against the number of specimens. In doing so he used an evenly spaced scale but each increment of the scale did not in all cases represent an equal increase in values of the same variable along the scale. The result is a graphic representation of relationships between the number of species and soil variables and between the number of snail specimens and soil data.

The present study utilizes a much different approach for graphical representation of the data. Descriptive statistics were obtained for the raw soil data (Table 4). A frequency distribution was constructed for each variable using the respective mean as the midpoint and the appropriate standard deviation as the increment. These data and the frequency distributions showed all soil variables, except exchangeable potassium, to have a near normal distribution. To compare these data with those of Burch an even increment was used. To obtain a similar scaling effect for all parameters the range of each was divided into six equal parts and plotted against the number of species, then against the number of specimens.

Inspection of Figures 2A and 2B shows some relationships between the number of species and soils and between the number of specimens and soil data, although in both sets of graphs there is a great deal of variation. Rather than illustrating causal affinities (the 'relationships' of Burch) between

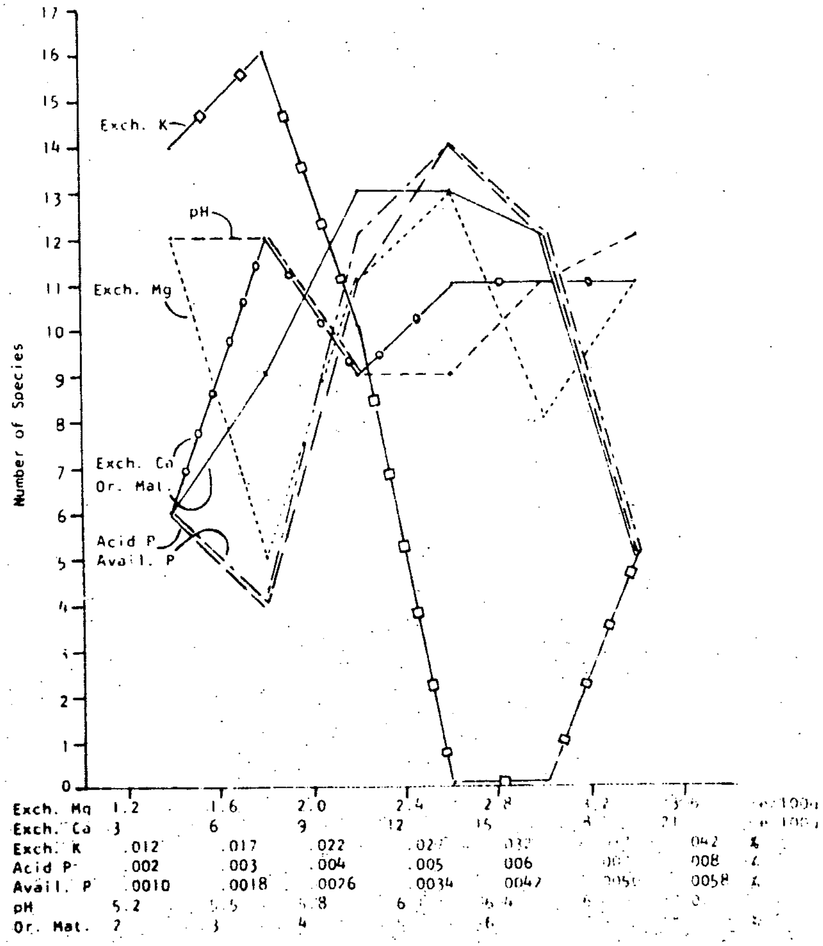

Figure 2A. Even increment plot of soil data a [illegible]

