Statistical Interpretation of Species Composition

Dean BILLHEIMER, Peter GUTTORP, and William F. FAGAN

The relative abundance of different species characterizes the structure of a biological community. We analyze an experiment addressing the relationship between omnivorous feeding linkages and community stability. Our goal is to determine whether communities with different predator compositions respond similarly to environmental disturbance. To evaluate these data, we develop a hierarchical statistical model that combines Aitchison's logistic normal distribution with a conditional multinomial observation distribution. In addition, we present an algebra for compositions that includes addition, scalar multiplication, and a metric for differences in compositions. The algebra aids interpretation of treatment effects, treatment interactions, and covariates. Markov chain Monte Carlo (MCMC) is used for inference in a Bayesian framework. Our experimental results indicate that a high degree of omnivory can help to stabilize community dynamics and prevent radical shifts in community composition. This result is at odds with classical food-web predictions, but agrees with recent theoretical formulations.

KEY WORDS: Compositional data; MCMC; Multinomial regression; Random effects; Species assemblage.

1. INTRODUCTION

Species composition, the relative abundance of different species (or of different functional groups of species), has long been a key measure for evaluating biological communities (Fisher, Corbet, and Williams 1943; May 1975; Cairns 1979). For example, in early research by MacArthur (1955) and others, patterns of relative abundance of species were used to infer the importance of interspecific competition. When extensive data are available, species composition can be used to predict the number of species missing from a community sample (May 1975; Fagan and Kareiva 1997). Moreover, temporal shifts in species composition within a community have been identified as valuable early warning indicators of pollution (Patrick 1972; Schindler et al. 1985; Marmorek, Bernard and Ford 1988). Likewise, spatiotemporal patterns of relative abundance of different taxa can provide insight into the dynamics of ecological processes by highlighting community responses to environmental stressors and identifying aspects of community dissolution and reassembly (e.g., Patrick 1949; Edmondson and Litt 1982; Davis 1986).

Here, we use relative abundance of different (groups of) species to evaluate the role of food-web structure on community stability in the presence of disturbance. Omnivory–defined as feeding on more than one trophic level–is an important, often divisive, issue in food-web ecology. Classical food-web theory (Pimm and Lawton 1978; Pimm 1982) predicts omnivory to be a destabilizing feature in ecological communities, and therefore rare in nature. Early analyses of food-web catalogs support this result (e.g., Cohen 1978; Cohen et al. 1986). More recent theoretical investigations suggests that the role of omnivory depends on the degree of species interaction (e.g., Yodzis, and Innes, 1992). Further, by constraining species interactions according to bioenergetic principles, new theoretical models show that omnivory may exert a stabilizing, rather than destabilizing, influence on multispecies dynamics (McCann and Hastings 1997).

Field studies add to this debate. Results by Sprules and Bowerman (1988), Hall and Rafaelli (1991), and Polis (1991) indicate that omnivory is actually quite common in natural systems, provided that adequate efforts are made to accurately characterize food webs. Experimental work by Fagan (1997) demonstrates that elevated omnivory can prevent major changes in species densities that would otherwise occur in response to disturbance. Communities lacking omnivores, instead dominated by specialist predators, produced the opposite results: large changes in abundance of some taxa in response to disturbance. This suggests that omnivory can act as a stabilizing factor rather than a destabilizing one.

Here, we describe an experiment at Mount St. Helens, Washington, investigating how the degree of omnivory influences an arthropod community's response to experimentally-imposed disturbance. This approach is similar to work reported in an earlier study (Fagan 1997), but features two key differences. First, the ecological disturbance affects the producer trophic level (rather than the herbivores in the previous study). Second, the analysis concentrates on stability at the community level rather than at the population level (i.e., shifts in community composition vs. changes in population densities).

Previous research (Fagan 1996) suggests that removing vegetation tends to increase the abundance of both specialist and generalist feeding herbivorous species. These herbivores may be attracted to and/or enjoy greater survival in areas with decreased plant density. In contrast, when large numbers of omnivorous spiders are present, these effects on community composition are hypothesized to be reduced or eliminated. Because omnivorous spiders eat both specialist and generalist feeding herbivores, they limit increases in the abundance of these groups, preventing compositional shifts. Thus, the goal of the experiment is to evaluate whether the shift associated with vegetation disturbance is equivalent for all predator manipulations. In classical linear models, this is described by the interaction between predator manipulation and vegetative disturbance.

We use trophic category composition (relative abundance) to summarize arthropod community structure. We posit that each predator–vegetation treatment combination supports a (conceptual) species assemblage (i.e., a vector of proportions). The data from each plot provide discretely sampled information about the corresponding assemblage. Note that we do not

Dean Billheimer is Assistant Professor of Biostatistics at Vanderbilt University, Nashville, TN 37205 (E-mail: *dean.billheimer@mcmail.vanderbilt.edu*). Peter Guttorp is Professor of Statistics at University of Washington, Seattle, WA 98195. William F. Fagan is Assistant Professor of Biology at Arizona State University, Tempe, AZ 85287-1501.

use total abundance as either a response variable or as a covariate. Whereas total abundance does provide important ecological information, it is less relevant to community composition. Moreover, because vegetation removal increases abundance of herbivores, we anticipate abundance to be strongly related to a subset of the treatments. Hence, its inclusion as a covariate might obscure interpretation of treatment effects.

To investigate the stability of community composition, we develop a hierarchical statistical model combining Aitchison's (1982, 1986) logistic normal (LN) distribution with a conditional multinomial observation model. This combination accommodates multivariate count data associated with arthropod counts, and allows the rich structure of the LN distribution to describe inter-category covariances. More generally, our modeling framework may be viewed as a random effects model for multinomial data. This approach allows extramultinomial variability that is typical of data in many biological problems (e.g., Pollard 1975, p. 129). To help interpret our modeling results, we develop an algebra for compositions. This algebra formalizes developments of Aitchison (1986, 1992), and provides intuitive definitions for addition, scalar multiplication, and a metric for differences in compositions. Further, it allows us to define "linear" statistical models directly in terms of the compositional quantities and operations on them. We make extensive use of the algebra in evaluating the omnivory–disturbance interaction.

Our hierarchical modeling approach is similar (in spirit) to Allenby and Lenk (1994, see also Albert and Chib 1993; Dellaportes and Smith 1993). They use logistic normal regression models in a hierarchical Bayesian setting to relate covariates to household purchase decisions. They also incorporate random effects and serial correlation in modeling purchase behavior. We note that Allenby and Lenk interpret their results on the logit scale with respect to a fixed category. Further, parameter estimates are interpreted qualitatively, and with respect to the baseline brand.

Section 2 describes the experimental design and data collection. Section 3 reviews Aitchison's LN distribution for analysis of compositional data. We also introduce an algebra for composition vectors and illustrate how the algebra, along with graphical analysis tools can be used to interpret and visualize statistical modeling results. In Section 4, we couple the conditional multinomial observation model with the logistic normal in a hierarchical Bayesian framework. Section 5 provides analysis results from the omnivory experiment. Finally, Section 6 discusses issues associated with this modeling approach.

