



A framework for estimating niche metrics using the resemblance between qualitative resources

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Despite the central importance of the niche concept for the ecological theory, current methods to quantify the species niche from qualitative resources, such as food or habitat types, remain insufficiently developed. Classically, information theory and diversity measures have formed the toolbox used for calculating resource niche metrics on species preference data for a set of qualitative resources. We provide a comprehensive framework that extends these classical approaches by incorporating the resemblance between resources into the calculation of resource niche metrics. This does not only allow estimation of the niche centre, breadth, overlap and displacement with greater accuracy, but also makes the estimates less influenced by the way the resources are subdivided. In addition, all niche metrics can be calculated while taking into account the variation in resource availability, and confidence intervals can be obtained by bootstrapping. We illustrate the utility of the framework with an analysis of dietary preferences in feral pigeons *Columba livia*.

The fundamental ecological niche of a species is the set of ecological requirements individuals need for survival in the absence of competition, predation, dispersal limitation, and natural or human disturbances (Hutchinson 1957). Thus, the niche concept underlies most ecological questions, from population growth and geographic expansion to community dynamics and ecosystem functioning (Austin and Smith 1989, Owens and Bennett 2000, Chase and Leibold 2003, Phillimore et al. 2006). Since the development of niche theory by MacArthur and his collaborators (summarized in Vandermeer 1972), field ecologists have been interested in measuring the niche of species. However, the fundamental niche of a species is usually impossible to quantify, and at the most we can try to measure the part of the fundamental niche actually occupied by the species after the constraints above-mentioned, the so-called realized niche (Hutchinson 1957, Pulliam 2000). The past decades have seen a proliferation of methods to quantify the realized niche of species based on quantitative environmental factors, such as climatic or soil variables (Peterson et al. 1999, Thuiller et al. 2004, Calenge and Basille 2008). In contrast, considerably less effort has been devoted to develop methods to estimate the niche defined as the preference for a set of qualitative resources (e.g. food types) required for survival and reproduction. Describing an operational method to measure the qualitative resource niche of organisms is the goal of the present paper.

Information theory and diversity measures have traditionally made up the toolbox used for calculating qualitative

resource niche metrics in the past (Horn 1966, Colwell and Futuyma 1971, Hanski 1978, Hurlbert 1978, Gordon and Illius 1989, Mysterud 2000, Blüthgen et al. 2006). These metrics are calculated from observed use or preference for either resources (e.g. the fraction of each prey consumed) or resource surrogates (e.g. the amount of individuals observed in a set of habitats). Unfortunately, most of the traditional measures do not take into account the fact that some pairs of resources may be more similar than others, and hence all resources are treated as equally distinct (Colwell and Futuyma 1971). Not taking into account unequal resource resemblance is problematic, because niche metrics are sensitive to how resource categories are defined and weighted. For example, dividing a given resource into two similar subcategories can artificially inflate niche breadth because a species preferring the initial resource will also show high preference for the two subcategories. Such biases can only be prevented if resource distinctness is incorporated into the niche breadth measure. Colwell and Futuyma (1971) were the first to propose niche metrics that accommodated resource distinctness. However, their approach only allowed to estimate niche breadth and overlap, and was deemed difficult to interpret by some researchers (Hanski 1978). Later developments of resource niche metrics did not further extend these novel ideas but instead concentrated on solving another limitation, that is, incorporating the variation of resource availability in the definition of metrics (Hurlbert 1978, Lawlor 1980, Feinsinger et al. 1981, Smith 1982).

The framework we describe in the present paper revisits Colwell and Futuyma (1971) ideas in an attempt to produce niche metrics that are more accurate and less affected by the way the different resources are defined. Like their approach, our method incorporates the resemblance between resources into the calculation of resource niche metrics. Unlike their approach, ours is more general, making it possible to estimate a large number of niche metrics, which we define either using existing indices, like Rao's (1982) diversity, or proposing new ones. In addition, our framework allows a graphical representation of the niche in the resource space. It also allows incorporating the variation in resource availability in the computation of resource metrics, for the cases where this is deemed necessary, and it may be implemented at different ecological levels (including individuals, populations, species and communities) and within different temporal and spatial scales (Bolnick et al 2003, Devictor et al. 2009). Finally, our framework makes it possible to estimate confidence intervals for resource niche metrics by using the bootstrap approach described in Mueller and Altenberg (1985), thus considering uncertainty in niche assessment.

