

Resource Selection:
Tests and Estimation using Null Models

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1 Introduction

Resource selection (usually either habitat choice or food preference) is modelled using Manly's alpha (Manly 1974; Manly, McDonald and Thomas, 1993; Chesson 1978, 1983). This measure uses ratios to allow for different availabilities of the resources. Resource selection models lead to measures of niche overlap between taxa, which is used in the description and analysis of biological community structure.

The taxa in this report are groups of organisms. They may be species, functional groups, size groups, or some other classification.

In this report, we construct null models (Gotelli and Graves 1996, Gotelli 2000) to evaluate and compare resource selection, using a unified approach which is appropriate for different kinds of raw data. The Bray-Curtis distance (an overlap statistic, see Schmid and Schmidt, 2006) is the measurement of distance used throughout, for comparing two statistical distributions, or comparing observed with expected values.

Definitions and notation are given in Sections 2.1 and 2.2. Sections 2.3 to 2.5 provide tests under the assumption that usage occurs as count data, and Section 3 gives adaptations of the tests for continuous data. Section 4 has a specially-developed test for two different types of resources which are measured on different scales, and a brief discussion of the tests is given in Section 5.

2 Resource Selection

The **electivity scores** proposed by Manly (Manly 1974, Chesson 1978, 1983) provide measures of the preference of a particular taxon for different types of food items or habitats, taking into account the availability of each food type (prey taxon) or habitat type.

2.1 Usage and Availability

For a given taxon at a given site, assume we have measures of both the usage (f_r) and the availability (g_r) of n_R different resources ($r = 1, 2, \dots, n_R$).

Two major applications are:

- **Habitat selection models:**

- **Usage** is measured as the number or biomass of individuals of this taxon found in each type of habitat:

$$f_r = \text{number or biomass of this taxon found in habitat } r, r = 1, \dots, n_R,$$

where there are n_R types of habitat available at the site. Examples include a species of fish on different substrates, or a species of lizard or bird in different vegetation types.

- **Availability** is measured as either the percentage or the proportion of ground covered by each habitat type, e.g.

$$g_r = \text{percentage cover of habitat type } r, r = 1, \dots, n_R,$$

with $\sum_{r=1}^{n_R} g_t = 100$ for percentages (or $\sum_{r=1}^{n_R} g_t = 1$ for proportions).

- **Food preference models:**

- **Usage** is measured as the number or weight of food items of each prey species found in the diets of the predator taxon of interest:

$$f_r = \text{number or weight of items of prey type } r \text{ in the diet, } r =$$

$$1, \dots, n_R,$$

where there are n_R different prey species available at the site.

- **Availability** may be a measure of the relative biomass of each prey type or species at the site,

$$g_r = \text{relative biomass of prey type } r, r = 1, \dots, n_R,$$

with $\sum_{r=1}^{n_R} g_r = 1$. Another example, relevant to grazing animals, could use proportion or percentage of ground cover of food types.

2.2 Electivity Scores: Manly's alpha

Manly's alpha α_r is the preference of the taxon of interest (at this site) for resource r , defined by

$$\alpha_r = \frac{\frac{f_r}{g_r}}{\sum_{j=1}^{n_R} \frac{f_j}{g_j}}, \quad (1)$$

giving a vector of values $(\alpha_1, \alpha_2, \dots, \alpha_{n_R})$ over the different resources. The scaling factor on the denominator of the formula ensures that the α values add to one. Hence α_r has the following properties:

1. Each α_r is between 0 and 1 inclusive, $0 \leq \alpha_r \leq 1$.
2. The α values add to one, $\sum_{r=1}^{n_R} \alpha_r = 1$.
3. If the taxon of interest completely avoids resource r , $f_r = 0$ and hence $\alpha_r = 0$.
4. If the taxon of interest has a complete preference for resource r to the exclusion of all others, $f_r > 0$ but all other $f_j = 0$ ($j \neq r$), and hence $\alpha_r = 1$.
5. If the taxon of interest shows no preferences, it merely uses each resource in proportion to its availability, and all α_r values are equal. Since they must add to 1, this means all $\alpha_r = \frac{1}{n_R}$.

Note that in the case of numbers of individuals in different habitats, α is essentially a measurement of **relative density** in each habitat. If the areas covered by habitat types 1 to n_R are a_1, a_2, \dots, a_{n_R} respectively, with a total area $A = \sum_{r=1}^{n_R} a_r$, they are related to the g_r proportions by

$$g_r = \frac{a_r}{A}$$

and Manly's α is unchanged by using a_r instead of g_r since

$$\frac{\frac{f_r}{a_r}}{\sum_{j=1}^{n_R} \frac{f_j}{a_j}} = \frac{\frac{f_r}{A \cdot g_r}}{\sum_{j=1}^{n_R} \frac{f_j}{A \cdot g_j}} = \frac{\frac{1}{A} \frac{f_r}{g_r}}{\frac{1}{A} \sum_{j=1}^{n_R} \frac{f_j}{g_j}} = \frac{\frac{f_r}{g_r}}{\sum_{j=1}^{n_R} \frac{f_j}{g_j}} = \alpha_r.$$

The numerators in this case are simple densities, numbers per unit area, and the denominator rescales them to make them add to one, so α_r is just the relative density of this taxon in habitat r .