2. EXPERIMENTAL METHODS

Fagan (1996, 1997) conducted a series of experiments to evaluate the factors affecting the stability of arthropod communities in the presence of environmental disturbance. The experimental protocol is described in detail by Fagan (1996). Briefly, experimental plots were constructed by surrounding isolated clones of fireweed (Epilobuim) and pearly-everlasting (Anaphalis) with fluon-treated, plastic garden edging. A total of 30 plots were constructed, each measuring 1.5 m × 1.5 m. The plots were isolated from each other by vegetation free buffer zones, 1 m in width. The fluon-treated edging impeded

Table 1. Treatment Structure for Arthropod Community Stability Experiment. The Codes OV, SV, and so forth, Denote the Predator–Vegetation Factor Treatment Combinations

Vegetation disturbance	Predator manipulation		
	Increased omnivores	Increased specialists	Control level
50% Removal	OV	SV	CV
Control	OC	SC	CC

ground movements of arthropods in and out of the experimental plots. This allowed the manipulated predator densities to be maintained at their specified levels.

Five plots were assigned to each of the six experimental treatments. The treatments were arranged in a two-way factorial structure with predator manipulation (3 levels) and vegetation disturbance (2 levels) as the factors. The levels of the predator manipulation are increased dominance by omnivores (Pardosa, wolf spiders), increased dominance by specialist predators (Geocoris), and no change (control). Increased omnivory was accomplished by adding 3 subadult Pardosa wolf spiders, while removing the resident Geocoris specialist predators. Conversely, increased specialization means adding 2 specialist predators per plot and removing resident wolf spiders. All manipulated predator densities are within the naturally occurring density range. The vegetative disturbance consists of removing 50% of the existing fireweed (Epilobium) and pearly-everlasting (Anaphalis). The treatment structure is summarized in Table 1.

Arthropods (insects and spiders) were counted on each of the 30 experimental plots 2, 4, and 6 weeks after treatment application. Here, we consider only the 6 week data. These data are available online at http://www.nrcse.washington.edu/research/reports/reports.asp. Note that experimentally manipulated species (Pardosa and Geocoris) are not included in the counts. Eleven different species of arthropods were observed and included in the analysis. These species were partitioned into three trophic categories: predators, generalist herbivores, and specialist herbivores. The number of arthropods in each category (for each plot) comprise the data for analysis.

3. LOGISTIC NORMAL DISTRIBUTION AND AN ALGEBRA FOR COMPOSITIONS

Compositional data are vectors of proportions describing the relative contributions of each of k categories to the whole. Mathematically, $\mathbf{z} = (z_1, z_2, \ldots, z_k)'$, where $z_i > 0$, for all $i = 1, 2, \ldots, k$ and $\sum_{i=1}^{k} z_i = 1$. Hence, $\mathbf{z}$ is an element of the $(k-1)$ dimensional simplex (∇^{k-1}). The summation constraint and bounded support require special analysis techniques. Aitchison (1982, 1986) introduces the LN distribution as a framework for analysis of compositional data. These methods rely on the additive logratio transform $(\phi(\cdot))$ to take observations from the $(k-1)$-dimensional simplex (∇^{k-1}) to $(k-1)$-dimensional Euclidean space $(\Re^{k-1})$. The additive logratio transform of $\mathbf{z} \in \nabla^{k-1}$ to $\Re^{k-1}$ is defined as

$$\phi(\mathbf{z}) = \left[\log\left(\frac{z_1}{z_k}\right), \log\left(\frac{z_2}{z_k}\right), \ldots, \log\left(\frac{z_{k-1}}{z_k}\right) \right].$$

This transformation is a bijection with inverse transformation denoted by ϕ^{-1}. Aitchison (1986) terms the inverse transformation the additive logistic transform.

Aitchison models the transformed data via the $(k-1)$ multivariate normal distribution. Assuming multivariate normality of the transformed data induces a distribution on ∇^{k-1}: the LN distribution. A key benefit of the multivariate normal assumption is that its rich covariance structure transfers to the logistic normal. This allows modeling of dependence (positive or negative) between pairs of the k elements beyond that induced by the summation constraint. In addition, inference tools developed for multivariate normal data can be applied to the transformed compositions.

The LN density function is

$$f(\mathbf{z} \mid \boldsymbol{\mu}, \boldsymbol{\Sigma}) = \left(\frac{1}{2\pi}\right)^{(k-1)/2} |\boldsymbol{\Sigma}|^{-1/2} \left(\frac{1}{\prod_{i=1}^{k} z_i}\right)$$
$$\exp\left[-\frac{1}{2}(\phi(\mathbf{z}) - \boldsymbol{\mu})' \boldsymbol{\Sigma}^{-1} (\phi(\mathbf{z}) - \boldsymbol{\mu})\right]$$

for $\mathbf{z} \in \nabla^{k-1}$, where $\boldsymbol{\mu}$ is the location parameter vector in $\mathfrak{R}^{k-1}$, and $\boldsymbol{\Sigma}$ is a $(k-1) \times (k-1)$ variance-covariance matrix. We denote the density function by $L^{k-1}(\boldsymbol{\mu}, \boldsymbol{\Sigma})$. Clearly, the parameters depend on the ordering of the elements of $\mathbf{z}$. However, the density is invariant with respect to permutations of the components. Aitchison (1986) also establishes moments and other properties of this distribution, including its role as a limit distribution of successive, independent perturbations (defined later), and as the limiting form of the Dirichlet distribution as the Dirichlet parameters become large (Aitchison 1986, pp. 125–128).

In the rest of this section, we make use of the following notation. Let $\mathcal{C}(\cdot)$ denote the composition of a positive k-vector. That is, for $\mathbf{u} = (u_1, u_2, \ldots, u_k)'$ such that $u_i > 0$ for all i,

$$\mathcal{C}(\mathbf{u}) \equiv \left(\frac{u_1}{\sum_{i=1}^{k} u_i}, \frac{u_2}{\sum_{i=1}^{k} u_i}, \ldots, \frac{u_k}{\sum_{i=1}^{k} u_i}\right)'.$$

Also, denote elementwise multiplication of two positive k-vectors $\mathbf{u}$ and $\mathbf{v}$ by

$$\mathbf{u} \cdot \mathbf{v} \equiv (u_1 v_1, u_2 v_2, \ldots, u_k v_k)'.$$

Associated with the additive logratio transform is a perturbation operator for compositional data (Aitchison 1982). Perturbations allow an error structure on ∇^{k-1} analogous to the usual additive error model used in other areas of statistics. An observed proportion vector, $\mathbf{z}$, can be modeled as a location vector ($\boldsymbol{\xi}$) "perturbed" by an error ($\boldsymbol{\alpha}$). For $\boldsymbol{\xi}, \boldsymbol{\alpha} \in \nabla^{k-1}$,

$$\mathbf{z} = \boldsymbol{\xi} \oplus \boldsymbol{\alpha} = \mathcal{C}(\boldsymbol{\xi} \cdot \boldsymbol{\alpha})$$

and $\mathbf{z} \in \nabla^{k-1}$. The vector $\boldsymbol{\alpha}$ need not be an element of ∇^{k-1} for the perturbation operator to be defined. It is sufficient that $\alpha_i > 0$ for all $i = 1, 2, \ldots, k$. Aitchison (1986) shows a number of properties of the perturbation operator including associativity, commutativity, an inverse perturbation, an identity element

$$\mathcal{J}_{k-1} = \left(\frac{1}{k}, \frac{1}{k}, \ldots, \frac{1}{k}\right)$$

and a power-transformation for compositions (Aitchison 1986, p. 120).