An important aspect of our framework is the estimation of the degree of distinctness between resources to be incorporated in the niche metrics. Colwell and Futuyma (1971) argued that this distinctness should be assessed from the point of view of the species perception, by using the information on resource preferences. However, computing resource distinctness in terms of the species perception has an element of circularity because preferences are used twice, first to quantify the distinctness between resources and then to estimate the niche parameters based on resource distinctness. A way to circumscribe this problem is to quantify the distinctness between resources based on features of the resource categories that are ecologically meaningful and relevant for the purpose of the study. For example, in a food sources analysis of a gaminivorous bird, like the one we present later on to illustrate the method, it may be appropriate to consider the size and hardness of the seeds as these attributes are known to affect foraging performance (Herrel et al. 2009).

In the following section, we describe the details of the proposed framework, and describe the metrics we suggest to define the qualitative resource niche of organisms. We also explain the derivation of bootstrap confidence intervals for niche metric estimates. We then move to an example of application where we explore the trophic niche of feral pigeons *Columba livia*. We conclude by discussing the advantages and limitations of the suggested framework as well as the applications that we envision in the future. All the proposed methodological developments have been implemented in an R package called 'resniche', which is currently available from the first author's website (<<http://sites.google.com/site/miqueldecaceres/>>).

The method of resource niche analysis

Resource use, availability and preference

Although, for simplicity, the following description focuses on niche analyses at the species lever, the method can be applied to other ecological levels (see worked example). Resource niche analyses are based on observations of species resource use. Let s be the number of species and r be the number of

resources used by those species (e.g. food types, habitats or substrates). Resource use data is often in the form of an $s \times r$ table \mathbf{U} where each u_{ij} value is a quantitative assessment of how much species i is using resource j (Fig. 1A). If resources are habitat types, a given u_{ij} value will typically be an assessment of the number of individuals, cover or biomass of the target species in habitat j . If resources are diet types, u_{ij} values will be assessments of food consumption, such as prey numbers, volumes or masses (Griffiths 1986, Vitt and Pianka 2005). Now let \mathbf{P} be the $s \times r$ table obtained after dividing each value u_{ij} by the sum of values of the corresponding row. Each p_{ij} value is hence a proportion expressing the 'relative resource use' that species j makes of resource i .

Resource use is not the same as resource preference, especially if resource availability differs within the area of study (Hurlbert 1978, Lawlor 1980, Feinsinger et al. 1981, Smith 1982). If a particular resource is relatively scarce it may represent only a small proportion of use, even if the species has a high preference for that resource. Conversely, some resources for which the species preference is low may be frequently used simply because they are abundant. Although in most real communities the distinction between resource use and preference will be difficult to make, we think that resource niche metrics should be computed on the basis of estimates of the species' resource preferences. Whether or not species resource use values can be taken as representing species preferences is a question that should be tackled before computing niche metrics. Let \mathbf{p} be the relative resource use vector of a given target species (i.e. a row of matrix \mathbf{P}), and let \mathbf{q} be a vector of availability values for these same resources (i.e. q_i is the proportion of resource i available for use, Fig. 1B). When there is information on resource availability, species relative preference values can be calculated as:

$$f_j = \frac{p_j / q_j}{\sum_r p_j / q_j} \quad (1)$$

If the distributions of the target species resource use and that of resource availability are equal, then the species has equal preference for all resources (Fig. 2A). If, however, the target species uses resources in equal proportions but those are not equally available then the relative resource preferences are uneven (Fig. 2B). Finally, note that if resource availability data are not available or are not taken into account, the relative species preference vector \mathbf{f} is equal to the vector of relative resource use, that is $f_j = p_j$ for all resources.