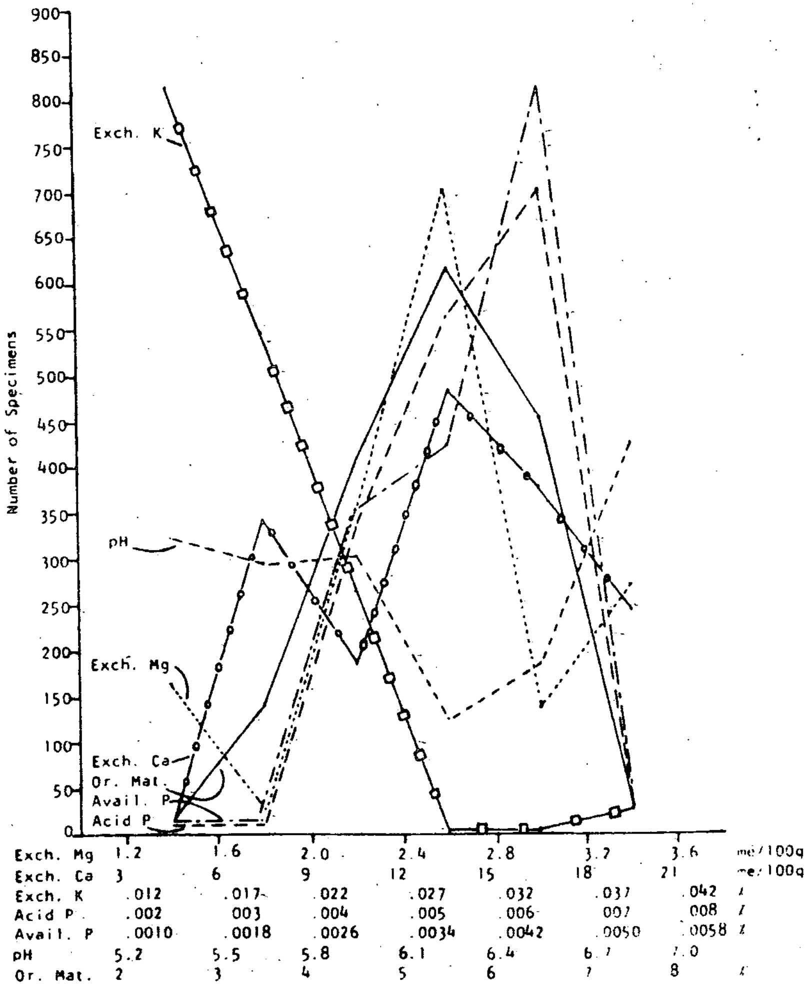

Figure 2B. Even increment plot of soil data against the number of snail specimens.

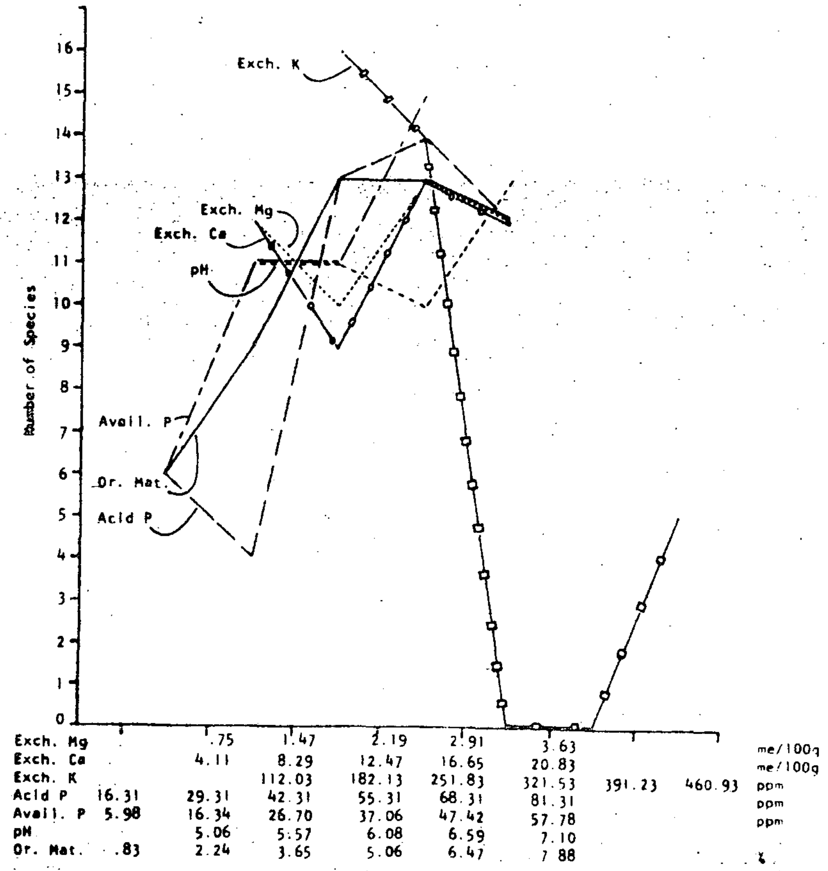

Figure 3A. Plot of soil data against number of species using standard deviation as the increment.

