A MORPHOLOGICAL APPROACH TO THE STUDY OF AVIAN COMMUNITY ORGANIZATION

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ABSTRACT.—We have undertaken a morphological approach to the analysis of community relationships among species of birds by using eight characters to define a morphological hypervolume. We describe methods of characterizing mophological space, estimating the total volume occupied, and calculating distances between species. Within this space, we examined 11 temperate-zone scrub communities described by Cody (1974). We used the total pool of species represented to generate two sets of randomly assembled communities; in one case, individual species were used to construct communities, and in the other, species synthesized from the pool of characters were used. We compared characteristics of the natural communities to those of the random communities to test the null hypothesis that species are added to communities independently of those already present.

Distance and regularity of spacing between nearest neighbors in natural communities did not differ significantly from randomly assembled communities. In comparisons between natural communities having different numbers of species, however, species were added at the edge of the morphological space, predominantly along novel morphological dimensions, rather than being drawn at random from the species pool.

Morphological separation and ecological overlap were inversely related in small communities, but this relationship was less pronounced in larger assemblages. Communities in California and Chile in similar habitats (chaparral and matorral) occupied morphological spaces that were superimposable in outline but showed no evidence of community convergence on a species-for-species level.

We suggest that morphology can be a powerful tool in the analysis of community structure. We feel that any evidence of community structure can be accepted only when tested statistically against a reasonable null hypothesis. Because morphological methods make possible the study of large samples of communities, they have a clearly defined role in the study of patterns of community organization. Received 25 June 1979, accepted 31 December 1979.

ALTHOUGH the organization of biological communities has figured prominently in the development of theory in ecology, empirical description of community structure has been limited primarily to the number and relative abundances of species. Recent theory concerning model communities, based on the Lotka-Volterra competition equations, suggests that a matrix of pair-wise coefficients of interaction between species may provide a useful description of community organization (MacArthur and Levins 1967, Levins 1968, May and MacArthur 1972, Vandermeer 1972, May 1975). In direct response to this theory, several authors have attempted to estimate these coefficients in natural communities by measuring the degree of ecological overlap among species (e.g. Cody 1968, 1974; Pianka 1973). At present, however, few ecologists believe that ecological overlaps measure the dynamics of interactions among species (e.g. Colwell and Futuyma 1971, Neill 1974, Schroder and Rosenzweig 1975, Seifert and Seifert 1976), although observed overlaps may be determined by these interactions (Schoener 1974).

Even as a primarily empirical description of community structure, ecological overlaps have several weaknesses. (a) Because field measurements are difficult, ecological overlaps are calculated from few parameters, which are mostly intuitive and the choice of which is rarely based upon preliminary studies of resource utilization. (b) Measures of overlap have sometimes included arbitrary combinations of morpho-

logical similarity, microhabitat overlap, activity patterns, feeding location, and feeding behavior and therefore comprise a mixed bag of metrics. (c) It is difficult to estimate confidence limits for indices of overlap and similarity (Ricklefs and Lau in press). Finally (d), because overlaps are measured against a background of habitat in ways specific to each taxon, results of different studies are rarely comparable and are not easily generalized.

In this paper, we advocate an alternative approach to describing community organization, based upon morphological similarities among species, and demonstrate its application to some problems in community ecology. The approach is founded on the premise that the adaptations of organisms reflect their ecological relationships, specifically that morphological space can be mapped closely onto ecological space. Evidence gathered thus far points to a strong correlation between morphological space and ecological space (see, for example, Hespenheide 1971, 1973; Karr and James 1975; Cody and Mooney 1978). But even if morphology and ecology are not strictly related, morphological analyses may reveal patterns that require explanation in the context of ecological and evolutionary theory.

We believe that morphological analysis presents several advantages for the study of community relationships (Ricklefs and Cox 1977). A variety of measurements is easily obtained, often from museum specimens or published accounts; morphological characteristics presumably weight the varying competitive pressures experienced during different seasons and throughout the lifetime of the individual in proportion to their influence on fitness; morphological traits can be measured independently of the structure of the habitat and, if properly analyzed, hold the potential for broad comparisons between habitats, regions, and higher taxa.

Multivariate analysis of morphology has previously been applied to the study of communities of bats (Fenton 1972; Findley 1973, 1976), birds (Karr and James 1975), and fish (Gatz 1979). In our opinion, these analyses were based on flawed statistical techniques. In particular, they used normalized ratios of characters to define the morphological space, making comparison and statistical interpretation of morphological distance difficult (e.g. Atchley et al. 1976).

In this paper, we introduce a procedure for morphological analysis that overcomes many of these limitations and may provide a uniform comparative approach to the study of community organization. This paper presents both a basic exposition of our methods and a preliminary test of some ideas concerning community structure. By way of example, we have analyzed bird communities in scrub habitats in the western United States and Chile described by Cody (1974) in his book, "Competition and the structure of bird communities." Cody provides both a set of censuses for habitats with simple vegetation structure and an ecological analysis of community structure that allow us to compare his ecological and our morphological approaches. It will become apparent that the two approaches may lead to strikingly different conclusions about the structure of bird communities, partly owing to the techniques of analysis and partly to the different concepts that motivated each of the studies. Above all, the results of our study should caution those who accept resource partitioning as evidence that competition plays a strong role in molding the structure and organization of bird communities.

METHODS

Morphological space.—Our analysis is based on the position of each member of a community in an n-dimensional morphological hyperspace of which the axes are the logarithms of n measurements. The

logarithmic transformation results in a more nearly normal distribution of data, tends to equalize the variances of the measurements, and allows one to identify ratios between variables from linear combinations of those variables [i.e. $\log(a/b) = \log(a) - \log(b)$] without the statistical problems inherent in the numerical analysis of ratios.

We describe the morphological space occupied by a set of species by means of a Principal Component Analysis (PCA) (Morrison 1967, Pielou 1969) of the n morphological dimensions based on the log-transformed measurements. Programs for the PCA were written by J. Travis based upon SSP subroutines. PCA provides n orthogonal coordinates, each of which is a linear combination of the original measurements. We calculate principal components from the covariance matrix, rather than the more traditionally used correlation matrix. As a result, the space described by the principal components is undistorted with respect to the space described by the logarithms of the original variables. In addition, the sum of the eigenvalues is equal to the sum of the variances of the original measurements, rather than to n as it is in a PCA based on a correlation matrix.