2.3 Testing for the Existence of Preference

In this section, f_r is assumed to be a count, not continuous data. For one taxon at one site, we wish to establish whether the taxon is showing any preferences at all, rather than just randomly selecting habitat or food in proportion to its availability. We first postulate the existence of underlying population parameters α_r for the “true” preferences, and regard equation 1 as providing an estimate $\hat{\alpha}_r$ of the unknown α_r for each resource r . We now test the overall hypothesis

$$H_0: \text{All } \alpha_r = \frac{1}{n_R}, \text{ versus } H_A: \text{At least one } \alpha_r \neq \frac{1}{n_R}.$$

More detailed tests for each resource separately (e.g. a two-sided test $H_0: \alpha_r = \frac{1}{n_R}$, versus $H_A: \alpha_r \neq \frac{1}{n_R}$) will give information about which (if any) resources are being selected or avoided. An adjustment for multiple testing is needed if each resource is tested.

One option for performing these tests would be to build generalized linear models with (for example) Poisson assumptions if f_r is count data, and use a likelihood ratio test (G^2) or a Pearson's χ^2 test. However, there could be excess zeros, which would invalidate the Poisson assumption, and the assumptions of large samples and independence may also not be met. Therefore we prefer to use randomization tests and null models, which are more robust and appropriate (Gotelli and Graves, 1996; Manly, 1997).

2.3.1 Randomization Tests

To construct a suitable randomization test (Manly 1997), we must:

- Select a test statistic which will differentiate the null from the alternative hypothesis.
- Evaluate the test statistic for the actual data.
- Decide the units for the randomization process.
- Do repeated randomizations assuming the null hypothesis is true, and in each run calculate the pseudo-value of the test statistic, thus building up a picture of the null distribution of the test statistic.
- Find where the data test statistic lies on the null distribution in order to determine the p value for the test.

2.3.2 Construction of the Overall Test

The null hypothesis is that the resource selection is occurring at random, in proportion to availability, with no preference shown. In the habitat preference model, this is the hypothesis of equal densities in all habitats.

The test is constructed by considering the expected usage values $E(f_r)$ under the assumption of random choice. Suppose we have count data for f_r (e.g. number of fish on substrate r , number of prey items of type r in the diet). We discuss the test construction in terms of relative density, which gives a heuristic argument for increased clarity, but the argument holds for other situations unrelated to density provided each f_r is a count.

If H_0 is true, the individuals are distributed over the habitats with an underlying process of equal density. Our sample will not show exactly equal density because of sampling fluctuation, but we are testing if the data are near enough to equal density for H_0 to be accepted. The availability g_r is the relative area of habitat r , where the relative areas sum to 1.

We have observed counts in each habitat, and the model gives us expected counts, as follows. If the underlying common density is λ , habitat r with area a_r has expected number λa_r . If a total of $F = \sum_{r=1}^{n_R} f_r$ individuals were observed, λ is estimated as $\frac{F}{A}$, where A is the total area searched, $A = \sum_{r=1}^{n_R} a_r$. Hence the expected number in habitat r , assuming H_0 is true, is

$$E(f_r) = \lambda a_r = F \cdot \frac{a_r}{A} = F \cdot g_r.$$

To check that this matches H_0 : all $\alpha_r = \frac{1}{n_R}$, we note that the expected frequencies above give

$$\alpha_r = \frac{\frac{E(f_r)}{a_r}}{\sum_{j=1}^{n_R} \frac{E(f_j)}{a_j}} = \frac{\frac{\lambda a_r}{a_r}}{\sum_{j=1}^{n_R} \frac{\lambda a_j}{a_j}} = \frac{\lambda}{\lambda \sum_{j=1}^{n_R} 1} = \frac{1}{n_R}.$$

Two possible test statistics for comparing observed with expected values would be the likelihood ratio statistic (deviance)

$$G^2 = 2 \sum_{r=1}^{n_R} f_r \log \frac{f_r}{E(f_r)}$$

or Pearson's chi-squared statistic

$$\chi^2 = \sum_{r=1}^{n_R} \frac{(f_r - E(f_r))^2}{E(f_r)},$$

where f_r and $E(f_r)$ are the observed and expected counts respectively for habitat r . However, both these statistics work best for large samples, and can be unstable for low expected values, so we choose instead to use the more robust Bray-Curtis index of dissimilarity, which also measures the discrepancy between two vectors (observed and expected values).