Unfortunately, as Aitchison (1986) and others (e.g., Pawlowski and Burger 1992) describe, interpretation of parameter estimates on the multivariate log-odds scale is difficult. Specifically, location parameters are $\mu_i = E(\log(z_i/z_k))$ for $i = 1, 2, \ldots, k-1$, and elements of the covariance matrix, $\sigma_{ij} = \text{cov}(\log(z_i/z_k), \log(z_j/z_k))$. While location parameters estimates can be transformed back to ∇^{k-1} via ϕ^{-1}, it is not clear how one should interpret interaction parameters (or effects) or regression parameter vectors estimated on the multivariate log-odds scale. Indeed, it can be challenging to understand these parameters (or their estimates) in terms of the motivating scientific problem.

A related difficulty is a suitable definition for a distance metric on ∇^{k-1}. Watson and Phillip (1989) and Aitchison (1992) debate metrics for distances between compositions. Watson and Phillip (1989) propose an angular measure of distance by considering transformed compositions as points on the $(k-1)$-dimensional sphere. Aitchison outlines desirable properties of a compositional metric, and proposes several forms meeting those properties. Specifically, he recommends the sum of squares of all logratio differences as a simple and tractable form.

3.1 Algebra for Compositions

Following Aitchison's (1986, 1992) suggestion, we use the perturbation operator to define an addition operator for compositions. Further, the power transformation allows us to define scalar multiplication of a composition $\mathbf{z}$ by a scalar a as,

$$\mathbf{z}^a \equiv \mathcal{C}(z_1^a, z_2^a, \ldots, z_k^a)$$

We show that ∇^{k-1} equipped with the perturbation operator and scalar multiplication constitutes a complete inner product space. (See Appendix I for details.) This additional mathematical abstraction allows the definition of a norm on ∇^{k-1}. Moreover, it provides a framework for algebraic operations on compositions. Once these operations are established, we see that difficulties with interpretation of regression parameters, interaction effects, and distances between compositions are alleviated. First, we show the inner product and norm, and then describe interpretation of parameters.

Define, $\mathcal{N} = [I_{k-1} + \mathbf{j}_{k-1}\mathbf{j}_{k-1}']$, where I_{k-1} is a $(k-1)$-dimensional identity matrix, and $\mathbf{j}_{k-1}$ is a $(k-1)$ column vector of ones. Note that

$$\mathcal{N}^{-1} = I_{k-1} - \frac{1}{k}\mathbf{j}_{k-1}\mathbf{j}_{k-1}'.$$

Definition 3.1. For $\mathbf{u}, \mathbf{z} \in \nabla^{k-1}$, let $\boldsymbol{\theta} = \phi(\mathbf{u})$, and $\boldsymbol{\eta} = \phi(\mathbf{z})$. Define by
$$\langle \mathbf{u}, \mathbf{z} \rangle = \boldsymbol{\theta}' \mathcal{N}^{-1} \boldsymbol{\eta},$$
the inner product of $\mathbf{u}$ and $\mathbf{z}$.

Definition 3.2. Define the norm for $\mathbf{u} \in \nabla^{k-1}$, $\|\mathbf{u}\|$, by $\langle \mathbf{u}, \mathbf{u} \rangle^{1/2}$.

Inclusion of the matrix $\mathcal{N}^{-1}$ ensures that the inner product and norm are invariant to permutations of components of $\mathbf{u}$. Also note that the norm defined above is a sum of squares of
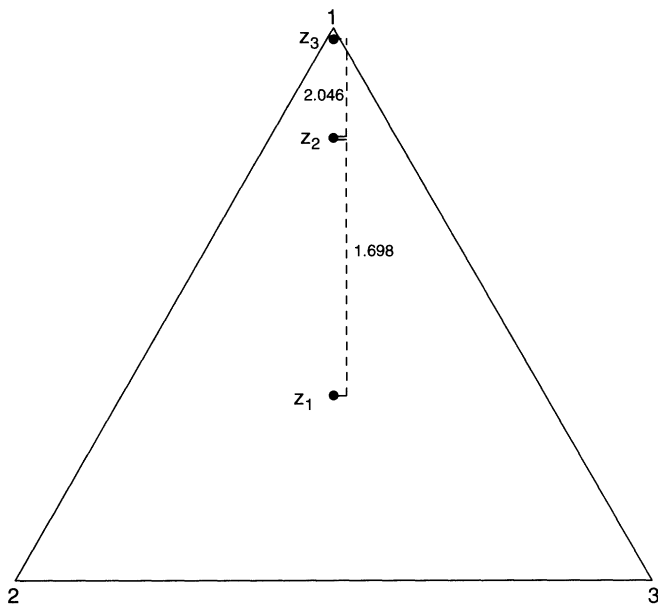
Figure 1. Graphical Display of 3 Three-Part Compositions in a Ternary Diagram. The points shown correspond to compositions of $z_1 = (1/3, 1/3, 1/3)$, $z_2 = (.80, .1, .1)$, and $z_3 = (.98, .01, .01)$. The numbers on the figure denote the distances between the points.

log-ratios. This is in the class of functions meeting Aitchison's (1992) criteria for a compositional metric.

We summarize a number of properties relating addition and scalar multiplication in ∇^{k-1} to images under the additive logratio transform. For $u, z \in \nabla^{k-1}$, and $a \in \Re$,

$$\phi(u \oplus z) = \phi(u) + \phi(z),$$

$$\phi(z^a) = a\,\phi(z),$$

$$\phi(\mathcal{J}_{k-1}) = \mathbf{0}_{k-1},$$

where $\mathbf{0}_{k-1}$ is a $k-1$ vector of zeros.

3.1.1 Differences Between Compositions. The definition of an (inverse) addition operation and a norm allow us to measure the difference between compositions. For demonstration, consider three compositions in ∇^2, $z_1 = \mathcal{J}_2 = (1/3, 1/3, 1/3)$, $z_2 = (.80, .10, .10)$, and $z_3 = (.98, .01, .01)$. For reference, we show these compositions in the ternary diagram of Figure 1. The ternary diagram has long been used in the geological sciences as a plotting region for 3-part compositions (e.g., proportions of sand, silt, and clay in soils). It may be viewed as the plane in the positive orthant of $\Re^3$ satisfying the summation constraint of a 3-part composition. For more details see Aitchison (1986, p. 5).

First, we note the norms of these compositions are

$$\|z_1\| = 0, \quad \|z_2\| = 1.698, \quad \text{and} \quad \|z_3\| = 3.744$$

Thus, the defined norm measures the distance of a composition from $\mathcal{J}_{k-1}$, the "center" of ∇^{k-1}.