The resource space

The key feature of our framework is the consideration of the geometric relationships between resources. These are described using an $r \times r$ distance matrix \mathbf{D} , where each element d_{jk} contains the distance between the pair of resources j and k (Fig. 1c). The d_{jk} values may be obtained from relevant attributes of the resources considered. For example, for a dietary analysis one could use features such as prey size, nutritional content or even palatability or toxicity. Although \mathbf{D} can be computed using any distance function, in order to facilitate the interpretation of some niche metrics we require that distance matrix \mathbf{D} be Euclidean (Gower and Legendre 1986) and the distance values be bounded between zero

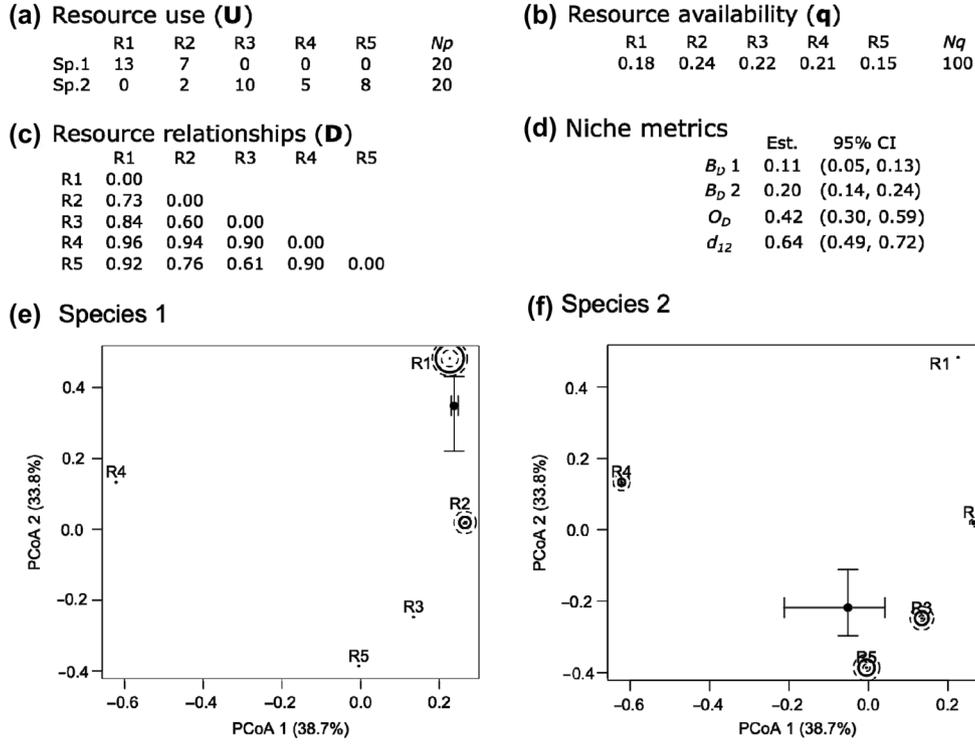


Figure 1. Example of the proposed framework for resource niche analysis. The table of observed resource use (a), the vector of resource availability (b) and the distance matrix among resources (c) are the input data of the method. Estimates for resource niche breadth, niche overlap and niche centre displacement, as well as the corresponding confidence intervals, are shown in (d). A principal coordinates analysis of matrix \mathbf{D} is used to display the resource space (e–f), where the species preferences are represented using circles whose sizes are proportional to the preference value. Dashed circles indicate the lower and upper values of the confidence interval for preference values. The niche centre can be displayed (black dots) along with the 95% confidence intervals in each resource dimension.