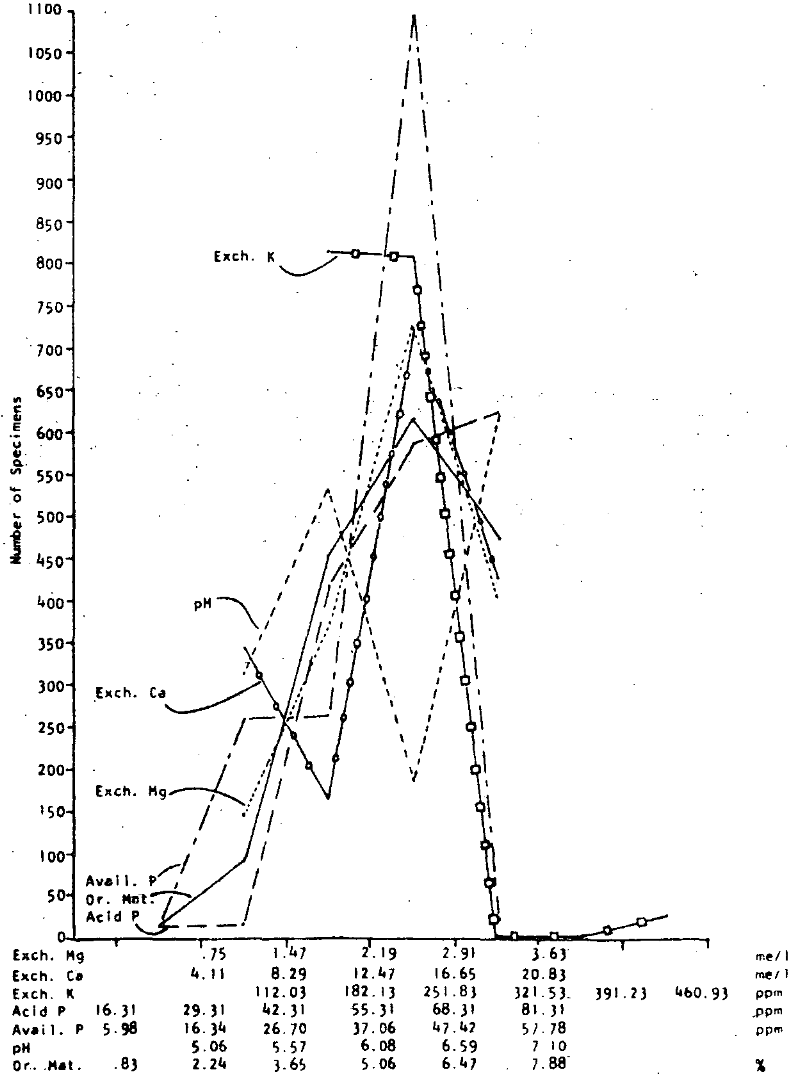

Figure 3B. Plot of soil data against number of specimens using standard deviation as increment.

Table 6. Percent of total variance explained by respective eigenvector.

Eigenvalues[1]	Fraction of Total Variance Individual[2]	 Cumulative
7.12823	35.64	35.64
2.94875	14.74	50.38
2.49691	12.48	62.87
1.97363	9.87	72.74

1 Eigenvalue = sum of the column of squared loadings for each factor. Measures the amount of variance accounted for by a factor.