Next, using the inverse of the perturbation operator, we find the difference between pairs z_1 and z_2, and z_2 and z_3. To find

the difference between two compositions, we perturb the second by the elementwise inverse of the first. That is,

$$z_2 \ominus z_1 \equiv z_2 \oplus z_1^{-1} = z_2,$$

because z_1 is the identity element. Similarly,

$$z_3 \ominus z_2 = \mathcal{C}\big([z_3]_1\,[z_2]_1^{-1},\,[z_3]_2\,[z_2]_2^{-1},\,[z_3]_3\,[z_2]_3^{-1}\big),$$

$$= (.860, .070, .070),$$

where $[z_i]_j$ is the jth element of the composition z_i. Thus, $(.86, .07, .07)$ is the composition by which we need to perturb z_2 to obtain z_3. By taking the norm of the difference composition, we measure the distance between z_2 and z_3.

$$\|z_3 \ominus z_2\| = \|(.86, .07, .07)\| = 2.046$$

Note that the distance from z_1 to z_2 is 1.698, whereas the distance from z_2 to z_3 is larger at 2.046. This demonstrates two points,

1. Interpretation of distances between compositions is difficult without a careful definition of a norm.
2. Graphical interpretation in the simplex (e.g., ternary diagram) is complicated by the (visual) compression of distances near the boundaries of the simplex.

An (invertible) addition operation and norm allow interpretation of differences in compositions. Specifically, if $\hat{\xi}_1$ and $\hat{\xi}_2$ are estimated location parameter vectors for treatments 1 and 2, respectively, we may easily obtain information about the direction and distance between them.

3.2 Interpretation and Visualization of Parameters

3.2.1 Interpretation of μ as a Composition. The location parameter of the LN distribution, μ, can be expressed as a composition via the additive logistic transformation. That is,

$$\phi^{-1}(\mu) = \xi, \quad \text{where } \xi \in \nabla^{k-1}.$$

Interpretation of ξ in the simplex is much simpler than interpreting μ on the multivariate logit scale. However, some of the statistical properties of μ are lost with the transformation to the simplex. Specifically, μ is the mean and mode of the multivariate normal logit (i.e., for $\phi(z)$). The $\phi^{-1}(\cdot)$ transform does not preserve these properties, although as $\phi^{-1}(\cdot)$ is monotone in each of the $(k-1)$ components of μ (Billheimer and Guttorp 1995), ordering of values is preserved under this transformation. Hence, $\xi = \phi^{-1}(\mu)$ can be interpreted as a componentwise multivariate median for the LN distribution in ∇^{k-1}. This interpretation is a useful characterization for point estimates of parameters, and as a "center" for the asymmetric LN distribution.

3.2.2 Covariates and Interactions. To incorporate the effect of covariates, the location parameter, μ, may depend on explanatory variables (see Aitchison 1986; sec. 7.6, p. 158). For a scalar covariate x_j, indexed by $j = 1, 2, \ldots, n$ observations, μ_j can be replaced in the density expression by $\beta_0 + \beta_1(x_j - \bar{x})$. Here, β_0 and β_1 are vectors in $\Re^{k-1}$, and $\bar{x}$ is

the mean of the observed covariate values. This parameterization allows interpretation of $\boldsymbol{\beta}_0$ as the location when $x_j = \bar{x}$, and $\boldsymbol{\beta}_1$ as the change in location for a unit change in x.

Equivalently, the regression expression $\boldsymbol{\mu}_j = \boldsymbol{\beta}_0 + \boldsymbol{\beta}_1(x_j - \bar{x})$ can be written as a perturbation of compositions. This is accomplished by taking the additive logistic transformation of both sides,

$$\phi^{-1}(\boldsymbol{\mu}_j) = \phi^{-1}(\boldsymbol{\beta}_0) \oplus \phi^{-1}(\boldsymbol{\beta}_1)^{(x_j - \bar{x})}.$$

We write this more compactly as

$$\boldsymbol{\xi}_j = \boldsymbol{\xi} \oplus \boldsymbol{\gamma}^{u_j},$$

where $\boldsymbol{\xi}_j = \phi^{-1}(\boldsymbol{\mu}_j)$, $\boldsymbol{\xi} = \phi^{-1}(\boldsymbol{\beta}_0)$, and $\boldsymbol{\gamma} = \phi^{-1}(\boldsymbol{\beta}_1)$. The scalar u_j is the centered covariate. In this parameterization, $\boldsymbol{\xi}$ is the overall location on the simplex. Further, the role of the regression composition parameter, $\boldsymbol{\gamma}$, is clear: the location parameter is the overall location ($\boldsymbol{\xi}$) perturbed by $\boldsymbol{\gamma}$ (for $u_j = 1$). Thus, $\boldsymbol{\gamma}$ is directly interpretable as a composition. It is the amount by which a location is shifted, via a perturbation, by a unit change in the covariate. Finally, deviations in $\boldsymbol{\gamma}$ from the identity composition, $\mathcal{J}_{k-1}$, indicate the direction and magnitude of the change. Note that $\boldsymbol{\gamma} = \mathcal{J}_{k-1}$ implies the covariate has no effect on the composition location. We find this much more informative than the alternative interpretation of linear regression on the log-odds scale. Also note that this formulation is directly applicable to parameter estimates from multinomial logistic regression.

Figure 2 shows the curves of $\boldsymbol{\xi}_j = \boldsymbol{\xi} \oplus \boldsymbol{\gamma}^{u_j}$ for different values of the regression composition, $\boldsymbol{\gamma}$. The 'effect' of a regression parameter is invariant to the starting composition (via the compositional algebra). However, the graphical display (in the ternary diagram) of the change in composition to a unit change in the covariate does depend on the starting location. This is analogous to the case of logistic regression where a unit change in an explanatory variable produces small changes in predicted probability near zero and one, but large changes when the probability is near .5.

Billheimer et al. (1997) demonstrate the use of covariate information in estimating species composition in an estuarine system. In this analysis, they show that relative abundance of pollution sensitive and pollution tolerant taxa are associated with a salinity gradient, but are (apparently) not related to depth or dissolved oxygen measurements in the Delaware Bay.