2.3.3 Test Statistic

Our **test statistic** is the **Bray-Curtis index of dissimilarity** between the observed and expected vectors,

$$\text{BCD} = \frac{\sum_{r=1}^{n_R} |f_r - E(f_r)|}{\sum_{r=1}^{n_R} (f_r + E(f_r))} = \frac{\sum_{r=1}^{n_R} |f_r - E(f_r)|}{2F} \quad (2)$$

which has a value between 0 (for completely matching vectors) and 1 (for the most extreme dissimilarity, where for each resource r either $f_r = 0$ or $E(f_r) = 0$).

The null distribution of the Bray-Curtis index will be found by randomization. Each randomization will take F individuals, and assign each independently to a habitat, with the probability of going to habitat r being g_r . This is a multinomial distribution, with the categories being the habitats.

2.3.4 Algorithm for Overall Test

The algorithm for the overall test incorporates random allocation using the multinomial distribution, as follows:

1. Calculate the expected values under the assumption of no selection, $E(f_r) = F \cdot g_r$, and then the data BCD values using Equation 2.
2. Do a large number of randomizations. Within each randomization:
 - (a) Allocate F individuals independently to habitats 1 to n_R , with probabilities (g_1, \dots, g_{n_R}) (a multinomial allocation).
 - (b) Use these pseudo-usages to calculate and store the pseudo-BCD value.
3. See where the data BCD falls in the distribution of different pseudo-BCD values. A high BCD value indicates a large distance between observed and expected values. The proportion of pseudo-BCD values which exceed the observed value is the p-value (exact significance level) for the test. If there are 1000 randomizations, the p value will be found to 3 decimal places.

2.3.5 Detailed Resource-Specific Tests

For each resource r , the distribution of the numbers in habitat r is binomial (F, g_r) (i.e. F trials, “success” with probability g_r), so if a significant difference via the Bray-Curtis index is found, tests of whether each habitat has higher or lower selection than expected may be done.

The two-sided test for selection or avoidance of one resource r could use as a test statistic the deviation of the α_r estimate from $1/n_R$, $D_r = \hat{\alpha}_r - n_R$. This is calculated for the original data, and then at each randomization, the pseudo-value of D_r is saved. At the end the data D_r value is compared with the null distribution of the saved pseudo-values.

The null distribution will be centred on zero. For a two-sided test, the p value for resource r is the proportion of D_r pseudo-values further from zero than the data D_r value. The direction of preference will also be clear, with data $D_r > 0$ indicating preference, and data $D_r < 0$ indicating avoidance.

If n_R such tests are performed, an adjustment for multiple testing, for example a sequential Bonferroni adjustment, should be done to the p-values.

2.4 Comparing Multiple Taxa at the Same Site

Suppose we wish to compare some or all of the taxa at the same site, to see if they have the same resource selection. Not all the available taxa need to be compared in the test. For example, the test has low power for rare taxa, and these may well be omitted as they contribute little information on resource selection.

Let n_T be the number of taxa to be compared. Assuming the usages are counts, let f_{tr} be the usage of resource r by taxon t ($t = 1, 2, \dots, n_T$). The test will be based on the expected usages for each taxon under an assumed null hypothesis of the taxa having the same preference vector. The data are shown in Table 1, with marginal totals F_t = total usage by taxon t , and U_r = total usage of resource r .

		Resource						Total	
		1	.	.	r	.	.		n_R
Usage	Taxon 1	f_{11}	.	.	f_{1r}	.	.	f_{1,n_R}	F_1

	Taxon t	f_{t1}	.	.	f_{tr}	.	.	f_{t,n_R}	F_t

	Taxon n_T	$f_{n_T,1}$.	.	$f_{n_T,r}$.	.	f_{n_T,n_R}	F_{n_T}
	Total	U_1	.	.	U_r	.	.	U_{n_R}	F
Availability		g_1	.	.	g_r	.	.	g_{n_R}	1

Table 1: Data for n_T taxa at one site.

2.4.1 Statistical Tests

The **overall test** is whether or not all n_T taxa have the same resource usage. The unknown population α values are tested:

H_0 : For each $r = 1, \dots, n_R$, $\alpha_{1r} = \alpha_{2r} = \dots = \alpha_{n_T,r}$, versus

H_A : For at least one pair of taxa (t and t') and at least one r , $\alpha_{tr} \neq \alpha_{t'r}$.

More **detailed tests** are:

- **Resource-specific tests:** Check each resource r separately, with hypotheses:

H_0 : $\alpha_{1r} = \alpha_{2r} = \dots = \alpha_{n_T,r}$, versus

H_A : For at least one pair of taxa (t and t'), $\alpha_{tr} \neq \alpha_{t'r}$.