2 $\frac{\text{Eigenvalue}}{\text{number of variables}} \times 100$ = Percent of total variance explained by the eigenvector.

snail species and soil variables. graphs such as these represent evidence of the optimal habitat of species within a range of given soil parameters; i.e. how diversity and frequency relate to a range in soil characteristics. The graphs consider all species present rather than ecological dominants or covariation between numbers of species or numbers of specimens, and soil parameters. This occurs due to the near-normal distribution of the values for nearly all of the soil variables. Most soil values are within one standard deviation of the mean value. Thus most of the snail samples also lie within these limits; i. e. the soil samples and the snail samples are the same points in space. This unavoidably increases the area and thus the number of species since the latter tends to increase in any population as the area of the sample increases (Odum 1971: 143-154). The use of an increment less than one standard deviation would even out the sharp inflections in the distribution curves. This however defeats the purpose of attempting to delineate patterns of relationship between gastropods and soils on a quantitative basis.

A pattern similar to even increment scaling is obtained when the soil data are plotted against the number of species and the number of specimens using the standard deviation of each variable as the increment (Figures 3A and 3B).

The use of the above analytical techniques facilitates interpretations about the assemblage as a whole but permits very few inferences about autecology and the significance of particular species in a particular habitat.

In conclusion, the optimal conditions in this habitat utilizing Figures 3A and 3B, considering the complex of soil variables measured, for nine to thirteen of the species represented, are characterized by exchangeable calcium levels of 8.29 to about 20.83 milliequivalents per 100 grams of magnesium. Acid soluble phosphorus levels would be from between 42.31 and 44.31 parts per million to less than 81.31 parts per million. Soil pH would range from 5.57 to about 7.0, and organic matter from 3.65 to 6.47 percent. This 'habitat' would predictably contain from 350 to around 700 individuals considering a sample size of about nine square feet.

Multivariate analysis

The univariate and bivariate statistics described previously are not sufficient to quantify a relationship between several variables which may be related in a multivariate and complex manner.

The principal tool used to delineate the quantitative covariation between snail species and soil variables discussed in this study was multivariate factor analysis. The computer program for the analysis was written in FORTRAN by Mr. Peter Guetter of the Department of Meteorology of the University of Wisconsin. The program was initially applied to climatic data but is applicable to a wide range of data sets. Included in the program is the generation of a number of factors here to be referred to as eigenvectors. The factors were generated from the data in Table 2; snail frequencies transformed by the $\sqrt{x + 1}$, and soil parameters. Each eigenvector 'summarizes' the mathematical relationships between a number of variables; i.e. the covariance of interrelated variables. As such the analysis implies no statistical significance (Rummel 1967). The intent of factor analysis is to

> 'express covariation in terms of k underlying factors that explain a large part of the variance and covariance of the original variables. The number of factors is much less than that of the number of variables in the study' (Sokal and Rohlf 1969: 542).

Eigenvalues measure the amount of mathematical variance accounted for by an eigenvector. The eigenvalues for the present analysis and the variance they account for, expressed as a percent, are summarized in Table 6. Fifteen eigenvectors were computed; those which explain less than ten percent of the total amount of variability (100 percent) are considered insignificant.

Table 7. Eigenvectors with factor loadings for each variable.

Variable		Eigenvector			
		1	2	3	4
1	Anguispira alternata	-.140406	-.222126	.005389	-.270861
2	Euconulus fulvus	-.232059	-.163953	-.066870	-.077894
3	Gastrocopta contracta	-.074472	.001533	-.400785	.352647
4	Gastrocopta pentodon	-.324577	-.131144	.022044	.053415
5	Hawaiia minuscula	-.266096	-.058836	-.134704	.383516
6	Helicodiscus parallelus	-.294690	-.264080	.051647	-.014480
7	Helicodiscus singleyanus	-.170687	-.209209	.196635	-.196011
8	Mesomphix friabilis	-.195757	.122171	-.461717	-.113591
9	Punctum minutissimum	-.311730	-.068208	-.158576	.235900
10	Retinella indentata	-.321627	-.224146	-.032492	.113066
11	Strobilops labyrinthica	-.344220	-.076658	.069540	-.075626
12	Succinea sp.	-.105983	-.201880	.253882	-.327742
13	Vallonia perspectiva	.107645	-.406303	-.012034	.182406
14	pH	-.061170	.316205	-.286369	-.223062
15	% Organic matter	-.230443	.297354	.140053	-.069531
16	Available phosphorus	-.129625	.235334	.420607	.335622
17	Acid soluble phosphorus	-.182229	.239256	.424116	.180917
18	Exchangeable potassium	.049858	.148663	.041001	.315285
19	Exchangeable calcium	-.260216	.326115	-.077150	-.275137
20	Exchangeable magnesium	-.267310	.280348	-.006743	-.069492