The compositional algebra easily extends to experimental factors (main effects and interactions). For example, the usual two-factor interaction in the standard linear model

$$\mu_{ij} - \mu_{i.} - \mu_{.j} + \mu_{..}$$

can be expressed in terms of compositional location parameters

$$\boldsymbol{\xi}_{ij} \ominus \boldsymbol{\xi}_{i.} \ominus \boldsymbol{\xi}_{.j} \oplus \boldsymbol{\xi}_{..}$$

via the additive logistic transform.
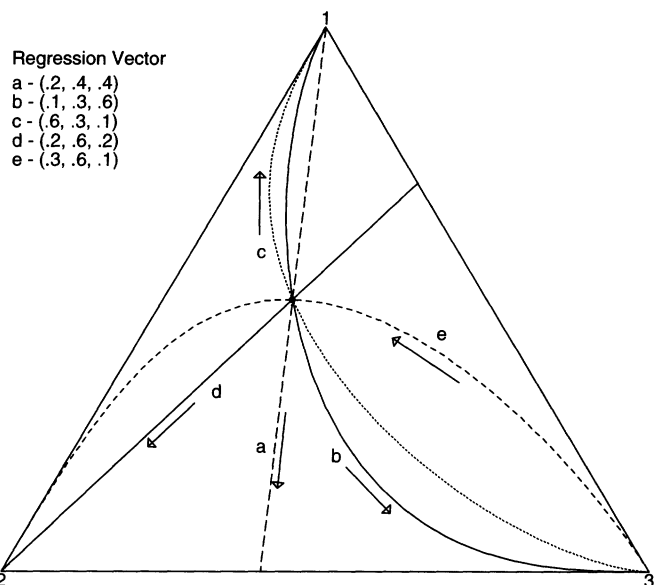
Figure 2. Regression Curves for Different Parameter Vectors. The curves shown are of the form $\boldsymbol{\xi}(u) = \boldsymbol{\xi} \oplus \boldsymbol{\gamma}^u$ for selected values of $\boldsymbol{\gamma}$, and $-\infty < u < \infty$. The arrows indicate direction as u increases. For all curves $\boldsymbol{\xi} = (.5, .3, .2)$, and the curves intersect at $\boldsymbol{\xi}$ for $u_j = 0$. For curve "a", $\boldsymbol{\gamma} = (.2, .4, .4)$, the covariate u has equal influence on elements 2 and 3. Similarly, in curve "d", $\boldsymbol{\gamma} = (.2, .6, .2)$, the covariate affects elements 1 and 3 equally.

4. STATE-SPACE MODEL FOR ARTHROPOD ASSEMBLAGE

To model the arthropod counts, we combine the logistic normal model for continuous compositions with a conditional multinomial observation distribution. We assume the arthropod count vector from treatment t, plot j, $\mathbf{y}_{tj}$, is conditionally multinomial given the latent composition vector $\mathbf{z}_{tj}$ ($\mathbf{z}_{tj} \in \nabla^{k-1}$ for t in $\{1, 2, \ldots, T\}$ treatments, and j in $\{1, 2, \ldots, n_t\}$ plots in treatment t). The compositions are modeled as independent draws from $L^{k-1}(\boldsymbol{\mu}_{tj}, \Sigma)$.

For the rest of this section, we assume that $\boldsymbol{\mu}_{tj} = \boldsymbol{\mu}_t$, ($\boldsymbol{\xi}_{tj} = \boldsymbol{\xi}_t$) for all $j = 1, 2, \ldots, n_t$ plots with treatment t. Thus, for each treatment, plot location parameters are (unobservable) realizations from a common LN distribution. The LN distribution "mean" is allowed to differ for each omnivory-disturbance combination. This framework produces a "random effects" approach to accommodate extramultinomial variability typical of ecological systems.

The model formulation is completed by specifying prior distributions for $\boldsymbol{\mu}_t$ and Σ. Let $\boldsymbol{\mu}_t$ have a $(k-1)$-dimensional multivariate normal distribution with mean vector $\boldsymbol{\eta}$, and variance-covariance matrix Ω. Typical choices for $\boldsymbol{\eta}$ and Ω are

$$\boldsymbol{\eta} = \mathbf{0}_{k-1}$$

and

$$\Omega = a\mathcal{N}$$

where

$$\mathcal{N} = I_{k-1} + \mathbf{j}_{k-1}\mathbf{j}'_{k-1},$$

$\mathbf{0}_{k-1}$ is a $(k-1)$-vector of 0s, I_{k-1} is a $(k-1)$ identity matrix, and $\mathbf{j}_{k-1}$ is a $(k-1)$-vector of ones. This is equivalent to specifying a LN prior distribution for $\boldsymbol{\xi}_t = \phi^{-1}(\boldsymbol{\mu}_t)$, centered at

$\mathcal{I}_{k-1}$ (for $k = 3$, (1/3, 1/3, 1/3)). Setting the hyperparameter $a = .5$ allows the 95% prior probability contour for ξ_t to reach at least .05 for each component.

For the variance-covariance matrix, we take the prior distribution for $\Sigma^{-1} \sim \text{Wishart}(\Psi^{-1}, \rho)$, where Ψ is a $(k-1) \times (k-1)$ positive definite matrix, and ρ denotes the degrees of freedom. A typical choice for Ψ is

$$\Psi = c\mathcal{N}$$

with $c = .1$. The value of ρ is set to $k - 1$; the smallest value allowable (least informative) that still maintains a proper Wishart distribution. By setting weak prior information on the variance-covariance structure, we allow dependence between species groups in the data to be reflected in the posterior distribution.

By combining the likelihood with the prior distributions, the posterior distribution can be written as follows (up to a constant of proportionality).

$$\pi(\mathbf{z}, \xi, \Sigma \mid \mathbf{y}) \propto \prod_{t=1}^{T} \left\{ \prod_{j=1}^{n_t} \left(\prod_{i=1}^{k} ([\mathbf{z}_{tj}]_i)^{([\mathbf{y}_{tj}]_i - 1)} \mid \Sigma \mid^{-1/2} \right. \right.$$
$$\times \left. \exp\left[-\frac{1}{2}(\phi(\mathbf{z}_{tj}) - \mu_t)'\Sigma^{-1}(\phi(\mathbf{z}_{tj}) - \mu_t) \right] \right)$$
$$\times \left. \mid \Omega \mid^{-1/2} \exp\left[-\frac{1}{2}(\mu_t - \eta)'\Omega^{-1}(\mu_t - \eta) \right] \right\}$$
$$\times \mid \Psi \mid^{\rho/2} \mid \Sigma \mid^{-(\rho-k)/2} \exp\left[-\frac{1}{2}\text{tr}(\Psi\Sigma^{-1}) \right]$$

The full conditional distributions for $\mathbf{z}_{tj}$, $\mu_t = \phi(\xi_t)$, and Σ^{-1} follow immediately from this expression (see, e.g., Besag et al. 1995).

Implementation of MCMC is straightforward using a combination of Gibbs sampling and Metropolis–Hastings steps. The conditional distribution for $\mathbf{z}_{tj}$ (given current values of μ_t and Σ) is sampled via Hastings' algorithm (Hastings 1970). For this we use a LN proposal distribution, centered at the current value of $\mathbf{z}_{tj}$. The Gibbs sampler is used to update μ_t and Σ because their conditional distributions are avaiable in closed form (see, e.g., Gelfand et al. 1990). The conditional distribution of μ_t is multivariate normal with mean $(\Omega^{-1} + n_t\Sigma^{-1})^{-1}(n_t\Sigma^{-1}\overline{\phi(\mathbf{z}_{t.})} + \Omega^{-1}\eta)$ (where $\overline{\phi(\mathbf{z}_{t.})} = 1/n_t \sum_{j=1}^{n_t} \phi(\mathbf{z}_{tj})$), and variance-covariance matrix $(\Omega^{-1} + n_t\Sigma^{-1})^{-1}$. In addition, Σ has an inverse Wishart distribtion with parameter matrix $(V + \Psi)$, where $V = \left[\sum_{t=1}^{T} \sum_{j=1}^{n_t} \phi(\mathbf{z}_{tj}) - \mu_t \right]\left[\sum_{t=1}^{T} \sum_{j=1}^{n_t} \phi(\mathbf{z}_{tj}) - \mu_t \right]'$, and $\sum_{t=1}^{T} n_t + \rho - k$ degrees of freedom.

