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Data-dependent permutation techniques for the analysis of ecological data

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Abstract

Two distribution-free permutation techniques are described for the analysis of ecological data. These methods are completely data dependent and provide analyses for the commonly-encountered completely-randomized and randomized-block designs in a multivariate framework. Euclidean distance forms the basis of both techniques, providing consistency with the observed distribution of data in many ecological studies.

Nomenclature: follows Harrington (1964). Manual of the plants of Colorado. Shallow Press, Chicago.

Abbreviations: MRPP = Multiresponse permutation procedure; MRBP = Ibid, randomized block analog

Introduction

Classical least squares (CLS) analysis has dominated the statistical literature for much of this century. The dominance and popularity of CLS analysis can be attributed to the fact that the underlying theory is simple, the applications are highly developed, and the methods are well documented. CLS statistics are optimal and result in maximum likelihood estimators of the unknown parameters of the model if the population is normal, or multivariate normal, with equal variances, or a variance-covariance matrix which exhibits compound symmetry (Huynh & Mandeville 1979). CLS is far from optimal in many non-Gaussian situations, especially when the population distribution is asymmetric and/or outlying values are present.

The problems generated by nonnormality are serious and are likely to be prevalent in ecological data (e.g., Austin 1987). Hampel *et al.* ((1986) review studies of data distributions in the natural sciences and conclude that normality seems to be the exception rather than the rule. A number of studies have demonstrated that even a modest departure from normality can seriously degrade the efficiency of CLS estimators (Andrews *et al.* 1972; Rey 1983; Wu 1985). In field studies these assumptions may be very difficult to satisfy. Many times the underlying distribution model of the population is not known and in many cases it is definitely non normal; for example, size of precipitation events in semiarid regions is better approximated by an exponential distribution than by a normal distribution (Sala & Lauenroth 1982; Soriano & Sala 1983). There are many cases involving vegetation analysis where comparisons are made between plant communities that have different spatial patterns of plant distribution. Under these circumstances, the assumption of equal variances does not hold. Even when the population is normally distributed, alternatives to CLS may be required, especially if the form of the model is not known.

One of the most satisfying robust alternatives to CLS is the analysis of absolute differences. Statistics based on absolute differences are resistant to outliers, do not require parametric assumptions of normality, and, as shown below, provide an attractive alternative to CLS estimators. In recent years, extensive work has been undertaken to develop statistics based on some form of absolute values. The literature is too vast to be summarized here, but the following provide summaries of the advancements in various fields and applications, and each contains an extensive bibliography of the area: Dielman (1984), Dietz *et al.* (1987), Dodge (1987), Harter (1974–1976), Huynh (1982), and Narula & Wellington (1982).

Two of these methods, multiresponse permutation procedure (MRPP) and its randomized block analog (MRBP), are described below. This is followed by examples involving real data sets that highlight the major characteristics of MRPP and MRBP.

Method description

Let $\Omega = \{\omega_1,\ldots,\omega_N\}$ be a finite population of N objects, let $x_I = [x_{1I},\ldots,x_{rI}]$ denote r commensurate response measurements for object ω_I ($I = 1,\ldots,N$), and let $S_1,\ldots,S_g$ designate an exhaustive partitioning of the N objects comprising Ω into g disjoint groups. Also, let Δ_{IJ} be a symmetric distance function value of the response measurements associated with the objects ω_I and ω_J. The statistic underlying MRPP is given by

$$\delta = \sum_{i=1}^{g} C_i \xi_i \tag{1}$$

where

$$\xi_i = \binom{n_i}{2}^{-1} \sum_{I<J} \Delta_{IJ} \Psi_i(\omega_I) \Psi_i(\omega_J) \tag{2}$$

is the average distance function value for all distinct pairs of objects in group S_i ($i = 1,\ldots,g$), $n_i \geq 2$ is the number of *a priori* classified objects in groups S_i ($i = 1,\ldots,g$), $N = \Sigma_{i=1}^{g} n_i$, $\Sigma_{I<J}$ is the sum over all I and J such that $1 \leq I < J \leq N$, $\Psi_i(\omega_I)$ is 1 if ω_I belongs to S_i and 0 otherwise, $C_i > 0$ ($i = 1,\ldots,g$), and $\Sigma_{i=1}^{g} C_i = 1$. The C_i value generally used is n_i/N. The underlying permutation distribution of δ (under the null hypothesis) assigns equal probabilities to the

$$M = N!/(\prod_{i=1}^{g} n_i!) \tag{3}$$

possible allocations of the N objects to the g disjoint groups.