- **Pairwise comparisons of taxa:** If $n_T > 2$, any two taxa may be compared over the n_R resources.

If multiple detailed tests are used, a correction for multiple testing (e.g. sequential Bonferroni) should be applied.

2.4.2 Expected Values under H_0

For the overall test, we will find contingency-table probabilities and expected values of the usages under the null hypothesis, in order to randomize from the appropriate distribution. We then compare the data $\hat{\alpha}$ values with the α values under the null hypothesis. The Bray-Curtis distance between the data and generated $\hat{\alpha}$ values will form the test statistic.

To find the expected usages, assume H_0 is true, i.e. that all n_T taxa select the resources in the same pattern. Then the individuals in taxon t have the same probabilities p_1, \dots, p_{n_R} of selecting resources 1 to n_R as the individuals in each other taxon. These common probabilities are estimated by pooling the n_T taxa to give an overall estimate of usage from all sources. The estimated probability for resource r is the total usage of resource r divided by the overall total usage,

$$p_r = \frac{U_r}{F} \quad \text{where} \quad U_r = \sum_{t=1}^{n_T} f_{tr} \quad \text{and} \quad F = \sum_{t=1}^{n_T} F_t.$$

This gives the expected usages (numbers of individuals) for taxon t as

$$E(f_{tr}) = p_r F_t, \quad r = 1, \dots, n_R.$$

Table 2 shows the expected usages under the null hypothesis. Note that this table has the same margins (row sums and column sums) as the table of observed usages (Table 1).

As a check, the resource selection parameter for the expected usage of resource r by taxon t is

$$\alpha_{tr} = \frac{E(f_{tr})/g_r}{\sum_{j=1}^{n_R} E(f_{tj})/g_j} = \frac{p_r F_t/g_r}{\sum_{j=1}^{n_R} p_j F_t/g_j} = \frac{p_r/g_r}{\sum_{j=1}^{n_R} p_j/g_j}$$

which is independent of t . Thus all taxa have the same distribution of α values across the available resources.

There is now enough information to construct the randomization test of H_0 . The probability vector (p_1, \dots, p_{n_R}) is calculated from the data, and at each randomization each taxon has pseudo-usages calculated from a multinomial distribution.

		Resource						Total	
		1	.	.	r	.	.	n_R	
Probability	$p_r = \frac{U_r}{F}$	p_1	.	.	p_r	.	.	p_{n_R}	1
Expected usage under H_0 $E(f_{tr})$	Taxon 1	$p_1 F_1$.	.	$p_r F_1$.	.	$p_{n_R} F_1$	F_1

	Taxon t	$p_1 F_t$.	.	$p_r F_t$.	.	$p_{n_R} F_t$	F_t

	Taxon n_T	$p_1 F_{n_T}$.	.	$p_r F_{n_T}$.	.	$p_{n_R} F_{n_T}$	F_{n_T}
Total		U_1	.	.	U_r	.	.	U_{n_R}	F
Availability		g_1	.	.	g_r	.	.	g_{n_R}	1

Table 2: Expected usages under H_0 .

For taxon t , F_t individuals are allocated to the resources with probabilities p_r , $r = 1, \dots, p_{n_R}$. This allocation has assumed the truth of H_0 .

2.4.3 Test Statistics

We will use as test statistics the Bray-Curtis distances between pairs of α vectors. For comparing two taxa, t and t' say, the distance is

$$d(t, t') = \frac{\sum_{r=1}^{n_R} |\hat{\alpha}_{tr} - \hat{\alpha}_{t'r}|}{\sum_{r=1}^{n_R} (\hat{\alpha}_{tr} + \hat{\alpha}_{t'r})} = \frac{1}{2} \sum_{r=1}^{n_R} |\hat{\alpha}_{tr} - \hat{\alpha}_{t'r}|, \quad (3)$$

with the denominator simplifying because α is scaled to add to 1 across the resources. The null hypothesis is that the distance between the true α vectors is zero; if this is true, a Bray-Curtis distance above zero is due to sampling fluctuation alone. Randomization will be used to generate the null distribution of BCD, under the null hypothesis of equal α vectors. Values of the test statistic close enough to zero will lead to an acceptance of H_0 , while values sufficiently far above zero will give evidence to reject H_0 .