Examination of MCMC realizations indicates that the algorithm converges to the limiting distribution in 50–100 Monte Carlo iterations. The convergence is not affected by changes in the (hyper)prior distribution scale parameters. Trial runs on simulated data were used to select Hastings proposal standard deviations for $\mathbf{z}_{tj}$ and ξ_t. These result in proposal acceptance probabilities of 50–60%. For inference, a sequence of 500 Monte Carlo iterations was used for "burn-in", and the subsequent 10,000 Monte Carlo realizations were collected for each of the updated components. Visual inspection of time series of

realized values, autocorrelations, and marginal posterior distributions based on multiple starting locations were used to evaluate MCMC sampling properties (see, e.g., Cowles and Carlin 1996, for a review). In addition, "gibbsit" (Raftery and Lewis 1992, 1995) was used to provide an objective evaluation of Markov chain convergence. All diagnostic procedures indicate that MCMC run length is adequate.

Point estimates were constructed for each treatment location parameter vector by computing sample means of the MCMC realizations. Similarly, credible regions for location parameter vectors were constructed from a convex hull of retained MCMC realizations. For each treatment, the location parameter realizations were ordered according to their LN likelihood (using the above point estimates as the parameters). The convex hull was constructed to contain the 95% of realizations with highest likelihood.

To evaluate the omnivory–vegetative disturbance interaction, we consider the effect of vegetation removal separately for each of the predator manipulations. This is easily accomplished by taking differences, $\xi_t \ominus \xi_{t'}$, from realizations of the posterior distribution.

5. STABILITY IN ARTHROPOD FOOD WEBS

The total number of observed arthropods ranged from 7 (on plots 1 and 2 of the SC treatment) to 34 (on plot 5 of the SV treatment). Consequently, plots with the most arthropods provide more information about the treatment location (i.e., species composition) than do plots with the fewest arthropods. Because none of the plots yield a large total number of arthropods, estimates of the latent species assemblage are subject to substantial sampling variability. Moreover, it is notable that no predators (other than those of the manipulated species) were observed in four of the experimental plots.

Table 2 shows point estimates of species composition (i.e., location parameter vectors) for the six omnivory–vegetation treatments. Each composition vector is presented in the order (predators, generalist herbivores, specialist herbivores). In addition, the compositional difference from "control–control" and the magnitude of the difference (the norm in Section 3) are computed for each treatment. Difference compositions near $(1/3, 1/3, 1/3)$ (with norm near zero) indicate that treatments with increased omnivory exhibit species assemblages similar

Table 2. Point Estimates of the Location Parameter Vectors for Each of the Six Treatments

Treatment	Estimated species composition	Change from CC	Magnitude of change
OV	(.27, .44, .28)	(.39, .36, .26)	.31
SV	(.06, .28, .67)	(.09, .25, .67)	1.43
CV	(.08, .37, .56)	(.12, .33, .55)	1.12
OC	(.19, .38, .43)	(.27, .32, .40)	.28
SC	(.07, .41, .52)	(.11, .37, .52)	1.15
CC	(.23, .41, .36)	(.33, .33, .33)	0

NOTE: In addition, we show the difference composition of each treatment from the control treatment, and the magnitude of the difference. The trophic category order for all the compositions is (predator, generalist herbivore, specialist herbivore). The table shows that treatments with increased omnivory exhibit species assemblages similar to control. Conversely, background and reduced omnivory show decreases in predators and increases in specialist herbivores.

to that of the control treatment. Conversely, vegetation disturbance (without omnivory) and increased specialist predators (reduced omnivory) exhibit shifted species compositions. The shifts show decreases in unmanipulated predators and increases in specialist herbivores.

The observed plot compositions and location point estimates are shown in Figure 3. The figure shows the location of compositional parameter estimates in relation to the data, as well as the direction and magnitude of composition shifts due to treatments.

To better evaluate the variability in species composition estimates and differences, approximate 95% credible regions were constructed for all omnivory-vegetation location parameter vectors. Two of these, the CC and CV treatments, were selected for display in Figure 4. The other treatment credible regions were omitted to reduce clutter on the graph. All credible regions exhibited similar variability.

The credible regions show a separation of the CC and CV treatments. The CC region shows substantial overlap with those from OV and OC treatments. (Indeed, it contains both OV and OC composition point estimates.) This suggests that these treatments have a similar effect in maintaining arthropod group compositions. Similarly, the 95% credible region for CV contains the location point estimates for the SC and SV treatments. This suggests that the increasing specialist predators does not mitigate the species composition shift caused by reduced vegetation. Indeed, increasing specialist predators appears to shift species assemblage even without vegetation removal.

Finally, we consider the omnivory-vegetation interaction effect. Formally, this interaction can be written as

$$\xi_{ij} \ominus \xi_{i.} \ominus \xi_{.j} \oplus \xi_{..}$$

for selected omnivory-vegetation treatment combinations (comprising two degrees of freedom). We choose to interpret this interaction as the "vegetation removal effect" across
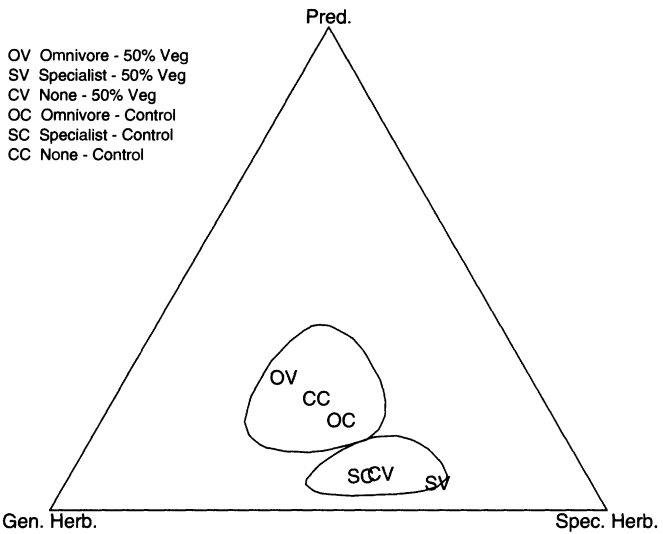
Figure 4. Ninty-Five Percent Credible Regions for Selected Species Compositions. Credible regions are plotted for CC and CV omnivory-vegetation disturbance compositions. Regions for other treatments exhibit similar variability. The small overlap between CC and CV regions suggests a shift in composition associated with vegetation removal.

omnivory manipulations. That is,

$$\xi_{iV} \ominus \xi_{iC}$$

where i denotes increased omnivory, increased specialist predators, or control levels. This evaluation of "difference of differences" is equivalent to the interaction expression above. Although single degree of freedom contrasts can be evaluated in this manner, construction of a joint (two degrees of freedom) posterior distribution for interaction is a topic of future research.