The symmetric distance function (Δ_{IJ}) is extremely important since it defines the structure of the underlying analysis space of MRPP. The form of the symmetric distance function considered in this paper is the Minkowski distance function,

$$\Delta_{IJ} = (\sum_{k=1}^{r} |x_{kI} - x_{kJ}|^p)^{1/p}. \tag{4}$$

When $p = 2$, the result is a Euclidean metric and (4) reduces to

$$\Delta_{IJ} = [\sum_{k=1}^{r} (x_{kI} - x_{kJ})^2]^{1/2}, \tag{5}$$

which is the normed distance of choice in this paper, since only $p = 2$ yields results which are unaffected by a rotation of the r response measurements (Mielke 1987).

Since small values of δ imply a concentration of response measurements within at least some of the g groups, the null hypothesis is rejected when the observed value of δ is small. The exact P-value (i.e., the probability under the null hypothesis of a value of δ being as or more extreme than the observed value of δ) is the proportion of all M values of δ which are equal to or less than the observed value of δ. Although an efficient algorithm for calculating the exact P-value for an observed value of δ has been developed (Berry & Mielke 1984), this procedure is extremely expensive when M is large (e.g., $M > 10^6$). Approximate P-values can be calculated with the use of the Pearson type III distribution which compensates for the fact that the underlying permutation distribution is often substantially skewed (Brockwell *et al.* 1982; Mielke 1984, 1986).

If δ_j denotes the jth value among the M possible values of δ then, under the null hypothesis, the first three moments of δ (i.e., mean, variance, and skewness) are given by

$$\mu_\delta = M^{-1} \sum_{j=1}^{M} \delta_j \, , \tag{6}$$

$$\sigma_\delta^2 = M^{-1} \sum_{j=1}^{M} \delta_j^2 - \mu_\delta^2 \, , \tag{7}$$

and

$$\gamma_\delta = (M^{-1} \sum_{j=1}^{M} \delta_j^3 - 3\mu_\delta \sigma_\delta^2 - \mu_\delta^3)/\sigma_\delta^3 \, , \tag{8}$$

respectively. Efficient computational techniques for obtaining μ_δ, σ_δ^2, and γ_δ are described in Mielke *et al.* (1976) and Mielke (1984). The standardized test statistic given by $T = (\delta - \mu_\delta)/\sigma_\delta$ is approximated, under the null hypothesis, by the Pearson type III distribution with the density function given by

$$f(y) = \frac{(-2/\gamma_\delta)^{4/\gamma_\delta^2}}{r(4/\gamma_\delta^2)} [-(2+y\gamma_\delta)/\gamma_\delta]^{(4-\gamma_\delta^2)/\gamma_\delta^2} \exp^{-2(2+y\gamma_\delta)/\gamma_\delta^2} , \tag{9}$$

where $-\infty < y < -2/\gamma_\delta$ and $\gamma_\delta < 0$. The probability value (p) for a realized value of δ, say δ_o, and correspondingly, $T_o = (\delta_o - \mu_\delta)/\sigma_\delta$, is given by

$$p = P(\delta \leq \delta_o) \doteq \int_{-\infty}^{T_o} f(y)dy \, . \tag{10}$$

Example

The general concepts of MRPP can best be illustrated by considering a comparison between two mutually exclusive groups of objects (A and B) where two measured responses (x_1 and x_2) have been obtained from each object in the two groups. Figure 1 shows how these responses could be represented in a two-dimensional diagram where the responses of the