(when the two resources are completely equivalent) and one (when the two resources are completely distinct). For distance functions that do not produce Euclidean distance matrices (e.g. the Bray–Curtis and Gower distances), the \mathbf{D} matrix can usually be made Euclidean by taking the square root of the d_{jk} values (Legendre and Legendre 1998, Table 7.2). If similarity values are available, one can easily transform them into distances. An advantage of having the distance relationships between resources is that one can display resource niches in an ordination diagram. To this aim, we suggest conducting a principal coordinate analysis (PCoA, Gower 1966) from table \mathbf{D} . Using this procedure, we obtain a table \mathbf{X} with r rows (resources) and m principal coordinate axes (where m is between 1 and $r - 1$) that represents the resource relationships in an Euclidean space. We will refer to these axes as defining the ‘resource space’. The species resource preferences can then be displayed in the resource space by using symbol sizes proportional to the resource preference values (Fig. 1e–f).

Resource niche metrics

In our framework one uses the resource space (i.e. either matrix \mathbf{X} or, equivalently, matrix \mathbf{D}) in the computation of resource niche metrics. In what follows, we use vector \mathbf{f} as description of the resource preference of the target species. For niche metrics aimed at comparing two niche configurations (corresponding to either two distinct species or to one

species in two distinct situations), we will represent the two vectors of relative resource preferences by \mathbf{f}_1 and \mathbf{f}_2 .

Niche centre – The centre of the species niche in the resource space is computed by averaging the coordinates of the resources preferred by the species, that is

$$\bar{x}_l = \sum_{j=1}^r f_j x_{jl} \quad (2)$$

where x_{jl} is the position of the j th resource on the l th axis of the resource space. If the species equally prefers all resources (i.e., if $f_j = 1/r$) then the niche centre will be at the overall centre of \mathbf{X} .

Niche breadth – Early studies on niche analysis with qualitative resources measured the niche breadth with diversity measures, such as the Shannon–Wiener information index or the inverse of Simpson’s concentration (Levins 1968, Colwell and Futuyma 1971, Hanski 1978, Griffiths 1986). In order to assess niche breadth while taking into account the relationships among resources, we suggest using Rao’s quadratic entropy (Rao 1982), which is a general diversity measure that has been recently recommended to assess both functional and taxonomic diversity, and whose mathematical properties have been extensively studied (Shimatani 2001, Champely and Chessel 2002, Pavoine et al. 2005, Ricotta and Szeidl 2006, Ricotta and Marignani 2007). We chose the following notation for Rao’s entropy:

$$B_D = \frac{1}{2} \sum_{j=1}^r \sum_{k=1}^r f_j f_k d_{jk}^2 \quad (3)$$

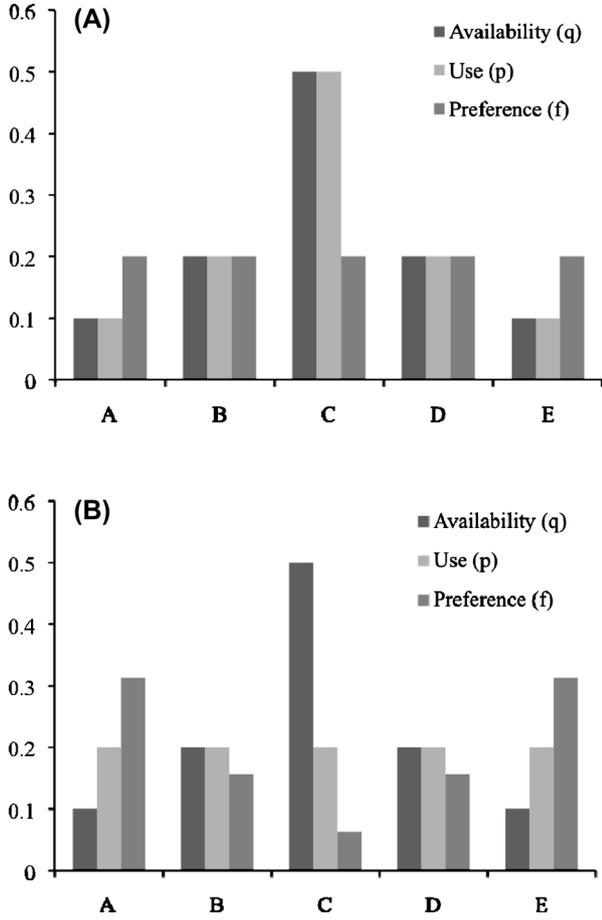


Figure 2. Two examples of how resource availability in the sampled area and target species resource use determine the species resource preference as calculated using Eq. 1.