For an **overall comparison** of two or more taxa ($n_T \geq 2$) over all n_R resources at this site, we let the test statistic be the sum of the Bray-Curtis distances between all possible pairs of different taxa:

$$\text{Overall Test Statistic} = D = \sum_{t=1}^{n_T-1} \sum_{t'=t+1}^{n_T} d(t, t') \quad (4)$$

where $d(t, t')$ is the Bray-Curtis distance between taxa t and t' . There are $\frac{n_T(n_T-1)}{2}$ different pairs contributing to D . For a more detailed **resource-specific test** for a single resource r , we may use the Bray-Curtis contribution for that resource only,

$$\text{Test Statistic for resource } r = D_r = \sum_{t=1}^{n_T-1} \sum_{t'=t+1}^{n_T} \frac{1}{2} |\hat{\alpha}_{tr} - \hat{\alpha}_{t'r}| \quad (5)$$

If the overall test gives significant differences of resource selection, the individual resources may be tested as above, with a correction (e.g. sequential Bonferroni) for multiple testing.

2.4.4 Algorithm to Compare Taxa (same site)

The procedure for an overall comparison and resource-specific tests of n_T taxa at the same site, with $n_T \geq 2$, is:

1. Calculate the (estimated) α_{tr} values for each taxon t and each resource r .
2. Calculate and save the data BCD, $d(t, t')$, between the α values for each pair of taxa, t, t' , using Equation 3.
3. Calculate and save the overall sum D (Equation 4) and the vector of D_r values (Equation 5).
4. Calculate the overall probability vector which holds if H_0 is true:

$$p_r = U_r/F \text{ for } r = 1, 2, \dots, n_R$$

where U_r is the total usage of resource r and F is the overall sum of the usages.

5. Do a large number of randomizations. Within each randomization:
 - (a) For each taxon t , independently allocate F_t individuals to resources 1 to n_R , with probabilities p_1 to p_{n_R} (a multinomial allocation). This gives an $n_T \times n_R$ matrix of pseudo-usages.
 - (b) Calculate the associated $n_T \times n_R$ matrix of pseudo-alphas.
 - (c) Calculate and store the pairwise pseudo- $d(t, t')$ distances, the overall pseudo-test statistic D , and the resource-specific pseudo-distances D_r , as in steps 1–3 above.

6. After the randomizations, see where the data D value falls in the distribution of pseudo- D values. If there are fewer than 5% of the pseudo- D values above D , there is a significant difference of resource selection among taxa 1 to n at a 5% significance level. The p-value is

$$p = \frac{\text{No. pseudo-}D \text{ values} > \text{data } D}{\text{No. randomizations}}.$$

7. If there are significant differences, resource-specific tests may be done. For each resource r compare the data D_r value with the distribution of stored pseudo- D_r values, finding a p-value for each resource. Apply a multiple-testing adjustment to the resource-specific p-values.
8. If $n_T > 2$, pairwise tests of taxa may be done to find which pairs differ and which are similar. Compare the data $d(t, t')$ values with the generated pseudo-values, and do a correction for multiple testing. These tests may help to identify functional groups of taxa, with similar resource selection within groups.

2.5 Comparing One Taxon Across Multiple Sites

In this section, we compare the resource usages of one taxon over two or more sites, which will have different resource availabilities. The taxon must be present at all the sites. If the taxon has varying preferences over the different sites, this could possibly indicate adaptative differences. Although we refer to different sites, these tests may instead be used for the same site at different times. For example, a seasonal change in resource availability may occur in food preference data, or perhaps there is a long-term trend for changing resource selection as habitats are modified during succession or interference.

Arthur *et al.* (1996) discussed a similar problem of changing availability, but details of the application differ from ours and so the models also differ.

To compare a group of sites, we must restrict the analysis to resources which are available over all the sites being compared, since any resource missing at one site will yield no estimate of possible usage at that site.

We construct two types of tests, an overall test to compare two or more sites (with a resource-specific version), and a pairwise test for two sites. The testing is again based on finding what usages we would expect if the null hypothesis is true.

Assume our restricted data set has n_S sites and n_R resources (available at all sites), and that the usages are counts. The data are shown in Table 3.

2.5.1 Statistical Tests

The **overall test** has a null hypothesis that the resource selection pattern is the same over all the sites, versus an alternative that at least two sites show some difference in resource selection. If α_{rs} is the selection (preference) for resource r at site s ($r = 1, 2, \dots, n_R$, $s = 1, 2, \dots, n_S$), the hypotheses are

$$\begin{aligned} H_0: & \text{for each resource } r, \alpha_{1r} = \alpha_{2r} = \dots = \alpha_{n_S, r}, \text{ versus} \\ H_A: & \text{for at least one resource } r \text{ and one pair of sites } s \text{ and } s', \alpha_{sr} \neq \alpha_{s'r}. \end{aligned}$$

More **detailed tests** are:

- **Resource-specific tests:** Check each resource r separately, with hypotheses:
$$H_0: \alpha_{1r} = \alpha_{2r} = \dots = \alpha_{n_S, r}, \text{ versus}$$
$$H_A: \text{for at least one pair of sites } s \text{ and } s', \alpha_{sr} \neq \alpha_{s'r}.$$
- **Pairwise comparison of sites:** If $n_S > 2$, any two sites s and s' may be compared over the n_R resources, using