The first principal component is the vector through an n-dimensional cluster of data points that maximizes the variance among projections of the data points along itself. Subsequent components are constructed to account maximally for the remaining variance, subject to the constraint that they be orthogonal to all other components. By definition, the distributions of species along each principal component are independent of their distributions along all other components.

We ascertained the significance of the principal components by χ^2 test of the null hypotheses that the last r characteristic roots (eigenvalues) of the covariance matrix are equal. If the null hypothesis were true, the last r components would not define statistically significant axes, but rather would be part of an infinite set of geometrically arbitrary coordinates for a spherical cluster of points. Each χ^2 statistic is calculated by the expression:

$$\chi^2 = -(n - 1) \sum_{j=q+1}^{q+r} \left[\ln(\lambda_j) + (n - 1)r \ln\left(\frac{\sum \lambda_j}{r}\right) \right],$$

where n is the sample's size, r the number of roots being compared, $q + r$ the total number of roots, and λ_j the jth eigenvalue (Anderson 1963, Morrison 1967). The number of degrees of freedom is

$$df = [r(r + 1)/2] - 1.$$

Community analysis.—We define the Euclidean distance between a pair of species i and j as:

$$d_{ij} = \left[\sum_{k=1} (X_{ik} - X_{jk})^2 \right]^{1/2},$$

where X_{ik} is the value of the logarithm of original measurement k for species i, X_{jk} is the value of measurement k for species j, and d_{ij} is the distance between species i and species j. Because the PCA does not distort the morphological space, Euclidean distances based on original measurements and on principal components are identical.

For each community, we calculated the average nearest-neighbor distance (NND) as a measure of the density of species packing and the standard deviation of the nearest-neighbor distance (SDNND) as a measure of the evenness of species packing.

We calculated the standard deviations of projections of the member species onto each principal component (SC_{ij}) as an index to the size of that dimension (i) for a particular community (j). We calculated the volume (V_j) occupied by community (j) as the produce of the standard deviations of either the first four or all eight principal components:

$$V_j = \prod_i SC_{ij}.$$

Because we permit two species to be each others' nearest neighbors, marked clumping within the morphological space could bias the average nearest-neighbor distance as an estimate of the density of species packing within the community. To check for this potential bias, we constructed shortest spanning trees, or Prim networks (Prim 1957), for each of the communities. The Prim network is the shortest composite line that connects all the species in the community. The Prim network of an n-species community has $n - 1$ segments. In this study we calculated the mean and standard deviation of the segment lengths, which are analogous to the mean and standard deviations of the nearest-neighbor distances.

Random communities.—Hypotheses about community organization predict certain attributes of community structure, several of which are discussed in this paper. For example, the theory that relates competition to community organization predicts that species should be more or less regularly distributed

in ecological space and, by implication, morphological space. One result of limiting similarity theory suggests that nearest-neighbor distance should be independent of species number, provided niche breadth remains constant (May and MacArthur 1972, May 1975). To test these predictions statistically, one must have a null hypothesis. In this study, we have generated a number of random communities in which each species is chosen independently of all the others. The species in the random communities occupy the same morphological space as in the natural communities, but their spacing is independent of any interactions among them.

Random communities were generated by two methods. One set of 80 random communities was generated by assigning random numbers to the total set of species in all of Cody's study areas and drawing 20 random communities of each of 5, 9, 13, and 17 species. The only restriction on species composition was that no species could be placed in a community more than once. Any one species could occur in as many different communities as its number arose.

The second set of 80 random communities was produced by randomly generating synthetic species within the principal component space occupied by the species in Cody's study. The factor score for each synthetic species on each of the eight principal components was derived by a random normal deviate (RND) generator with a mean of zero and a standard deviation of unity. Each RND was multiplied by a factor equal to the standard deviation of the projections of the real species onto each principal component (the standard deviation equals the square root of the eigenvalue). We calculated matrices of Euclidean distances for each community from the synthesized factor scores and used the matrix to calculate morphological measures of community structure (NND and SDNND).

Field data.—To illustrate the application of our multivariate techniques and to test several predictions about community structure, we have analyzed the morphological relationships within communities of birds in the 11 scrub habitats described in Appendix A of Cody (1974). This analysis is not intended to review or evaluate Cody's data, which are accepted here at face value. Table 1 lists the 11 communities and Cody's assessment of ecological overlap among nearest neighbors.

Species.—The combined species lists of the 8 North American and 3 South American communities include 76 species of passerine birds. We excluded nonpasserines (mostly hummingbirds, doves, and cuckoos) from this analysis. We found that the morphological spaces occupied by nonpasserine and passerine species do not overlap. Therefore, morphological distances between species within the space occupied by passerines are not affected by deleting the peripherally located nonpasserines.

When the smaller sex of a species differed from the larger by more than 10% of the larger in any morphological character, the sexes were treated as separate morphological types. In this study, such dimorphism occurred in the Icteridae (4 out of 4 species), Corvidae (1 of 2), and Fringillidae (2 of 18), bringing the total number of morphological forms to 83. We use the term "number of species" interchangeably with "number of morphological types" unless stated otherwise. Note, however, that the rank orders of communities determined by either number are identical (Table 1).

Morphological characters.—In this analysis, we have described morphological space by eight characters, chosen according to availability of published data, ease of measurement, and lack of redundancy. The characters are lengths of (1) body, (2) wing, (3) tail, (4) tarsus, and (5) middle toe, and the length (6), depth (7), and width (8) of the beak.

For North American species, measurements of characters (1) through (5) were obtained from compilations in Ridgway (1901–1918). Bill measurements and all South American data were obtained from specimens at the Academy of Natural Sciences in Philadelphia. We measured specimens of the pertinent subspecies and, where possible, from the general locality of Cody's study areas. Samples included four–six individuals of each species (and of each sex in dimorphic species). We measured with a plastic ruler to the nearest millimeter (1) total length (tip of bill to tip of tail); (2) length of the folded wing, flattened along a stiff ruler, from the wrist to the tip of the longest primary; and (3) length of the tail, from the base to the tip of the longest retrix. We measured to the nearest 0.1 mm with dial calipers lengths of the (4) tarsus, (5) middle toe (to the base of the claw), and (6) culmen from the tip of the upper mandible to its kinetic hinge (Bock 1966), and the (7) depth and (8) width of the beak at the kinetic hinge. Our bill length measurement differs slightly from that of Ridgway, who recorded the length of the "exposed" culmen, the tip to the edge of the feathered portion. We replaced total length with a derived measure, body length minus the lengths of the culmen and tail, to reduce redundancy in our variables.