Figure 5 shows the effect of changing from background vegetation to 50% vegetation removal for each of the three predator manipulations. Approximate 95% credible regions for each difference are shown. Note that the credible regions are constructed by computing the compositional difference between random samples from the marginal posterior distributions for each omnivory manipulation. If there was no effect attributable to vegetation removal, then the differences would be centered at $\mathcal{J}_2$. Further, absence of an interaction effect would result in a substantial area covered simultaneously by all credible regions.

Figure 5 shows that the increased omnivory treatments respond differently to vegetation removal than do the control or increased specialist predator treatments. Specifically, plots with increased omnivorous predators show increased proportion predators and decreased proportion specialist herbivores when vegetation is removed. Conversely, the increased specialist and control predator treatments show a decrease in the proportion of predators and an increase in specialist herbivores with vegetation removal. The volume of compositions covered by the 95% credible regions indicates that the magnitude of these changes is difficult to pin down. This is likely attributable to the small number of plots per treatment (5) and the small number of arthropods observed per plot.
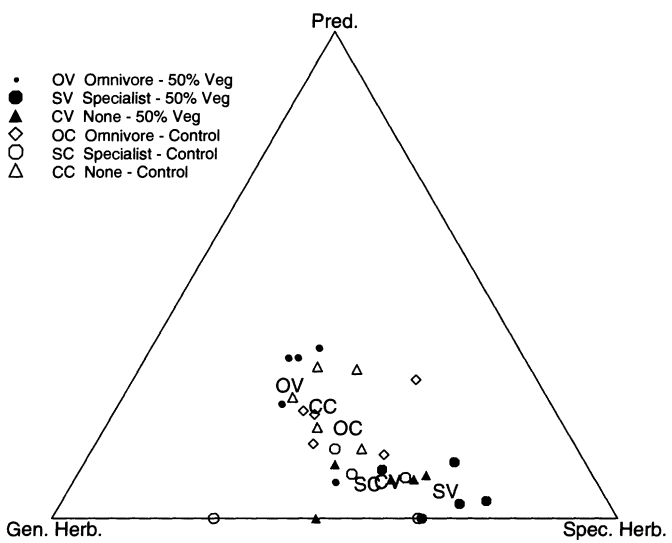

Figure 3. Observed Compositions and Species Composition Parameter Estimates for the Six Experimental Treatments. The treatment label (e.g., "OV") is plotted at its respective composition. Note that four of the experimental plots had no observed predators.
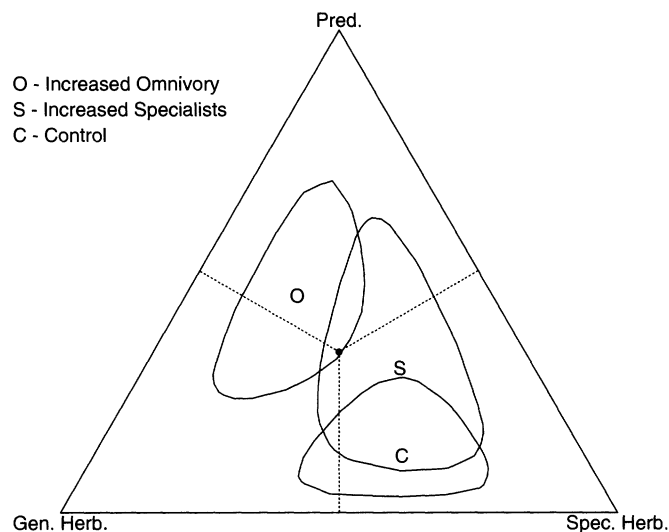
Figure 5. Point Estimates and 95% Credible Regions for the Effect of Vegetation Removal. For each omnivory treatment, we show the estimated species composition and credible region for the compositional difference associated with vegetation removal. Because increased omnivory and increased specialist regions contain $\mathcal{J}_2$, we cannot preclude that vegetation removal has no effect.

5.1 Diagnostics

A "leave-one-out" diagnostic procedure (Besag, Green, Higdon, and Mengersen 1995) was used to evaluate the adequacy of the statistical model. The (approximate) predictive distribution for a plot composition is obtained by setting its group counts equal to zero for all k groups, and collecting the MCMC realizations for the plot composition. One randomly selected plot from each treatment was withheld from the data, and the MCMC re-run with these data omitted. The compositions of the holdout plots were subsequently predicted from the model. The prediction region for the discrete observation can be constructed (under the model) by sampling from a multinomial distribution with parameter vector equal to the realized values of $\mathbf{z}_{tj}$, and sample size equal to $\sum_{i=1}^{k}[\mathbf{y}_{tj}]_i$.

For all six plots, the leave-one out procedure results in 95% prediction regions containing the omitted (observed) plot compositions. Although this is not a rigorous procedure for investigating model misspecification, it does suggest that the statistical model is adequate in capturing the observed variability in the data. Diagnostic procedures for hierarchical Bayesian models remains an area of ongoing research (see e.g., Albert and Chib 1997).

5.2 Conclusion

These results indicate that increased omnivory helps to maintain a stable species composition in the presence of 50% vegetation removal. Further, background predator levels or increased specialist predators do not facilitate this stability when vegetation is removed. The ecological conclusion is that the omnivores' broad diets allow them to feed on a diversity of species that would otherwise increase in abundance in response to the vegetation thinning; effectively buffering the community from compositional shifts induced by disturbance.

6. DISCUSSION

We present statistical analysis of an ecological experiment evaluating the effects of omnivory on reticulate food webs. Our approach can provide valuable insight into biological community structure. Previous analyses of community structure are typically summarized by either univariate indices (such as diversity or biotic integrity indices), or by ordination methods such as principal components analysis. These measures of community structure can be difficult to interpret, and may lose considerable information in their reduction of dimensionality. We believe it is more informative to evaluate biological communities directly in terms of the relative abundance of the species present.

Our framework allows interpretation of statistical modeling parameters via their direct effect on compositions. We find this approach much more informative than the alternative interpretation on the log-odds scale. Further, we believe that the compositional algebra is useful more generally, such as, for interpreting differences between compositions, or parameter estimates from multinomial logistic regression.

While the logistic normal distribution flexibly accommodates complicated covariance structure in general compositions, it exhibits a number of weaknesses. This distribution does not have "nice" mathematical properties of closure when combining elements of a composition (amalgamation), nor when marginalizing over a component. These do not appear to be serious limitations in the applications of the model. Alternative statistical models for compositional data include the Dirichlet distribution (Johnson and Kotz 1972), and the S^- distribution (Barndorff-Nielsen and Jørgensen 1991). Although both models exhibit attractive mathematical properties, neither allows modeling of the covariances between compositional elements. In both cases, the covariance is determined by the summation constraint. A novel approach, suggested by Stephens (1982), treats the square roots of proportions as directional data and uses the von Mises spherical distribution to model the compositions. This model appears to be used infrequently in applications, perhaps because of the relative complexity of the von Mises distribution. For an alternative approach to multivariate count data based on the log-normal Poisson distribution, see Aitchison and Ho (1989).