The first eigenvector explains 35.6 percent of the total variance in the data set of 20 variables. Each successive eigenvector explains a lesser portion of the remaining variance. The factor loadings for each variable (Table 7) indicate a general pattern of negative covariance between variables. The factor loadings being nearly all negative force more of a subjective approach toward emphasizing the variables which are important in the first eigenvector. *Gastrocopta pentodon*, *Punctum minutissimum*, *Retinella indentata*, and *Strobilops labyrinthica* are the variables which have the greatest similarity of covariance as expressed by factor loadings. Much of the variance is explained by the first eigenvector (Table 8: 75, 69.3, 72.7, and 84.5 percent respectively). The factor scores and the frequent occurrence of these species in most of the 16 samples provide the basis for the tentative conclusion that these species characterize the forest habitat.

Factor loadings for samples (Table 9) show that samples 3 and 13 are quite similar with respect to the information they contribute to the first eigenvector. These samples in addition to samples 8, 14, and 16 covary in a negative fashion with a similar amplitude, opposite to samples 5, 6, 7, and 9. These results indicate substantially different patterns of variation between the two groups of samples.

A second group of variables has a high degree of covariance in the first eigenvector. These variables are: *Hawaiia minuscula*, *Helicodiscus parallelus*, calcium, and magnesium. Although these have no significant linear correlations with each other (Table 5) they are summarized in the first eigenvector (Table 8).

The two groups of covarying species evident in the first eigenvector contain species which occur

Table 8. Percent of explained variance for each variable, first four eigenvectors.

	Variable	Eigenvector				
		1	2	3	4	Total
1	Anugispira alternata	14.05	14.55	.00	14.48	43.08
2	Euconulus fulvus	38.39	7.93	1.12	1.20	48.64
3	Gastrocopta contracta	3.95	.00	40.11	24.54	68.60
4	Gastrocopta pentodon	75.10	5.07	.12	.56	80.85
5	Hawaiia minuscula	50.47	1.02	4.53	29.03	85.05
6	Helicodiscus parallelus	61.90	20.56	.67	.04	83.17
7	Helicodiscus singleyanus	20.77	12.91	9.65	7.58	50.91
8	Mesomphix friabilis	27.32	4.40	53.23	2.55	87.50
9	Punctum minutissimum	69.27	1.37	6.28	10.98	87.90
10	Retinella indentata	73.74	14.81	.26	2.52	91.33
11	Strobilops labyrinthica	84.46	1.73	1.21	1.13	88.53
12	Succinea sp.	8.01	12.02	16.09	21.20	57.32
13	Vallonia perspectiva	8.26	48.68	.04	6.57	63.55
14	pH	2.67	29.48	20.48	9.82	62.45
15	% Organic matter	37.85	26.07	4.90	.95	69.77
16	Available phosphorus	11.98	16.33	44.17	22.23	94.71
17	Acid soluble phosphorus	23.67	16.88	44.91	6.46	91.92
18	Exchangeable potassium	1.77	6.52	.42	19.62	28.33
19	Exchangeable calcium	48.27	31.36	1.49	14.94	96.10
20	Exchangeable magnesium	50.93	23.18	.01	.95	75.07

in nearly all of the samples and which have the highest frequencies. These species are concluded to be characteristic of the habitat of the sample area. The lack of significant correlations (Table 5) between these species and soil variables, and the lack of evident covariance based on factor scores, suggests that they are responding predominantly to other ecological parameters. At least fifty percent of the variance of these species is explained by the first eigenvector.