RESULTS

Logarithmic transformation eliminated most significant differences between the variances of the original measurements. Standard deviations of the log-transformed

TABLE 1. Parameters of the 11 scrub communities reported by Cody (1974).

Habitat	Location[a]	Number of passerine species	Number of morphological types (S)	Family diversity (F)[b]	Average nearest-neighbor overlap (a_{max})[c]	Average nearest-neighbor distance (NND)	Standard deviation of NND (SDNND)	Average Prim segment length (P)	Morphological volume	
									V_4[d]	V_8[e]
1. Sagebrush	Wyoming (2)	5	6	1.01	0.548		0.102	0.198	1.77	0.13
2. Saltbush	Colorado (3)	5	6	1.33	0.575	0.185	0.112	0.250	4.16	1.75
3. Coastal scrub	Chile (9)	5	7	1.27	0.641	0.265	0.078	0.193	1.78	1.68
4. Mojave desert	California (4)	8	8	1.91	0.724	0.199	0.087	0.264	4.36	5.39
5. Mesquite	Arizona (7)	8	8	1.42	0.680	0.269	0.143	0.230	1.93	0.98
6. Sonoran desert	Arizona (6)	9	9	1.97	0.706	0.219	0.111	0.250	5.48	5.09
7. Willows	Wyoming (1)	11	11	1.36	0.669	0.173	0.073	0.169	1.18	1.22
8. Chaparral	California (5)	12	12	2.06	0.727	0.173	0.059	0.215	2.07	2.71
9. Savanna	Chile (11)	13	16	1.91	0.724	0.218	0.056	0.222	3.56	12.13
10. Matorral	Chile (10)	15	16	2.17	0.741	0.221	0.062	0.231	4.45	19.43
11. Pine-oak	Arizona (8)	16	17	2.33	0.639	0.189	0.088	0.220	3.16	7.20

[a] Numbers in parentheses refer to order of study sites in Cody (1974).
[b] $F = \exp(-\Sigma p_i \log_e p_i)$ where p_i is the proportion of species in family i.
[c] Compiled from overlap matrices for each community in Appendix B of Cody (1974); a_{max} is the average of the largest value of a for each species.
[d] Values $\times$ 10^4.
[e] Values $\times$ 10^{10}.

TABLE 2. Factor loadings of each variable on the first five principal components, proportion of the variance explained by each component, test of significance, and distribution parameters of each component.

Variable (log$_{10}$)	Principal component factor loadings				
	I	II	III	IV	V
Length	0.355	−0.054	−0.157	−0.150	−0.271
Wing	0.317	−0.250	−0.537	−0.180	−0.239
Tail	0.345	0.079	0.201	0.866	0.164
Tarsus	0.335	0.450	−0.296	0.145	−0.390
Midtoe	0.342	0.156	−0.227	−0.182	−0.437
Culmen	0.390	0.530	−0.155	0.371	0.635
Depth	0.409	−0.497	0.645	0.031	−0.301
Width	0.326	−0.417	−0.259	−0.055	0.075
Eigenvalue[a]	0.1444	0.0133	0.0105	0.0065	0.0037
Standard deviation[b]	0.380	0.115	0.102	0.081	0.061
Variance explained					
Percent	0.792	0.073	0.057	0.036	0.020
Cumulative	0.792	0.865	0.922	0.958	0.978
χ^2	—	240.0	177.2	102.8	43.3
df	—	27	20	14	9
P	—	<0.005	<0.005	<0.005	<0.005

[a] Variance of the factor scores of each species projected onto the principal component; eigenvalues for the last three principal components were 1.6, 1.4, and 1.0×10^{-3} ($P > 0.05$).

[b] Square root of the eigenvalue.

(base 10) variables varied between 0.139 and 0.180, with only one value (culmen depth) greater than 0.168. Within this range, ratios of variances (F-ratios) significantly greater than 1.0 result from differences between standard deviations in excess of about 0.30. Therefore, culmen depth may be significantly more variable among species than some of the other characters.

Principal component analysis.—Each principal component is an eigenvector of the covariance matrix of the original variables. The linear combinations of characters that define each principal component are described by coefficients of linear relationship (Table 2). Each column in Table 2 lists the loadings or coefficients of each character in the equation for that particular principal component. Because measurements were transformed to logarithms, positive loadings in a linear combination of variables imply multiplication; negative loadings, division. The coefficients describe the allometric relationships among the characters. For example, component II has large positive loadings on tarsus (0.45) and bill length (0.53) and large negative loadings on bill depth (−0.50) and width (−0.42); component II thus represents variation in the ratio (tarsus length$^{0.45}$ bill length$^{0.53}$ bill depth$^{-0.50}$ bill width$^{-0.42}$). Other components may be interpreted similarly. A chi-squared test of significance of the eigenvalues revealed that components VI through VIII cannot be distinguished statistically from arbitrary vectors drawn through a spherical cloud of points.

The first principal component basically measures overall size, even though some allometric shape information is included; that is, all the coefficients are not identical. It accounts for 79% of the total variance in morphological space. Species having the extreme values of this component (Table 3) weigh less than 10 g at one extreme and more than 100 g at the other.

The second component (tarsus culmen/depth width) accounts for 7% of the morphological variance among species. At one end of the component, with long legs and long, thin bills, are the thrashers *Toxostoma* ssp. (Mimidae) and the gnatcatcher

TABLE 3. Species occupying extreme positions on each of the first five principal components.