Equation 3 has been referred to as the Euclidean diversity coefficient (Champely and Chessel 2002). We can see that B_D can be interpreted as ‘half the average squared distance among the resources preferred by the target species’. An advantage of using d^2 instead of d for Rao’s entropy is that in the former case it becomes equal to ‘the total variability among resources using the relative preference values as weights’:

$$B_D = \sum_{l=1}^m \left[\sum_{j=1}^r f_j (x_{jl} - \bar{x}_l)^2 \right] \quad (4)$$

Therefore, the same quantity can be obtained using table **X** instead of **D** (Champely and Chessel 2002). The minimum niche breadth is 0; this value is obtained when all resources used are equal or when a single resource is used. For completely distinct resources (i.e. when the $d_{jk}^2 = 1$ for $j \neq k$) B_D becomes the half the Gini–Simpson index (Shimatani 2001, Pavoine et al. 2005):

$$B_D = \frac{1}{2} \left(1 - \sum_{j=1}^r f_j^2 \right) \quad (5)$$

and the upper bound of B_D occurs for equal preference (i.e. $f = 1/r$). In general, however, the preference vector that yields a maximum value of B_D will vary depending on the resource distance values (Shimatani 2001).

Distance between niche centres – The distance between niche centres is a simple and intuitive measure to compare the niche of two species, or to assess temporal displacements of the centre for a single species. This distance can be calculated from either **X** or **D** (Cuadras et al. 1997, Champely and Chessel 2002):

$$d_{12}^2 = \|\bar{\mathbf{x}}_1 - \bar{\mathbf{x}}_2\|^2 \quad (6a),$$

$$d_{12}^2 = \sum_{j=1}^r \sum_{k=1}^r f_{1j} f_{2k} d_{jk}^2 - B_{D1} - B_{D2} \quad (6b)$$

Niche overlap – Resource niche overlap was defined in multiple ways in the past (Horn 1966, Schoener 1970, Colwell and Futuyma 1971, Pianka 1974, Sale 1974, Hurlbert 1978) and comparative studies exist (Ricklefs and Lau 1980, Linton et al. 1981, Mueller and Altenberg 1985). A measure that was frequently used was the cosine of the angle between the two vectors of relative resource preferences (Pianka 1974, Lawlor 1980, Rotenberry and Wiens 1980, Slobodchikoff and Schulz 1980):

$$O = \frac{\sum_{j=1}^r f_{1j} f_{2j}}{\sqrt{\sum_{j=1}^r f_{1j}^2 \sum_{j=1}^r f_{2j}^2}} \quad (7)$$

which is symmetrical and ranges from 0 (no overlap) and 1 (complete overlap). We suggest here generalizing Eq. 7 to take into account the resemblance between resources (Appendix A.1.1):

$$O_D = \frac{\sum_{j=1}^r \sum_{k=1}^r f_{1j} f_{2k} (1 - d_{jk}^2)}{\sqrt{\sum_{j=1}^r \sum_{k=1}^r f_{1j} f_{1k} (1 - d_{jk}^2) \sum_{j=1}^r \sum_{k=1}^r f_{2j} f_{2k} (1 - d_{jk}^2)}} \quad (8)$$

This index of overlap is also bounded between 0 (no overlap) to 1 (complete overlap). O_D will only yield zero overlap if the two vectors of preferences do not share any resource, and the resources preferred in one niche are completely distinct from the resources preferred in the other. This means that two species, one species preferring one resource only and the other preferring another resource, will still have some degree of niche overlap if the two resources have some similarity. When the two vectors of preferences are equal, the overlap is always one regardless of the resemblance between resources.