Much of the remaining variance of *Helicodiscus parallelus* and *Retinella indentata* is explained by the second eigenvector (Table 8). With much of their variance already accounted for, these species and *Anguispira alternata* and *Helicodiscus singleyanus* show a general pattern of covariance of similar amplitude as six of the seven soil variables (excluding potassium). The covariance of the snail species, however, is in a direction opposite that of the soil variables. Samples 1, 4, 9, 10, 11, 13, and 16 contribute most of the variance accounted for by the second eigenvector (Table 9). These samples also suggest a pattern of distribution of the variance between sample points that is opposite to the pattern indicated by samples 3, 5, 6, 7, and 14.

Following the computation of the second eigenvector 50.4 percent of the total variance of the assemblage has been accounted for(Table 6). In the third eigenvector, the last one considered to be of

Table 9. Eigenvectors with factor loadings for each observation (sample).

Sample	Eigenvector			
	1	2	3	4
1	1.208321	- .336089	-1.056477	1.189470
2	- .126662	1.225691	1.281039	- .228042
3	-4.692862	-2.754288	1.911508	- .595574
4	1.293829	1.070858	.639006	-2.156628
5	4.813039	-2.822209	-1.419051	-1.193376
6	3.621002	- .239646	-1.288072	- .644324
7	2.281698	-1.696686	.931875	.410141
8	-2.053272	- .516163	.747936	-2.749899
9	2.520461	1.487161	- .207997	2.112110
10	1.920869	1.073838	.487117	.765144
11	.363201	3.011929	2.092990	.548227
12	- .391342	- .148436	- .191281	- .858923
13	-4.349376	1.190759	-4.685825	- .120355
14	-2.302820	-2.963130	.299530	3.031444
15	-1.735203	.998141	.997426	.497122
16	-2.370887	1.418273	- .539726	- .006536

pertinent value in this analysis, *Gastrocopta contracta* and *Mesodon friabilis* have factor scores of similar amplitude but which covary negatively with available and acid soluble phosphorus (Table 5). The remaining species tend to covary negatively or to have little relationship to soil variables.

The results of the eigenvector analysis, in addition to the results of the simple correlations (Table 5), permit the conclusion that the soil parameters measured in this study are of secondary or tertiary importance with respect to the distribution of the species included in the factor analysis.

Qualitative habitat differentiation

During field study the sample area appeared to contain two habitats which could be distinguished on the basis of apparent cover; a sparse grass-and-moss association on top of the mound and a humus layer increasing in thickness on the sides and toe-slope of the mound. It was hypothesized that the analytical method used to study covariance of species could provide data justifying a qualitative distinction between the two habitats.

Inspection of the transformed data matrix (Table 2) and Figure 1 permit the conclusion that the two habitats do contain markedly different data sets with respect to snail frequencies and soil parameters. On close inspection a third habitat is distinguishable. The east slope of the mound differs from the west slope; the former has a higher frequency of *Punctum minutissimum* and *Gastrocopta pentodon*, a generally higher frequency of other species (excluding species not included in the factor analysis), and a generally greater organic matter content per unit area. The samples included in arriving at this conclusion are 3, 13, and 14.

The top of the mound (samples 5, 6, 9, and 10) is separable from the other microhabitats due to generally lower snail frequencies, particularly of *Gastrocopta pentodon* and *Punctum minutissimum*, and lower organic matter content.

Due to the transformation of the raw frequency matrix a conclusion regarding differences in species diversity between habitats must be based on Table I. Again, the samples from the top of the mound are conspicuous because of the fewer species per unit area than samples from the west side of the mound. Samples from the east side of the mound are also conspicuous because the species diversity of these is greater than in any of the remaining samples (Table I).

The habitat differentiation is also supported by the eigenvector analysis. *Hawaiia minuscula*, *Helicodiscus singleyanus*, and *H. parallelus* tend to predominate among the species present in the samples from the top of the mound (Table 7 and Figure 1). *Hawaiia minuscula* and *Helicodiscus parallelus*, in addition to magnesium and calcium, had a high degree of covariation in the first eigenvector. This is due in part to the pattern of variation of these variables in samples from the top of the mound, even though the same species occur in other samples in higher frequencies. Other species found to covary in the first eigenvector included *Gastrocopta pentodon*, *Punctum minutissimum*, *Retinella indentata*, and *Strobilops labyrinthica*. These species occur in all of the samples but attain their highest frequencies in samples 3, 13, and 14; i. e. on the east side of the mound.