Component and extreme species	Family	Score
Component I (overall size)		
Aphelocoma ultramarina (♂)	Corvidae	0.81
A. ultramarina (♀)	Corvidae	0.74
A. coerulescens	Corvidae	0.63
Troglodytes aedon	Troglodytidae	−0.59
Polioptila melanura	Silviidae	−0.62
Psaltriparus minimus	Paridae	−0.63
Component II (tarsus culmen/width depth)		
Toxostoma redivivum	Mimidae	0.24
T. lecontei	Mimidae	0.22
Polioptila melanura	Silviidae	0.20
Tachycineta thalassina	Hirundinidae	−0.21
T. leucopyga	Hirundinidae	−0.22
Progne subis	Hirundinidae	−0.24
Component III (depth/wing)		
Passerella iliaca	Fringillidae	0.16
Calamospiza melanocorys	Fringillidae	0.15
Cardinalis sinuatus (♂)	Fringillidae	0.14
Tachycineta thalassina	Hirundinidae	−0.25
Progne subis	Hirundinidae	−0.30
Tachycineta leucopyga	Hirundinidae	−0.35
Component IV (tail culmen)		
Leptasthenura aegithaloides	Funariidae	0.23
Chamaea fasciata	Chamaeidae	0.15
Phainopepla nitens	Ptilogonatidae	0.11
Aphelocoma ultramarina (♂)	Corvidae	0.11
Sitta carolinensis	Sittidae	−0.19
Sturnella neglecta	Icteridae	−0.20
Sitta pygmea	Sittidae	−0.22
Component V (culmen depth/tarsus midtoe)		
Myiarchus tuberculifer	Tyrannidae	0.18
Contopus sordidulus	Tyrannidae	0.18
Empidonax traillii	Tyrannidae	0.11
Pteroptochos megapodius	Rhinocryptidae	−0.12
Cattarus ustulata	Turdidae	−0.16

Polioptila melanura (Silviidae); at the other end, with short legs and stout bills, are three species of swallows (Hirundinidae).

Component III (bill depth/wing length) accounts for 6% of the variance. Three finches, with stout bills, have the extreme high values, while the swallows, with their long wings and flattened bills, occupy the other end of the component. The remaining components account for only 8% of the total variance, but, although they separate relatively few species, two are morphologically interpretable as tail culmen (IV) and bill length depth/tarsus midtoe (V). Component IV separates nuthatches (*Sitta*) from other species, and component V appears to isolate several flycatchers (Tyrannidae). The remaining three components are not statistically meaningful, but, as we shall demonstrate below, they measure variation that is important biologically. Inasmuch as the higher taxonomic categories of birds are distinguished partly by size and shape, it is not surprising that the families of birds included in this study occupy distinct regions within the morphologically defined space (Fig. 1). The Ty-
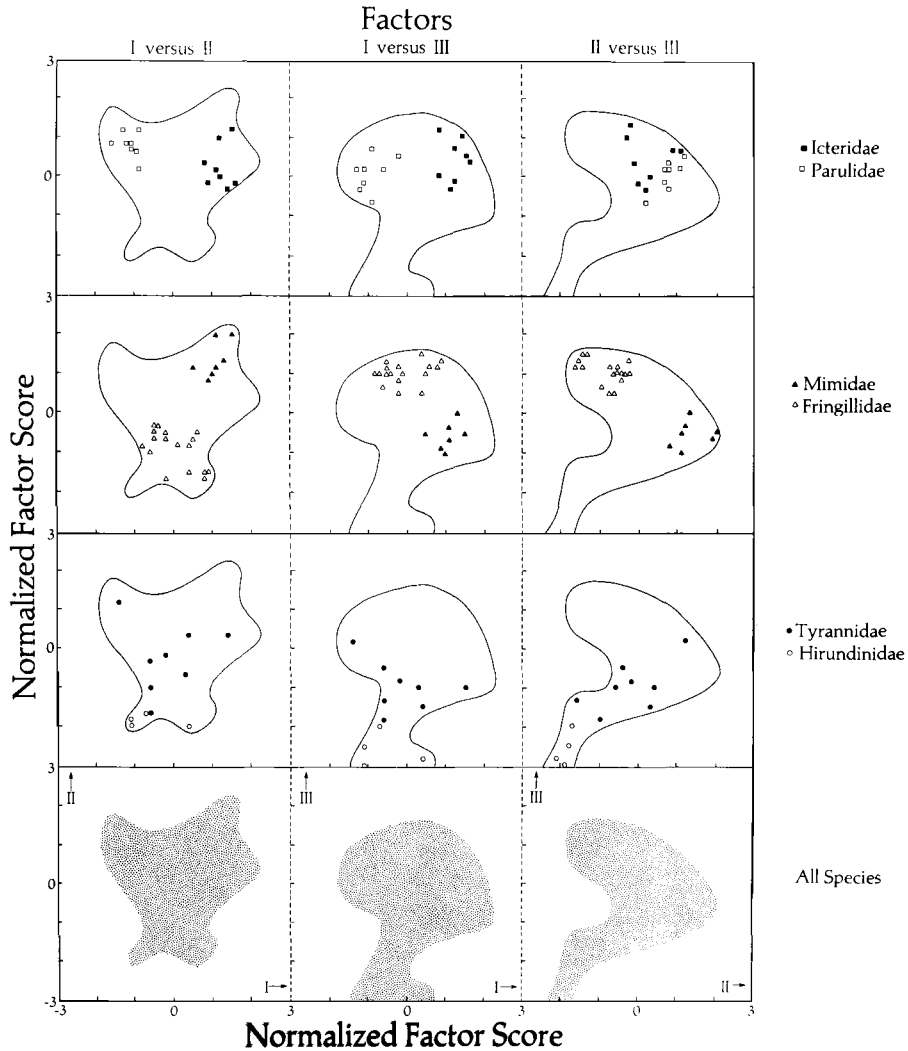
Fig. 1. Positions of species in a variety of families represented in scrub communities with respect to the first three principal components in the morphological space defined by all 83 species and forms. Projections on factors are presented in pairwise fashion. Factor scores were normalized by the mean and standard deviation of the species' projections. The shaded areas in the bottom set of boxes represent the area occupied by all 83 species and forms in morphological space. These areas are outlined in the boxes above.

rannidae are the most diverse morphologically, overlapping many other families within the three morphological planes defined by the first three principal components. The distinctly irregular shape of the morphological space derives primarily from the extreme morphological positions of the swallows (Hirundinidae), the only aerial foragers in the sample of species.