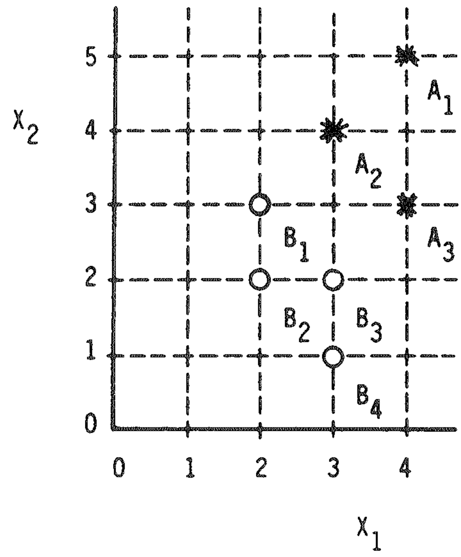

Fig. 1. Scatter diagram showing the points of the two groups (A and B) plotted as a function of the measured responses x_1 and x_2.

three objects in group A are plotted as crosses and the responses of the four objects in group B are plotted as circles. Although a visual impression suggests that groups A and B are separated, a more rigorous and objective characterization of this separation is needed before a quantitative evaluation or inference can be made.

One way to test the difference between the groups is by first examining the Euclidean distances

$$\Delta_{IJ} = [\sum_{i=1}^{2} (x_{iI} - x_{iJ})^2]^{1/2}$$

between all distinct pairs of points in the diagram. The seven points of Fig. 1 imply that there are $\binom{7}{2} = 21$ pairs of points and, consequently, 21 distances to be computed. These 21 distances are listed in Table 1 and ordered from the lowest to the highest value. Table 1 confirms the visual impression of clustering since the distances between points of a common group tend to be smaller than the distances between points of different groups. A natural way to consider this clustering tendency is to form an average of the between-point distances for each group. Thus, for the three distances of group A, the average is

$$\xi_A = (1/3) \sum_{A} \Delta_{I,J} = 1.6095$$

Table 1. Ordered distances between all 21 pairs of the seven points shown in Fig. 1 where distances between points in either group A or group B are indicated by crosses (x) or circles (o), respectively.

Rank	Points	Distance
1	B_1B_2	1.000 (o)
2	B_2B_3	1.000 (o)
3	B_3B_4	1.000 (o)
4	A_1A_2	1.414 (x)
5	A_2A_3	1.414 (x)
6	A_2B_1	1.414
7	A_3B_3	1.414
8	B_1B_3	1.414 (o)
9	B_2B_4	1.414 (o)
10	A_1A_3	2.000 (x)
11	A_2B_3	2.000
12	A_3B_1	2.000
13	A_2B_2	2.236
14	A_3B_2	2.236
15	A_3B_4	2.236
16	B_1B_4	2.236 (o)
17	A_1B_1	2.828
18	A_2B_4	3.000
19	A_1B_3	3.162
20	A_1B_2	3.606
21	A_1B_4	4.123

and for the six distances of group B, the average is

$$\xi_B = (1/6)\sum_{B} \Delta_{I,J} = 1.3441.$$

A measure which describes the separation between the points of groups A and B is the simple weighted mean given by

$$\delta = (3/7)\ \xi_A + (4/7)\ \xi_B = 1.4578.$$

Small values of δ indicate a tendency for clustering while large values of δ indicate a lack of clustering. The problem is to determine whether or not the observed statistic ($\delta = 1.4578$) for this particular partition (A and B) is unusual with respect to other possible partitions with the same size structure that could have been made with these seven objects. Now, N objects can be partitioned into two groups (A and B) with fixed number of points n_A and n_B, respectively, in precisely $M = N!/(n_A!n_B!)$ ways. Since $M = 35$ for this example, all values of δ can be obtained by complete enumeration. These 35 values of δ are listed in Table 2 and ordered from the lowest to the highest value. It can be seen that the observed statistic ($\delta = 1.4578$) obtained for the realized partition (A and B) is indeed unusual since each of the remaining 34 values is greater than 1.4578. Because each partition could have occurred with equal chance (the null hypothesis), the observed significance level or P-value is $1/35 = 0.0286$.