The previous qualitative distinctions give further indication that microhabitat differentiation within a macrohabitat is possible and is quantifiable with this form of eigenvector analysis, with the advantage of quantitative definition of relationships between many variables simultaneously.

SUMMARY AND CONCLUSIONS

The species which tended to covary throughout the eigenvector analysis were those which occurred in all or nearly all of the 16 samples and which had the highest raw and normalized frequencies. This group, characteristic of the sample area, includes *Gastrocopta pentodon*, *Punctum minutissimum*, *Retinella indentata*, and *Strobilops labyrinthica*. Additional species form a group of secondary importance but the members still covary; *Hawaiia minuscula* and *Helicodiscus parallelus*. *Anguispira alternata* and *Helicodiscus singleyanus* form a group also of secondary importance.

Species included in the primary group have been shown by numerous investigators to be characteristic of forested habitats (Burch 1956; Douglas 1963; Atkins 1966; Elwell and Ulmer 1971). Nearly all of the remaining species in the assemblage are common in other forested habitats, with the exception of *Vallonia perspectiva* and *Gastrocopta armifera*. All of the species of this assemblage could be expected to occur in a range of habitats; i. e. many species may occur in areas more open than the Mueller-Ringhausen forest, particularly *Hawaiia minuscula*, *Helicodiscus parallelus*, *Vallonia perspectiva*, and *Gastrocopta armifera*.

Previous authors (Burch 1955, 1956) have concluded that potassium, phosphorus and pH have an indirect effect on the distribution of land snails. Burch's study considered the relationships of soil variables and snails on a regional level. At the local scale of the present analysis two species were found to have significant simple correlation with soil pH; *Mesomphix friabilis* and *Vallonia perspectiva*, the latter having a negative correlation. *Mesomphix friabilis* was also significantly correlated with calcium and magnesium.

The latter species, in addition to *Gastrocopta pentodon*, *Punctum minutissimum*, and *Strobilops labyrinthica*, were highly correlated with magnesium. Using multivariate techniques, however, i. e. examining all the variables simultaneously, there was no definite pattern of covariance between any of the above species, which were the most frequently occurring ones, and soil variables. When examined bivariately these species appear to be responding to the pattern of variation in principally magnesium, but also to calcium.

There is an absence of significant bivariate correlations between other species and organic matter, available phosphorus and exchangeable magnesium. The eigenvector analysis showed all of the soil variables to be of secondary importance with respect to their effect on the distribution of snails. The major covarying variables are complexes of species rather than species and soil variables.

These results also disagree with Burch's conclusion regarding the effect of organic matter on the distribution of snails. In the present study organic matter is concluded to be of minor importance in terms of its covariance with a complex of snail species characteristic of the local area.

During the preceding analysis an attempt was made to assess qualitatively the relationships between gastropods and several soil variables. A quantitative approach was then used to delineate statistically significant relationships in several cases where two variables were examined together. A factor analysis was utilized to summarize the multivariate relationships between 20 variables, 7 of which were soil parameters.

The humid temperate weathering regime of the Illinois Valley and surrounding regions is the primary factor affecting the development and maintenance of the expansive deciduous forests of the Prairie Peninsula. It is in the deciduous forests, where soils are acidic and on acidic soils of transition zones between forests and prairie, where the quantitative ecology of land snails adapting to soil, cover, and moisture conditions will be most substantially understood. This is due primarily to the lack of significant effects brought about by the preservation of shells, as happens in alkaline environments. In addition, refined sampling techniques can be expected to result in qualitative measurement of intra- and inter-seasonal variation in the molluscan assemblages, and thus in quantitatively based analyses of changes in gastropod communities.

The quantitative definition of habitat groups, similarity of covariance of a complex of species, has distinct advantages over subjective assessment of species lists and the comparison of only a few species at a time. Continued use of multivariate techniques and refined data collecting techniques will contribute to a more complete understanding of the relationship between land snails and their physical environment. Such improvements will facilitate more detailed interpretations of past molluscan assemblages, and thus more accurate reconstructions of past environments based on terrestrial mollusks.

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