Nearest-neighbor distances.—Nearest-neighbor distances (NND) within the morphological space are portrayed for various subsets of species in Fig. 2. NND's within genera (**E**) resemble the distribution of NND's within the scrub habitat avifauna as a whole (**A**). Those genera with NND'S exceeding 0.20 were *Myiarchus* (Tyranni-
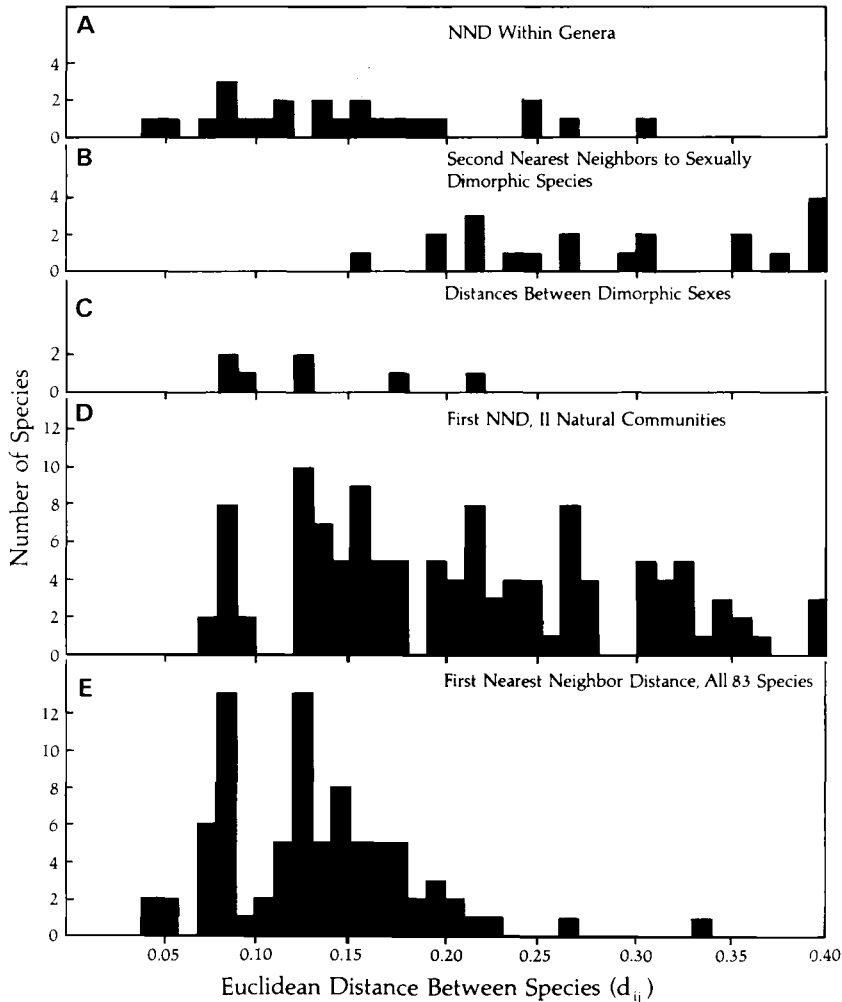
Fig. 2. Distribution of neighbor distances for selected groups of comparisons. For explanation see text.

dae), *Parus* (Paridae), *Sitta* (Sittidae), and *Zonotrichia* (Fringillidae). The within-genus distances tended to be much smaller than distances among all members of each family: Tyrannidae (8 species, d = 0.46 ± 0.24 SD), Hirundinidae (4, 0.36 ± 0.20), Paridae (4, 0.26 ± 0.12), Mimidae (7, 0.22 ± 0.08), Parulidae (8, 0.15 ± 0.15). This is not surprising, as taxonomists rely on many of the morphological measurements included in this study. Because distances within genera did not differ markedly from NND's more generally, we were not surprised to find four cases of sympatric congeners: *Sitta* (d = 0.31), *Dendroica* (0.07), *Pipilo* (0.08), and *Melospiza* (0.13) in the 11 communities.

The range of nearest-neighbor distances within the communities (Fig. 2. **D**, n = 118, i.e. several species occurred in more than one community) was greater than the range of NND's within the sample as a whole (**E**, n = 83). But the smallest NND's within communities (**D**), were similar to those within the sample as a whole (**E**),

suggesting that NND does not place a major constraint on the assembly of species into communities.

The distance between the sexes in species that we designated as dimorphic (**C**) resembled the distribution of nearest-neighbor distances among all 83 species and forms (**E**). Hence the degree of morphological differentiation between dimorphic sexes is similar to that between closely related species within the scrub habitat avifauna analyzed here. In every case, the two sexes of a dimorphic species were each other's nearest neighbors in the 11 natural communities. Furthermore, the second nearest-neighbor distances for each sex of dimorphic species in natural communities (**B**) were distributed as second NND's as a whole rather than first NND's. Hence, marked sexual dimorphism is correlated with an absence of morphologically similar species.

Community characteristics.—Morphological characteristics of the 11 communities are presented in Table 1. To determine the relationships of these characteristics to number of species, we calculated regressions of our morphological indices upon number of species. Because we transformed variables to their logarithms, the regressions reveal the percentage rate of change of one variable with respect to another. Hence, the slope of the relationship is independent of the particular scale of measurement used.

Cody's nearest-neighbor measure of ecological overlap (a_{max}) increased with increasing number of species in the community (slope $b = 0.17 \pm 0.06$ SE, $F(1,9) = 6.8$, $P \leqslant 0.05$). In contrast, the slopes of regressions relating our morphological measures of nearest-neighbor distance and average segment of the Prim network to number of species did not differ significantly from zero ($b = -0.11 \pm 0.13$, $F(1,9) = 0.8$, $P \geqslant 0.05$ and $b = -0.01 \pm 0.11$, $F(1,9) = 0.1$, $P \geqslant 0.05$). Because a_{max} depends upon both niche separation and niche breadth, the ecological and morphological results could be reconciled if niche breadth increased in proportion to number of species. Cody's (1974) Fig. 29 indicates that the habitat component of niche breadth is unrelated to number of species among the eight North American sites. He did not tabulate the vertical-foraging-height component of niche breadth.

The standard deviation of nearest-neighbor distance decreased significantly with increasing number of species in the community ($b = -0.45 \pm 0.21$, $F(1,9) = 4.7$, $P \leqslant 0.05$).

Comparisons with random communities.—To determine whether or not the morphological arrangement of species in communities reflected internal organization, we compared NND's and SDNND's in natural and randomly generated communities (Fig. 3). The null hypothesis in these comparisons is that the species in natural communities are drawn at random from a pool representing the total morphological diversity of species in the 11 communities studied by Cody. Because the largest natural community contained only 20% of the species in the pool, biases caused by the makeup of the pool were unlikely, but we could not rule them out completely.