This example of MRPP involved only a two-group analysis. The procedure is easily extended to a multigroup analysis. A variation of this method applied to a randomized block design follows.

Randomized blocks

MRBP is the MRPP analog for cases when randomized block designs are used. Let b blocks and g treatments be associated with a randomized block design. Let $x_{ij}' = [x_{1ij},...,x_{rij}]$ denote r commensurate response measurements corresponding to treatment i and block j. The modified MRPP statistic for this situation is given by

$$\delta = [g\tbinom{b}{2}]^{-1} \sum_{i=1}^{g} \sum_{j<k} \Delta\ (x_{ij}, x_{ik}) \qquad (11)$$

Table 2. Ordered values of δ for all 35 partitions of the seven points shown in Fig. 1 into two groups (A and B) having fixed sizes $n_A = 3$ and $n_B = 4$.

Rank	Value	Rank	Value
1	1.4578	19	2.1381
2	1.5421	20	2.1480
3	1.6939	21	2.1591
4	1.7505	22	2.1646
5	1.8389	23	2.1709
6	1.8547	24	2.1740
7	1.8935	25	2.1769
8	1.9898	26	2.1891
9	1.9915	27	2.1939
10	1.9988	28	2.2025
11	2.0060	29	2.2169
12	2.0157	30	2.2258
13	2.0176	31	2.2280
14	2.0522	32	2.2470
15	2.0575	33	2.2518
16	2.0829	34	2.2812
17	2.0944	35	2.2935
18	2.1158		

where $\Delta(x, y)$ is the symmetric distance function value of the points $x' = [x_1,...,x_r]$ and $y' = [y_1,...,y_r]$ defined in equation (5). The underlying permutation distribution of δ (the null hypothesis) assigns equal probabilities to the $M = (g!)^b$ possible allocations of the g r-dimensional measurements to the g treatment positions within each of the b blocks.

In a manner analogous to MRPP, small values of δ imply a concentration of the response measurements associated with each of the g treatments (i.e., over blocks). Therefore, $P(\delta \leq \delta_o)$ is again the P-value associated with δ_o (the realized value of δ). When M is large, the Pearson type III distribution is used to approximate P (Mielke 1984).

Simulation

Since a demonstration that the Pearson type III approximation is superior to other conceptual approximation is very satisfactory. Ten thousand indepenintended to show that the Pearson type III approximation is very satisfactory. Ten thousand independent random samples were drawn from a two-dimensional Poisson population[1] for two values of the Poisson parameter λ and two sample sizes, with each sample being randomly partitioned into two groups of equal size: $\lambda = 5$, $n_1 = n_2 = 10$; $\lambda = 5$, $n_1 = n_2 = 20$; $\lambda = 10$, $n_1 = n_2 = 10$; and $\lambda = 10$, $n_1 = n_2 = 20$. For each of the four simulations, 10000 MRPP probability values were calculated, using the Pearson type III approximation. The probability values were assigned to eight disjoint and exhaustive categories given by $p > 0.50$, $0.50 \geq p \geq 0.25$, $0.25 \geq p > 0.10$, $0.10 \geq p > 0.05$, $0.05 \geq p > 0.01$, $0.01 \geq p > 0.005$, $0.005 \geq p > 0.001$, and $0.001 \geq p$. The results of the Monte Carlo analyses are summarized in Table 3. The chi-square goodness-of-fit test statistic used for these comparisons is given by

$$\sum_{i=1}^{8} (O_i - E_i)^2/E_i,$$

where O_i is the observed frequency in the ith among the eight categories given above and $E_1 = 5000$, $E_2 = 2500$, $E_3 = 1500$, $E_4 = 500$, $E_5 = 400$, $E_6 = 40$, $E_7 = 40$, $E_8 = 10$. If the Pearson type III approximation with 10000 replications is inadequate, then a small chi-square probability value would be expected. However, the four chi-square goodness-of-fit probability values with 7 degrees of freedom were all greater than 0.5, indicating that the distribution of the MRPP statistic follows the Pearson typw III distribution in a reasonable manner.