		Resource						Total	
		1	.	.	r	.	.		n_R
Usage	Site 1	f_{11}	.	.	f_{1r}	.	.	f_{1,n_R}	F_1

	Site s	f_{s1}	.	.	f_{sr}	.	.	f_{s,n_R}	F_s

	Site n_S	$f_{n_S,1}$.	.	$f_{n_S,r}$.	.	f_{n_S,n_R}	F_m
Total		U_1	.	.	U_r	.	.	U_{n_R}	F
Availability	Site 1	g_{11}	.	.	g_{1r}	.	.	g_{1,n_R}	1

	Site s	g_{s1}	.	.	g_{sr}	.	.	g_{s,n_R}	1

	Site n_S	$g_{n_S,1}$.	.	$g_{n_S,r}$.	.	g_{n_S,n_R}	1
Average		V_1	.	.	V_r	.	.	V_{n_R}	1

Table 3: Data for one taxon at n_S different sites.

H_0 : for each resource r , $\alpha_{1sr} = \alpha_{s'r}$ versus
 H_A : for at least one resource r , $\alpha_{sr} \neq \alpha_{s'r}$.

Multiple testing should have a correction (e.g. sequential Bonferroni) applied to the p values.

2.5.2 Expected Values under H_0

The expected usages under H_0 are found to be similar to those in Section 2.4, but with an adjustment for different availabilities. Each usage is adjusted to be the expected usage under average availability V_r (averaged over the sites). The expected usage of resource r at site s is

$$E(f_{sr}) = \frac{F_s U_r g_{sr} / V_r}{\sum_{j=1}^{n_R} U_j g_{sj} / V_j} \quad (6)$$

As a check, the resource selection parameter for the expected usage at site s of

resource r is

$$\alpha_{sr} = \frac{E(f_{sr})/g_{sr}}{\sum_{k=1}^{n_R} E(f_{sk})/g_{sk}} = \frac{F_s U_r / V_r / \left(\sum_{j=1}^{n_R} U_j g_{sj} / V_j \right)}{\sum_{k=1}^{n_R} \left[F_s U_k / V_k / \left(\sum_{j=1}^{n_R} U_j g_{sj} / V_j \right) \right]} = \frac{U_r / V_r}{\sum_{k=1}^{n_R} U_k / V_k}$$

which is independent of s . Hence these expected values represent the same distribution of α values across the different sites.

The probability estimates vary from site to site, because of the different availabilities. For site s , the estimated probabilities under H_0 are

$$p_{sr} = E(f_{sr})/F_s = \frac{U_r g_{sr} / V_r}{\sum_{j=1}^{n_R} U_j g_{sj} / V_j} \quad (7)$$

for resources $r = 1, \dots, n_R$, and $\sum_{r=1}^{n_R} p_{sr} = 1$ for each site s . Under the null model, the usages at site s follow a multinomial distribution with F_s trials, and probabilities $\{p_{sr}\}$ for the different resources.

2.5.3 Test Statistics

We will again use Bray-Curtis distances as test statistics.

For **comparing two sites**, s and s' say, the distance is

$$d(s, s') = \frac{\sum_{r=1}^{n_R} |\hat{\alpha}_{sr} - \hat{\alpha}_{s'r}|}{\sum_{j=1}^{n_R} (\hat{\alpha}_{sj} + \hat{\alpha}_{s'j})} = \frac{1}{2} \sum_{r=1}^{n_R} |\hat{\alpha}_{sr} - \hat{\alpha}_{s'r}|. \quad (8)$$

with the denominator simplifying because α is scaled to add to 1 across the resources.

The **overall test** among three or more sites has test statistic

$$\text{Overall Test Statistic} = D = \sum_{s=1}^{n_S-1} \sum_{s'=s+1}^{n_S} d(s, s') \quad (9)$$

The more detailed **resource-specific test** for selection of a single resource r over the different sites has test statistic

$$\text{Test Statistic for resource } r = D_r = \sum_{s=1}^{n_S-1} \sum_{s'=s+1}^{n_S} \frac{1}{2} |\hat{\alpha}_{sr} - \hat{\alpha}_{s'r}| \quad (10)$$

These distance-based test statistics all lead to rejection of H_0 if the observed distance is greater than would be expected by chance.

2.5.4 Algorithm to compare Sites (one taxon)

For two or more sites, using the same taxon, the test procedure uses randomizations from the multinomial distribution, with the probabilities (equation 7) which were used in deriving the expected values under H_0 .