In the random communities, log NND decreased significantly with log species number ($b = -0.36 \pm 0.04$, $F(1,78) = 177$, $P \leqslant 0.001$). To test the homogeneity of the slopes of this regression for random and natural communities, we calculated a value of t (df $= 10$) from the difference between the slopes $[-0.11 - (-0.36) = 0.25]$ in the numerator and the standard error of the slope for natural communities (0.13) in the denominator. The resulting value ($t = 1.92$) is marginally significant ($P = 0.05$) in a one-tailed test, but not in a two-tailed test. Hence the result is ambiguous.
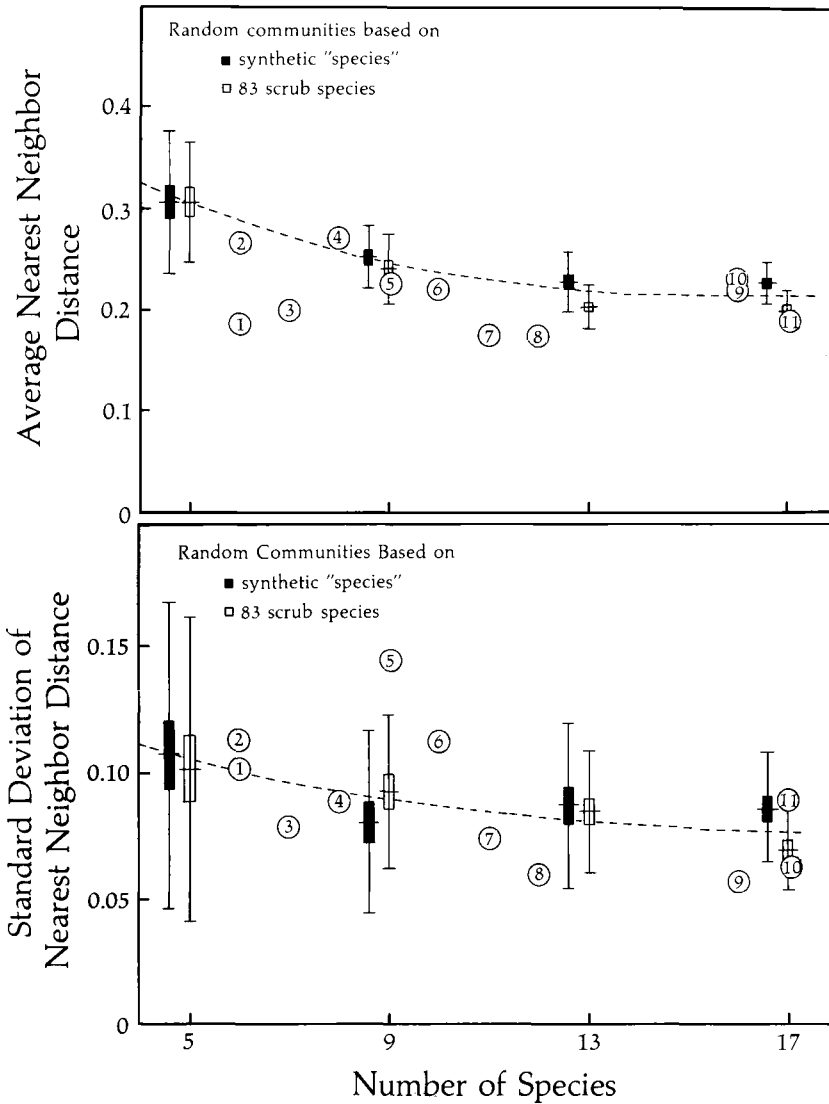
Fig. 3.   Above: Relationship of average nearest-neighbor distance to number of species in randomly generated communities and in 11 scrub communities, keyed by number in Table 1. Below: Relationship of the standard deviation of the nearest-neighbor distance to number of species in randomly generated communities and in 11 scrub communities. The values for the random communities are based on 20 replicates of each size. The vertical lines show the standard deviations, and the boxes show the standard errors of the mean. The dashed lines were drawn through the random community data by eye to suggest the trend.

The NND's of 8 of the 11 natural communities fall below the regression line for the random communities. This distribution does not differ significantly from the expectation of the null hypothesis that half the communities fall above and half below the line according to either a binomial test ($P = 0.11$) or χ^2 test ($\chi^2_1 = 2.27$, $P \geq 0.10$). The mean deviation of values of NND from the regression line for random communities, however, is significantly less than 0 ($t = -2.35$, $P \leq 0.05$).

TABLE 4. Regressions of logarithms of the lengths of morphological dimensions (standard deviations of species projections on principal components) upon logarithm of species number for 11 natural communities.

Component	$b \pm SE$	F
I	0.29 ± 0.18	2.79
II	-0.07 ± 0.24	0.10
III	-0.11 ± 0.16	0.47
IV	0.15 ± 0.28	0.31
V	0.90 ± 0.18	23.81[a]
VI	0.15 ± 0.14	1.20
VII	0.79 ± 0.16	22.93[a]
VIII	0.58 ± 0.25	3.00

[a] $P < 0.001$.

The standard deviation of nearest-neighbor distance is a measure of regularity of spacing in the morphological space. It is extremely variable, particularly in small communities, but its average value and variation decrease somewhat with increasing number of species indistinguishably in both natural and random communities (Fig. 3).

Species number and community morphological volume.—In random communities, species are added without regard to the presence of others. Because each community is a random sample of the total species pool, the morphological volumes of the random communities and the lengths of each morphological dimension do not vary with respect to number of species. Logarithmic regressions of the community morphological volumes, V_4 and V_8, upon number of species had slopes of $b = 0.27 \pm 0.42$ [$F(1,9) = 0.4$, $P \geq 0.05$] and $b = 2.78 \pm 0.84$ [$F(1,9) = 10.9$, $P \leq 0.01$). These results indicate that the four smaller principal components taken together do expand in direct relation to the number of species in the community, in spite of the fact that the last three components are not unique morphological dimensions (see Table 2). Regressions of dimension length (standard deviations of projections) against species number (Table 4) indicated that components V, VI, and perhaps VIII increased in direct proportion to species number (b significantly greater than 0 and not significantly different from 1.0).