Statistical inference on resource niche metrics

Niche metric estimates should be reported along with an indication of variance or a confidence interval (Fig. 1D). Studies have been published that develop analytical approximations to the variance of resource metrics (Smith 1982, Mueller and Altenberg 1985) or generate confidence intervals for estimates on the basis of re-sampling methods (Ricklefs and Lau 1980, Mueller and Altenberg 1985). All resource niche metrics presented here can be easily incorporated in the bootstrap framework described by Mueller and

Altenberg (1985) and we will only briefly repeat it. An important point is that we consider the resource space (\mathbf{D} or \mathbf{X}) as fixed, whereas both the species resource use and resource availability are random variables. Assume we obtained the estimates of relative resource use $\hat{\mathbf{p}}$ from a sample of size N_p . If each of the N_p observations is independent and identifies the use of a single resource (e.g. the species was observed once hunting that prey or in that habitat), then bootstrap samples $\hat{\mathbf{p}}^*$ can be generated by using a multinomial distribution with sample size N_p and probability values taken from the sample estimates. However, if the target niche (for a population or a species) is described by directly measuring \mathbf{u} (or \mathbf{p}) on several individuals (e.g. for every individual we assessed the proportions of food types from his stomach content), then individuals are the units to be re-sampled with replacement. One pools the resource use vectors of re-sampled individuals in order to obtain $\hat{\mathbf{p}}^*$ for the bootstrap sample. Moreover, if relative resource availability estimates $\hat{\mathbf{q}}$ are available from a sample of size N_q , then bootstrap samples $\hat{\mathbf{q}}^*$ can also be generated using a multinomial distribution. Each pair $\hat{\mathbf{p}}^*$ and $\hat{\mathbf{q}}^*$ of bootstrap samples is then used to calculate the bootstrap estimate for the species preference vector $\hat{\mathbf{f}}^*$ (Eq. 1) and, assuming the resource relationships to be fixed, the bootstrap estimate for any resource niche metric. After generating many pairs of bootstrap samples one obtains a bootstrap distribution of the resource niche metric and calculates confidence intervals (Manly 1997).

Example: diet preferences in two populations of feral pigeons *Columba livia*

We provide here an example of resource niche analysis where the main goal is to quantify the differences in foraging niche breadth of feral pigeons based on diet preferences. We used information from an ongoing food preference experiment. In brief, we captured free-ranging feral pigeons in two localities (Moià and Barcelona) in Catalonia (northeastern Spain),

located 50 km apart. After capture, individuals were kept in outdoor aviaries for acclimatization during two weeks. Food consisted in a mixture of seeds containing the six food types later used in the experiments. After acclimatization, birds were placed in individual cages and habituated for two days. The food choice experiment started after 18 h of food deprivation, when individuals were offered a six-section circular plexiglas feeder containing 10 g of six different seed types (green peas, oats, popcorn maize, soybeans, sunflower seeds and wheat). Pigeons rarely consumed more than 10 g of seeds during an experiment, which ensured that food consumption closely reflects food preferences of individuals. Individuals were allowed to feed for 20 min, after which we removed the feeder and measured the remaining amount of each food type with a digital precision balance. The quantity of each seed type consumed by each individual was estimated by subtracting this quantity from the initial amount of 10 g. All animal care, husbandry and experimental procedures were in accordance with the Spanish code of practice for the care and use of animals for scientific purposes and were approved by the Generalitat de Catalunya (0152S, Dept de Medi Ambient i Habitatge).

We characterized the six seed types using descriptors of nutritional content (hydrocarbons, fats and proteins), as well as length and width (Table 1a). These variables were standardized in order to remove differences due to units of measurement and the transformed variables were used to calculate the Euclidean (i.e. Pythagorean) distance between pairs of seed types. We then divided the resulting distance matrix by its maximum value so as to obtain distances bounded between zero and one (Table 2). Popcorn, oats and wheat seeds were the most similar food types, solely differing in seed dimensions (Table 1a). In contrast, the maximum distance value was obtained between wheat and sunflower. Whereas wheat seeds are richer than sunflower seeds in carbohydrates content, the latter are richer in proteins and especially fat. Moreover, sunflower seeds are much longer than wheat seeds (Table 1a). We studied diet resource niche at two ecological levels: individual and population.