1. Restrict the data to the n_S sites at which this taxon is present, and the n_R resources which are available at all these n_S sites. Rescale the availabilities to add to 1 at each site.
2. Calculate the (estimated) α_{sr} values for each site s and each resource r .
3. Calculate and save the data BCD, $d(s, s')$, between the α values for each pair of sites, t, t' , using Equation 8.
4. Calculate and save the overall sum D (Equation 9) and the vector of D_r values (Equation 10).
5. Calculate the $n_S \times n_R$ probability matrix which holds if H_0 is true, using Equation 7.
6. Do a large number of randomizations. Within each randomization:
 - (a) For each site s , independently allocate F_s individuals to resources 1 to n_R , with probabilities p_{s1} to p_{s,n_R} (a multinomial allocation). This gives an $n_S \times n_R$ matrix of pseudo-usages.
 - (b) Calculate the corresponding $n_S \times n_R$ matrix of pseudo-alphas.
 - (c) Calculate and store the pairwise pseudo- $d(s, s')$ distances, the overall pseudo-test statistic D , and the resource-specific pseudo-distances D_r , as in steps 2–4 above.
7. After the randomizations, see where the data D falls in the distribution of pseudo- D values. If fewer than 5% of the pseudo- D values are above D , there is a significant difference of resource selection over sites 1 to n_S at a 5% significance level. The p value is the proportion of pseudo- D values above the data D value.
8. If there are significant differences, resource-specific tests may be done. For each resource r compare the data D_r value with the distribution of stored pseudo- D_r values, finding a p-value for each resource. Apply a multiple-testing adjustment to the resource-specific p-values.
9. If $n_S > 2$, pairwise tests of sites may be done to find which pairs differ and which are similar. Compare the data $d(s, s')$ values with the generated pseudo-values, and do a correction for multiple testing. These tests may help to identify groups of sites, e.g. into different habitat types.

3 Continuous Usage Measures

In the definition of selectivity, the usages may be either counts or continuous data. Either way, the α values may be calculated.

The discussion so far has assumed the usages are counts, e.g. numbers of animals using a certain habitat, or numbers of items of different prey types in the diet. This restriction was imposed in order to have independent units to permute or allocate in the randomization tests.

However, the usage data obtained may be continuous. In habitat studies, if animals are tracked through habitats by radiotelemetry, time intervals in different habitats are available (e.g. Hoare *et al.*, 2007). In diet analyses, the weights of different prey types are likely to be recorded, with counts of individual items being impossible.

In these cases, there is no natural unit for random allocation in the randomization tests. The conservative approach is to set the randomization units high enough for independence to be assured. At worst, this may result in the loss of some power in the testing.

With continuous records of animals over different habitats, one could sample the locations at time points far enough apart for the animal to have had a choice of staying or moving to a different habitat in the intervening interval. This will depend on the mobility of the animal and the size of the habitat patches.

With weights of diet items in stomach contents, a reasonable assumption would be that each prey type in one stomach represents an independent choice. There may well be independence down to a finer level, e.g. different bites, but we don't know this. We make the conservative assumption that each "morsel" (type of prey, with associated weight) in one stomach was selected independently. This morsel is used in the randomization tests as the unit to be randomized, retaining its associated weight.

This conservative approach will help to keep the Type I error controlled, although the tests will have less statistical power than those with independence assumed down to a finer level.

4 Combining Different Availability Measures

With food preference data, there may be different prey categories which cannot be measured on the same scale. For example, omnivore predators may be grazing vegetation and hunting mobile animals. The abundance of vegetative (sessile) availability is best described by percent cover per unit of area; whereas mobile, benthic or pelagic prey availability is best described by the total number of individuals per unit of area for both terrestrial and aquatic habitat. In an aquatic environment, mobile or sessile prey or habitat availability can also be described by units of volume of water; for example, when mobile prey is pelagic (e.g. fish, salps, etc) or when the biomass of sessile prey or habitat occurred on a three-dimensional space (e.g. kelps). While α values may be calculated for each prey category separately, these do not give meaningful comparisons between predators - for example they may appear to have similar usage within each category, but one predator may really have a strong preference for vegetation and the other for animal prey, a fact which cannot show up in separate analyses. Resource selection estimates would give more meaningful comparisons among predator species if a unified overall measure of availability is used. In such cases we need to estimate the relative importance of each type of measure.

We propose a **comparability coefficient** κ to convert one availability measure to another. One prey category is taken as the standard, and the availabilities of any other prey categories $1, 2, \dots, N$ are converted to the standard using the coefficients $\kappa_1, \kappa_2, \dots, \kappa_N$ respectively. The following discussion refers to data with just two categories of prey, mobile and sessile, but the argument may be extended to multiple categories.

If the predators are fish species (the taxa), the mobile prey are measured in units of weight per unit of area or volume of water, while the sessile prey units are % substrate cover. We take the mobile prey as the standard, and use the data to construct a comparability coefficient κ to convert from sessile prey availability to a measure comparable with the mobile prey.