The regression of principal component dispersion on species number shows that species are not added to communities at random. Diverse communities appear to have a larger proportion of species occupying extreme positions on the shorter morphological dimensions. We can see this by analyzing the occurrence of species occupying extreme positions in the morphological space. For each dimension (principal component), we determined the three species out of the total pool of 83 that occupied each end of the distribution (see Table 3). We then asked how many of these species were found in the 4 most diverse communities, having a total of 61 species, and in the 7 least diverse communities, having a total of 57 species. For the first 4 principal components, there were 17 occurrences of the extreme species in the more diverse communities and 14 in the less diverse communities. This distribution was not significantly different from random by χ^2 test. For the last 4 principal components, 27 of the extreme forms occurred in the 4 more diverse communities and only 8 in the 7 less diverse communities, a significantly nonrandom distribution ($\chi^2_1 = 12.9$, $P \leq 0.005$).

Diversity and taxonomic composition.—The taxonomic composition of the scrub community varies considerably from locality to locality, and between North and

South America. One manifestation of this variation is seen in the diversity of families ((F) represented in each community, which varies in direct relation to number of species in a logarithmic regression ($b = 0.58 \pm 0.14$, $F(1,9) = 17.7$, $P \leq 0.01$). In part, this relationship reflects a property of small samples: a sample of one species, for example, can include only one family ($F = 0$). But if sampling bias were the major cause of the family diversity/species number relationship, we would expect the less common families to be poorly represented in communities with few species. For families with 5 or fewer forms represented in the sample communities, there were 22 occurrences of those species in the 4 largest communities, with about one-half of the total number of species occurrences (61), and 15 occurrences of those species in the 7 smallest communities with a total of 57 species occurrences. A χ^2 test showed that the smaller families were not significantly associated with occurrences in the larger communities. Representation of the larger families in small and large communities was, however, decidedly nonrandom. Flycatchers were significantly associated with large (principally South American) communities, 18 vs. 4 ($\chi^2_1 = 8.0$, $P \leq 0.005$), whereas finches were associated primarily with the smaller (principally North American) communities 19 vs. 8 ($\chi^2_1 = 5.3$, $P \leq 0.025$).

As each family occupies a distinct position within the morphological space (see Fig. 1), the diversity of families should strongly influence the total overall volume (V) occupied by a community. A multiple regression analysis of the relationship between the logarithm of volume and the logarithms of both species number (S) and family diversity (F) yielded the following equations:

$$\log V_4 = -0.096 - 0.032(\pm 0.023)\log S + 0.517(\pm 0.215)\log F \quad [F(2,8) = 2.28,$$
$P \geq 0.10$], and
$$\log V_8 = -1.625 + 0.020(\pm 0.047)\log S + 1.070(\pm 0.433)\log F \quad [F(2,8) = 11.1,$$
$P \leq 0.005$].

For the 11 communities included in this sample, family diversity varied by a factor of 2.3, almost as great as that for number of species (2.8).

Community convergence.—Cody (1974: 189–201) stated that, although North and South American communities of birds have diverse taxonomic origins, they nonetheless have similar numbers of species and variety of morphological and behavioral types. He went further to make species-for-species matches between birds of the Chilean matorral and California chaparral habitats. Two issues are raised here. One is a general convergence in the overall range of ecological types in similar habitats. The second is species-for-species matching, suggesting unique and discrete roles for each pair of convergent species in physiognomically similar habitats.

In this study we have examined both community and species-level convergence with respect to morphological characters of species in the matorral and chaparral communities. To assess community convergence, we compared the means and standard deviations of factor scores of species in the two communities on the first five principal components (Table 5). Our null hypothesis is that the means and standard deviations of the factor scores in the two communities do not differ. The only significant difference in means was for factor III (ratio of bill depth to wing length). The larger value for the chaparral community probably reflects the smaller number of flycatchers and swallows in the chaparral community (two species) compared to the matorral community (five species). But the overall similarity of the means and standard deviations of the factor scores suggest that the communities nearly coincide morphologically, at least in broad outline.

TABLE 5. Means and standard deviations of scores for factors I through V for the Chilean matorral and California chaparral communities.

	Factor				
	I	II	III	IV	V
Mean score					
Chaparral[a]	0.007	0.021	0.043	0.037	0.015
Matorral[b]	0.066	−0.005	−0.044	0.006	0.014
Standard deviation					
Chaparral[a]	0.399	0.117	0.068	0.067	0.044
Matorral[b]	0.423	0.114	0.111	0.083	0.064

[a] Number of species = 12.
[b] Number of species = 16.

We assessed convergence on a species-for-species level by comparing nearest-neighbor distances within and between communities. If ecological roles converged precisely and if they were paralleled by morphological convergence, we would expect each species to be more similar to its analog in the convergent community than to its nearest neighbor in the same community. If species were distributed more or less at random within the community niche space, we would expect the distance of a species to its nearest neighbor in a convergent community to approach the nearest-neighbor distance within the same community. Our analysis indicated that a species' nearest neighbor in a convergent community was almost exactly as distant as its nearest neighbor in the same community (chaparral, $\bar{x} = 0.173 \pm 0.017$ SE vs. 0.173 ± 0.010; matorral, $\bar{x} = 0.228 \pm 0.015$ SE vs. 0.229 ± 0.022). To double check this result, we combined both species lists into a single community and determined whether the nearest neighbor of each species belonged to its own community or to the convergent community. A 2×2 contingency table relating the location of each species to the location of its nearest neighbor revealed no association between Californian and Chilean species ($\chi^2_1 = 0.108$, $P \geqslant 0.05$). Hence, we found no evidence for morphological convergence on the species-for-species level; many species did not even have close morphological counterparts.

DISCUSSION

The value of a morphological approach to describing the organization of bird communities depends upon the relationship of morphological characters to the ecology of species. That behavior and morphology are generally correlated is well known (e.g. Karr and James 1975, Bierregaard 1978, Cody and Mooney 1978). Because Cody (1974) did not tabulate his observations of feeding behavior for each species, however, we could not examine the degree to which they matched our morphological characters. The relationship between Cody's ecological overlap (a; Appendix A of Cody 1974) and our morphological distance (d) is shown in Fig. 4. In communities with few species, Cody's overlap is inversely related to distance, as one would expect. In more diverse communities, this relationship is largely obliterated.