A serious shortcoming common to these compositional models is that all elements are required to be nonzero. A zero proportion actually results in a $(k-1)$ component assemblage (in the $(k-2)$-dimensional simplex). Further, the $\phi(\cdot)$ transformation is not defined when one or more components are zero. This restriction of no "structural zeros" may be a severe limitation in applications where one or more components are known to be absent, or where inference of absence is important.

More work is also needed in extending analyses to $k > 3$ categories. While the algebra and modeling methods apply to an arbitrary number of groups, graphical methods are not easily generalized. We are working to extend the ternary diagram (2-dimensional simplex) to higher dimensions using a dynamic graphics environment. (Xgobi, Swayne, Cook, and Buja 1991). In addition, Billheimer (2001) demonstrates a method for static viewing of higher dimensional compositions. Such methods, coupled with the norm defined in Section 3,

can provide effective inference methods with four or more categories.

APPENDIX A: MATHEMATICAL PROPERTIES OF THE COMPOSITIONAL ALGEBRA

Theorem A.1. ∇^{k-1} is a vector space with addition defined by the perturbation operator and scalar multiplication defined as $\mathbf{u}^a = \mathcal{C}(u_1^a, u_2^a, \ldots, u_k^a,)$ for the scalar a.

Proof. To show ∇^{k-1} is a vector space, the following four properties must hold.

1. There is an identity scalar multiplier.
   Clearly, $a = 1$ is the identity scalar multiplier.
2. Scalar multiplication is associative,

$$(\mathbf{u}^a)^b = \mathbf{u}^{ab}$$

$$
\begin{aligned}
(\mathbf{u}^a)^b &= \left(\mathcal{C}\left(u_1^a, u_2^a, \ldots, u_k^a\right) \right)^b \\
&= \mathcal{C}\left(\left(\frac{u_1^a}{\sum_{i=1}^k u_i^a} \right)^b, \left(\frac{u_2^a}{\sum_{i=1}^k u_i^a} \right)^b, \ldots, \left(\frac{u_k^a}{\sum_{i=1}^k u_i^a} \right)^b \right) \\
&= \mathcal{C}\left(u_1^{ab}, u_2^{ab}, \ldots, u_k^{ab} \right) \\
&= \mathbf{u}^{ab}.
\end{aligned}
$$

3. $(\mathbf{u} \oplus \mathbf{z})^a = \mathbf{u}^a \oplus \mathbf{z}^a$

$$
\begin{aligned}
(\mathbf{u} \oplus \mathbf{z})^a &= [\mathcal{C}(\mathbf{u} \cdot \mathbf{z})]^a \\
&= \left(\frac{(u_1 z_1)^a}{\sum_{i=1}^k (u_i z_i)^a}, \frac{(u_2 z_2)^a}{\sum_{i=1}^k (u_i z_i)^a}, \ldots, \frac{(u_k z_k)^a}{\sum_{i=1}^k (u_i z_i)^a} \right) \\
&= \mathcal{C}(\mathbf{u}^a \cdot \mathbf{z}^a) \\
&= \mathbf{u}^a \oplus \mathbf{z}^a.
\end{aligned}
$$

4. $\mathbf{u}^{a+b} = \mathbf{u}^a \oplus \mathbf{u}^b$.

$$
\begin{aligned}
\mathbf{u}^{a+b} &= \left(\frac{u_1^{a+b}}{\sum_{i=1}^k u_i^{a+b}}, \frac{u_2^{a+b}}{\sum_{i=1}^k u_i^{a+b}}, \ldots, \frac{u_k^{a+b}}{\sum_{i=1}^k u_i^{a+b}} \right) \\
&= \mathcal{C}(\mathbf{u}^a \cdot \mathbf{u}^b) \\
&= \mathbf{u}^a \oplus \mathbf{u}^b.
\end{aligned}
$$

Theorem A.2. Let $\mathbf{u}$ and $\mathbf{z}$ be elements of ∇^{k-1}, and $\boldsymbol{\theta} = \phi(\mathbf{u})$ and $\boldsymbol{\phi} = \phi(\mathbf{z})$. Then $\langle \mathbf{u}, \mathbf{z} \rangle = \boldsymbol{\theta}' \mathcal{N}^{-1} \boldsymbol{\phi}$ is an inner product.

where $\mathcal{N} = I_{k-1} + \mathbf{j}_{k-1} \mathbf{j}_{k-1}'$. Note, $\mathcal{N}^{-1} = (I_{k-1} - \frac{1}{k} \mathbf{j}_{k-1} \mathbf{j}_{k-1}')$ (Rao 1973, p. 33).

Proof. It is straightforward to show that this definition meets the conditions of an inner product.

Theorem A.3. ∇^{k-1} is a Hilbert space (a complete, inner product space).

Proof. It remains to show completeness of the space. That is, we require that every Cauchy sequence, $\{\mathbf{z}_n\} \in \nabla^{k-1}$, converges in ∇^{k-1}.

Suppose $\{\mathbf{u}_n\} \in \nabla^{k-1}$ is a Cauchy sequence. Then, for every $\epsilon > 0$, there is an integer, N, such that $m, n > N$ imply $\|\mathbf{u}_m \ominus \mathbf{u}_n\| < \epsilon$.

Let $\boldsymbol{\theta}_n = \phi(\mathbf{u}_n)$. Then $\boldsymbol{\theta}_n \in \mathfrak{R}^{k-1}$ for all n. Note that for the norm defined above

$$
\begin{aligned}
\|\mathbf{u}_m \ominus \mathbf{u}_n\|^2 &= (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m)' \mathcal{N}^{-1} (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m) \\
&= (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m)' \left[I_{k-1} - \frac{1}{k} \mathbf{j}_{k-1} \mathbf{j}_{k-1}' \right] (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m) \\
&\leq (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m)' (\boldsymbol{\theta}_n - \boldsymbol{\theta}_m)
\end{aligned}
$$

with equality holding only when $\boldsymbol{\theta}_n - \boldsymbol{\theta}_m$ is equal to the zero vector. Note that this final expression, $(\boldsymbol{\theta}_n - \boldsymbol{\theta}_m)'(\boldsymbol{\theta}_n - \boldsymbol{\theta}_m) = \sum_{i=1}^{k-1}(\theta_{ni} - \theta_{mi})^2$ is the square of the usual L^2 norm for vectors in $\mathfrak{R}^{k-1}$. By the completeness of $\mathfrak{R}^{k-1}$ (under L^2 norm), the limit of $\{\boldsymbol{\theta}_n - \boldsymbol{\theta}_m\} \in \mathfrak{R}^{k-1}$. By the above inequality, limit points under the L^2 norm are also limits under the norm defined above. Furthermore, because the $\phi(\cdot)$ transform is bijective, all limit points in $\mathfrak{R}^{k-1}$ can be transformed to points in ∇^{k-1}. Hence, any Cauchy sequence in ∇^{k-1} (as measured by the norm defined on ∇^{k-1}) has a limit in ∇^{k-1}, and ∇^{k-1} is complete. So, ∇^{k-1}, with the perturbation operator and scalar multiplication is a Hilbert space.

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