The prey types are first pooled into just the two categories, mobile and sessile. To estimate κ , the data set used must include:

- Two or more comparable sites, each having both prey categories available.
- A set of predator taxa, each of which
 - uses both prey categories,
 - occurs at all the chosen sites, and
 - may be assumed to have similar preferences over these sites.

We cannot use fish species which eat either mobile or sessile prey exclusively, as they provide no information to compare preferences between the two categories. The similar sites are needed to give some replication, so that an assumption of each predator taxon having similar preferences over the sites enables an estimate of κ to be made.

At a given site s , the availability measures are g_{sA} = weight per unit volume of water for mobile prey (category A), and h_{sB} = % cover for sessile prey (category B). The comparability coefficient κ will convert the h_{sB} measure to g_{sB} ,

$$g_{sB} = \kappa h_{sB}$$

where g_{sB} is now on a scale comparable with g_{sA} .

Since both mobile and sessile prey are available at the selected sites, Manly's α values are indicating true preferences of each predator taxon, without any restriction of choice which would occur with unavailability. Let α_{tsA} and α_{tsB} be the preferences of predator taxon t at site s for mobile (category A) and sessile (category B) prey respectively.

If κ were known, estimates of these α values could be found. The formula for simultaneous conversion from h_{sB} to g_{sB} and estimation of $\hat{\alpha}$ is

$$\hat{\alpha}_{tsA} = \frac{\frac{f_{tsA}}{g_{sA}}}{\frac{f_{tsA}}{g_{sA}} + \frac{f_{tsB}}{\kappa h_{sB}}} \quad \text{and} \quad \hat{\alpha}_{tsB} = \frac{\frac{f_{tsB}}{\kappa g_{sB}}}{\frac{f_{tsA}}{g_{sA}} + \frac{f_{tsB}}{\kappa h_{sB}}}$$

where f_{tsA} and f_{tsB} are the usages, for example weights of mobile and sessile prey respectively in the stomachs of fish species t at site s . Note that $\hat{\alpha}_{tsA} + \hat{\alpha}_{tsB} = 1$.

Since Manly's α adjusts for site (and availability) differences, the value of α_{tsA} should be similar across sites for each taxon t . The estimates $\hat{\alpha}_{tsA}$ should vary between taxa but be similar across sites within taxa.

We try different values of κ , and select the one which maximises the species differences in $\hat{\alpha}_{tsA}$ while minimising the site differences. (This is similar to discriminant analysis, and some types of cluster analysis, in which a between-groups difference is maximised in relation to the within-groups difference.) For each taxon t , the mean over the sites, $\bar{\alpha}_{t,A}$, is an estimated expected (or fitted) value for α_{tA} .

Three criteria which could be used for choosing κ are:

1. Minimise the sum of squares of deviations of observed from expected values (as is done in least squares regression),
2. Minimise the sum of absolute values of deviations of observed from expected values, which will be less sensitive to outliers than 1., or

3. Minimise the Bray-Curtis distance between the observed and fitted values, which is less sensitive to outliers and to small expected values.

The Bray-Curtis distance proved the most consistent in the experiment which inspired the development of the comparability coefficient (Pérez Matus, 2007, in prep.).

Once the comparability coefficient has been estimated numerically, it may be used for more detailed analyses in which there are many prey types, some mobile and some sessile. All sessile prey types have their measured availability (% cover) adjusted by κ to make them comparable with the mobile prey.

The analyses of Sections 2.3 (existence of preference), 2.4 (different taxa, same site) and 2.5 (same taxon, different sites) are now feasible.

5 Discussion

Tests have been given for comparing several taxa at one site, or several sites with one taxon. A generalization would be possible, giving an overall test over several sites and taxa, using the same methods.

A graphical representation of results using non-metric multidimensional scaling is a useful adjunct to these tests. For several taxa at one site, the Bray-Curtis distances between taxa, $d(t, t')$ (Equation 3) have been calculated. A scaling can illustrate in two dimensions which taxa are most alike, and which are most different. This and clustering methods could provide an objective method of determining functional groups of taxa, grouped by their selection of resources. Similarly, for one taxon and several sites, a non-metric multidimensional scaling or a clustering of the site by distances $d(s, s')$ (Equation 3) will group the sites for similarity of selectivity by that prey taxon.

Note that the independent allocation used in the randomization process implies that this test does not allow for density dependence mechanisms (e.g. intra- or inter-specific competition). With habitat usage, each individual is assumed to choose on the basis of habitat area alone, without reference to other occupiers. With diet data, each individual at one site has the same availability of food as the other individuals; selection is based on food availability, independently of other users.

R programs for these analyses are available from the first author.

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