Cody calculated a as the average of overlaps in habitat distribution and vertical foraging height (α_H, α_V) and differences in rates of foraging movements and bill dimensions (α_F). Because a is scaled between 0 and 1, it is insensitive to variation in the region of low overlap. Morphological distance, however, preserves relationships without distortion. As species diversity increases, the overall range of a_{ij}'s in
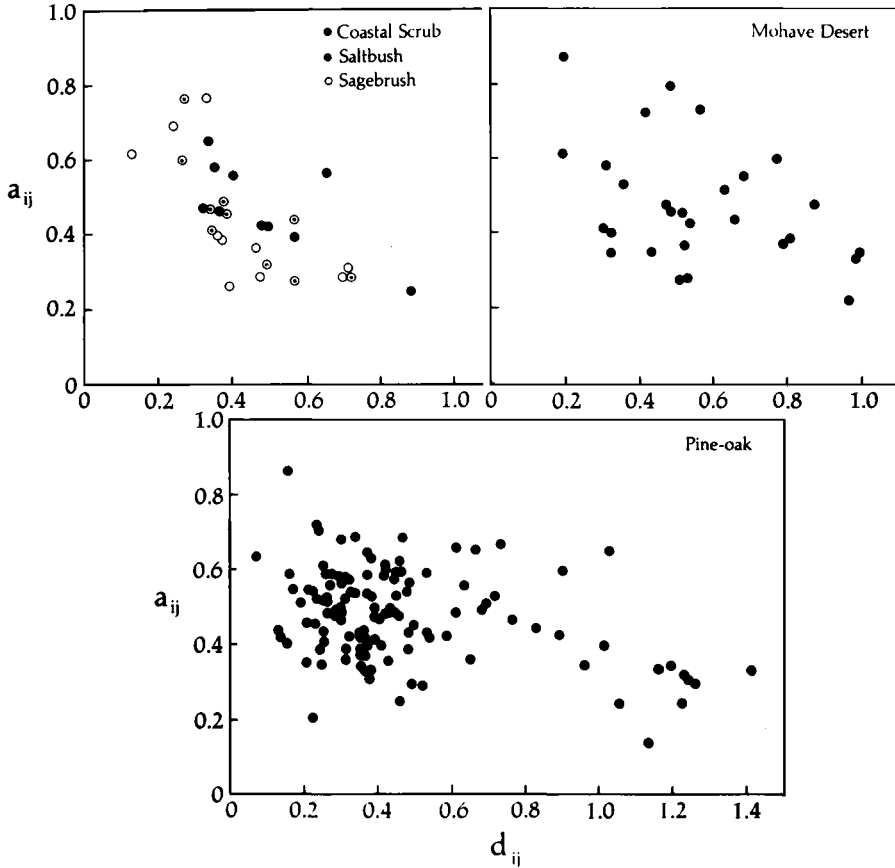
Fig. 4. Relationship between morphological distance (d_{ij}) and Cody's measure of ecological overlap (a_{ij}) in five communities. When species i was dimorphic, we averaged the distances of each sex to species j.

a community remains nearly constant, while the range of morphological distances (d_{ij}) increases (Fig. 4). It appears that, whereas a may be a sufficient measure of species relationships in simple communities, it fails to incorporate additional dimensions of resource partitioning employed by species in more diverse assemblages. We have seen that more diverse communities occupy a greater number of morphological dimensions than do less diverse communities.

We attempted to identify patterns of organization in bird communities from an analysis of morphological attributes of community structure. These were of two types. On the one hand, we examined the relationship between similar morphological types by the means and standard deviations of nearest-neighbor distances within communities. On the other, we examined the total morphological volume occupied by each community by the dispersions of species along each principal component in the morphological space. When we tested observed patterns against null hypotheses, we were able to draw several conclusions.

First, we could find no evidence that the density or regularity of species packing was determined by interactions among species. Whereas competition between species

presumably would be expressed in NND's greater than predicted by the null hypothesis, species only in smaller communities tended to be packed more densely (smaller NND's) than predicted (Fig. 3).

Second, total community volume increased in direct proportion to number of species. Most of the expansion occurred along the smaller, indeed insignificant, principal components of the morphological space occupied. According to our null hypothesis, community volume should have been independent of the number of species.

Third, comparisons of communities in similar habitats revealed general convergence or conservatism of the overall morphological space occupied but no indication of species-for-species counterparts.

Our analyses suggest that species are added to communities in a decidedly non-random fashion, although there is no evidence that the patterns we observed result from local ecological interactions among species. All the communities appear to have a core of species occupying a common morphological space defined by the first three or four principal components. Species added to make up the more diverse communities appear to occur on the periphery of the morphological space occupied by the core species in directions orthogonal to principal component vectors defining the core. This pattern suggests that the core of the community niche may be ecologically saturated and that species can be added only onto secondary, or novel, dimensions. If morphological space were saturated, we would expect that nearest-neighbor distance should not vary with species number: in randomly assembled communities, NND decreases with increasing diversity. Because of our small sample size ($n = 11$), our results did not rule out the null hypothesis completely. An alternative explanation for the pattern that species are added to the periphery of a core is that the ecological conditions of less diverse communities are favorable only to core-type species, in which case ours would not be appropriate null hypothesis against which to test community organization.

Because we could not distinguish patterns in the internal structure of natural communities from those of randomly generated communities, one might conclude that communities lack organization. But in accepting this view, one would fail to recognize two sources of sampling error. First, the detection of organization within communities depends in large degree upon statistical statements about community attributes, including their relationship to number of species in the community. To test the statistical relationship between natural and randomly generated communities, each natural community provides only a single data point. With so few degrees of freedom, the confidence limits on estimates of regression slopes and other statistics are broad, particularly for measures of internal organization like NND and SDNND. While we might not distinguish natural and random communities, we also might not distinguish natural communities from any reasonable model for highly organized communities.

Second, censuses of small, spatially defined areas, as in Cody's study, probably do not adequately sample the community relationships of any species. All species occur in a variety of habitats in which they interact with a wide spectrum of species. Although behavior may mold the species' niche in each habitat to the particular species it encounters there, there is little evidence for complete adjustment. In particular, most instances of ecological release in the absence of competitors are based upon habitat expansion, not change in patterns of feeding within habitats. Morphology certainly cannot respond to the local community experience. Furthermore,

the population of any species might be maintained in some habitats only by immigration from elsewhere. To understand fully the organization of a particular community, one might have to view each species over the whole range of habitats that it occupies. We feel that such an endeavor for a carefully selected group of species may be more fruitful than the continued analysis of local community interactions.

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