[1] Suggested by a reviewer.

Table 3. Summary of Monte Carlo computer simulation results with two group sizes ($n_1 = n_2 = 10$ and $n_1 = n_2 = 20$) and two Poisson parameters ($\lambda = 5$ and $\lambda = 10$) with 10000 replications for each combination.

Group size:	$n_1 = n_2 = 10$		$n_1 = n_2 = 20$	
Poisson parameter:	$\lambda = 5$	$\lambda = 10$	$\lambda = 5$	$\lambda = 10$
$p > 0.50$	4959	4984	4963	5013
$0.50 \geq p > 0.25$	2558	2539	2522	2544
$0.25 \geq p > 0.10$	1462	1479	1512	1448
$0.10 \geq p > 0.05$	494	484	479	500
$0.05 \geq p > 0.01$	423	401	418	393
$0.01 \geq p > 0.005$	56	59	60	54
$0.0005 \geq p > 0.001$	41	46	38	40
$0.001 \geq p$	7	8	8	8
Chi-Square:	5.68	4.39	4.76	3.45
P-value:	0.5771	0.7341	0.6898	0.8401

Applications

In this section, applications of MRPP and MRBP to two case studies in vegetation research are presented. The first case study comes from research on secondary succession (Biondini *et al.* 1985) and contained four treatments. Treatment 1 consisted of mechanical removal of vegetation with minimal disturbance to the topsoil (A and B horizons). In Treatment 2, the vegetation was mechanically removed and the topsoil was scarified to a depth of 30 cm. Treatment 3 consisted of mechanical removal of the topsoil and subsoil (C horizon) to a depth of 1 m; the material was mixed together and replaced. In Treatment 4, two layers of 1 m of soil were removed and replaced in a reverse order with the second layer placed on the surface. The hypothesis tested was that increased levels of soil disturbance significantly alter the direction of secondary succession. The main patterns of vegetation succession in this study were given by the changes through time of the following species groups (the groups were derived from a species ordination analysis): (1) perennial grasses (the dominant species being: *Agropyron riparium, A. smithii, Koeleria cristata, Oryzopsis hymenoides,* and *Stipa comata*), (2) perennial forbs (the dominant species being: *Sphaeralcea coccinea, Erigeron engelmanii, Phlox longifolia, Senecio multilobatus,* and *Trifolium gymnocarpon*), (3) annual forbs (the dominant species being: *Salsola iberica*) and (4) shrubs (the dominant species being: *Artemisia tridentata, Chrysothamnus nauseousus, C. viscidiflorus,* and *Gutierrezia sarothrae*).

The hypothesis was formally tested with MRPP. The percent relative cover of perennial grasses, perennial forbs, annual forbs, and shrubs shown in Table 4 were used as the multivariate observation which characterized the species composition of each treatment. Treatments were analyzed at two points in time: (1) one year into succession and (2) six years into succession. The data are ideal for a distribution-free permutation test based on Euclidean distances for two reasons: (1) the vegetation in the highly disturbed plots (Treatments 3 and 4) one year after natural succession was very unevenly distributed causing a higher variance for Treatments 3 and 4 when compared with Treatment 1; and (2) a few quadrats in Treatments 3 and 4 were located either in microsites with high annual forb cover or over bare soil causing some of the data points to look like outliers. This case is fairly typical of successional studies where in the early stages only a fraction of the soil is covered by vegetation. The results of the MRPP analysis are given in Table 5.

The second case study comes from a study associated with mine reclamation research (Redente *et al.* 1982). An area that had been shallowly disturbed was seeded with a combination of grasses, forbs, and shrubs and subjected to six treatments. The treatments were (1) no fertilizer, (2) low fertilizer (56 kg

Table 4. Mean percent relative cover of the dominant plant species groups of each treatment on years 1 and 6 of secondary succession (Biondini *et al.* 1985).

Species group	Treatment 1		Treatment 2		Treatment 3		Treatment 4	
	Yr 1	Yr 6	Yr 1	Yr 6	Yr 1	Yr 6	Yr 1	Yr 6
Grasses	49.04	62.15	14.27	38.07	1.27	43.80	0.04	5.44
Perennial forbs	33.90	32.86	13.39	21.05	1.14	25.31	1.48	11.79
Annual forbs	14.63	2.54	66.12	2.29	91.56	21.04	92.62	6.57
Shrubs	2.32	2.17	5.55	37.71	5.91	9.25	5.40	76.86

Treatment 1 – the vegetation was mechanically removed with minimal disturbance to topsoil (A and B horizons).
Treatment 2 – the vegetation was mechanically removed and the topsoil scarified to a depth of 30 cm.
Treatment 3 – topsoil and subsoil (C horizon) were removed to a depth of 1 m. The material was mixed together and replaced.
Treatment 4 – two layers of 1 m of soil were removed and replaced in a reverse order with the second layer placed on the surface.
The experiment consisted of two replications per treatment. Ten 0.25 m^2 quadrats per replication were used to estimate species basal cover.

Table 5. Results from the MRPP analysis run on data shown in Table 4 for years 1 and 6.

Test	Year 1 treatment				Year 6 treatment			
	1	2	3	4	1	2	3	4
MRPP	a	b	b	b	a	b	a	c

For each test, treatments within a year that have different letters are significantly different ($p<0.05$; multiple comparison).

N/ha + 28 kg P/ha), (3) high fertilizer (112 kg N/ha + 56 kg P/ha), (4) mulch (2.2 MT/ha of wood fiber hydromulch) and no fertilizer, (5) mulch and low fertilizer, and (6) mulch and high fertilizer. The experiment was organized in a randomized block design with three blocks (see Table 6). The biomass of three shrubs (*Atriplex canescens, Ceratoides lanata,* and *Ephedra viridis*) was used as the multivariate observation that characterized each treatment. The data were analyzed with the use of MRBP; the probability of no difference among treatments is p = 0.068.

Table 6. Biomass data on shrubs (gm^{-2}) for a reclamation study on a shallowly disturbed site (Redente *et al.* 1982). The three shrubs measured on each treatment are: *Atriplex canescens, Ephedra viridis,* low *Ceratoides lanata.* The treatments are (1) no fertilizer; (2) low fertilizer; (3) high fertilizer; (4) mulch and no fertilizer; (5) mulch and low fertilizer; and (6) mulch and high fertilizer.

	Treatment					
	1	2	3	4	5	6
Block 1	0.33	6.67	6.33	3.83	9.67	14.50
	1.00	5.00	8.50	8.00	1.33	0.50
	2.17	2.00	2.17	1.33	3.67	2.17
Block 2	2.50	18.67	4.17	11.50	8.33	21.67
	0.83	0.17	1.67	2.50	1.50	0.83
	4.33	2.83	2.17	3.50	2.50	2.17
Block 3	1.00	8.67	5.17	0.67	23.67	7.33
	0.50	0.50	3.33	7.00	0.50	7.50
	2.33	2.00	2.00	2.50	3.33	4.50

Note: The data for each block is the average of 6 0.5 m^2 quadrats.

Summary and conclusions

The parametric statistical tests commonly used in ecological research have limitations that can become a critical source of error in data interpretation. The assumptions of a normal distribution and equality of variance (or variance-covariance matrices) are often difficult to meet in field experiments. In this paper, a statistical test called multiple response permutation procedures (MRPP) and its randomized block design analog (MRBP) have been presented. These methods are based on Euclidean distances and are completely data-dependent. Consequently, they require no assumptions about the underlying distribution structure of the population under study. Computer programs to implement MRPP and MRBP in IBM compatible PC's are available from the authors.

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