Table 1. Seed nutritional and size characteristics (a), seed consumption (b) and calculated preference (c) for individuals of the two Pigeon populations: Barcelona (23 individuals) and Moià (19 individuals).

(a) Seed characteristics	Oats	Peas	Popcorn	Soy	Sunflower	Wheat	
Proteins (g in 100 g)	17	25	9	40	21	11	
Carbohydrates (g in 100 g)	66	60	74	33	20	75	
Fat (g in 100 g)	7	1	5	22	51	2	
Length (mm)	8.079	7.471	8.084	5.132	10.328	5.966	
Width (mm)	0.969	6.889	3.803	3.762	2.018	3.099	
(b) Seed consumption (g)	Oats	Peas	Popcorn	Soy	Sunflower	Wheat	Total
Barcelona population	7.1	0.2	4.1	3.4	65.8	63.9	144.5
Moià population	0.2	2.3	11.5	5.7	6.9	100.4	127.0
(c) Seed preference (with 95% CI)	Oats	Peas	Popcorn	Soy	Sunflower	Wheat	
Barcelona population	4.9% (0.4, 13.8)	0.1% (0.0, 0.4)	2.8% (0.4, 5.9)	2.4% (0.1, 8.2)	45.5% (27.0, 28.5)	44.2% (28.5, 61.8)	
Moià population	0.2% (0.0, 0.6)	1.8% (0.0, 6.7)	9.1% (3.1, 16.4)	4.5% (0.1, 11.2)	5.4% (0.5, 17.3)	79.1% (65.6, 87.9)	

Table 2. Matrix of distances between seed types.

	Oats	Peas	Popcorn	Soy	Sunflower
Peas	0.703				
Popcorn	0.371	0.507			
Soy	0.774	0.665	0.864		
Sunflower	0.766	0.977	0.878	0.867	
Wheat	0.395	0.571	0.284	0.774	1.000

Diet niche at the individual level

We calculated niche centres (Eq. 2) and niche breadths (Eq. 3 or 4) for each individual. Unfortunately, we did not have replicates of the experiment at the individual level, which prevented us from calculating confidence intervals for the different niche statistics. Individuals of the Barcelona population most often ate wheat and sunflower seeds, with a lot of variability in the proportions. In contrast, individuals of the Moia population ate either only wheat or combined with small amounts of other seed types, but generally avoided sunflower seeds (Fig. 3). Consequently, foraging niche should be broader for Barcelona than Moia individuals. This difference was significant when taking into account differences among seeds (Wilcoxon rank test, $W = 328$, $p = 0.005$) but not if seeds were considered equally distinct ($W = 262$, $p = 0.2729$). This result can be explained by the fact that the maximum distance occurred between sunflower and wheat seeds. Since Barcelona individuals ate mostly these two seed types, their niche breadths were quite similar regardless of resource distinctiveness. The Moia pigeons that ate wheat and similar seeds, such as popcorn, had much narrower foraging niche when resource distinctiveness was considered.

Diet niche at the population level

We assessed seed consumption at the population level by summing up the food consumptions of individuals belonging to each population (Table 1b). In this case, we were able to calculate bootstrap confidence intervals for niche metrics. We first calculated bootstrap estimates of seed consumption for a given population by re-sampling its individuals with replacement and summing up the food consumptions of the individuals in the sample. Bootstrap estimates of niche statistics were then computed using these bootstrapped seed consumption values. The preference values at the population level indicated the same differences in preference as appeared at the individual level (Table 1c): while in the Barcelona population seed preference is divided between wheat (45.5%) and sunflower (44.2%), in the Moia population wheat seems to be the preferred diet source (79.1%). Consequently, the niche centre for the Barcelona population occurred midway between wheat and sunflower seeds, whereas that of Moia was very close to wheat (Fig. 3). Foraging niche was again broader for the Barcelona population than for the Moia population, and the difference appeared to be larger when resource distinctiveness was taken into account (Table 3). Finally, we found a substantial overlap (Eq. 8) between the two populations sustained by the fact that both populations had a remarkable preference for

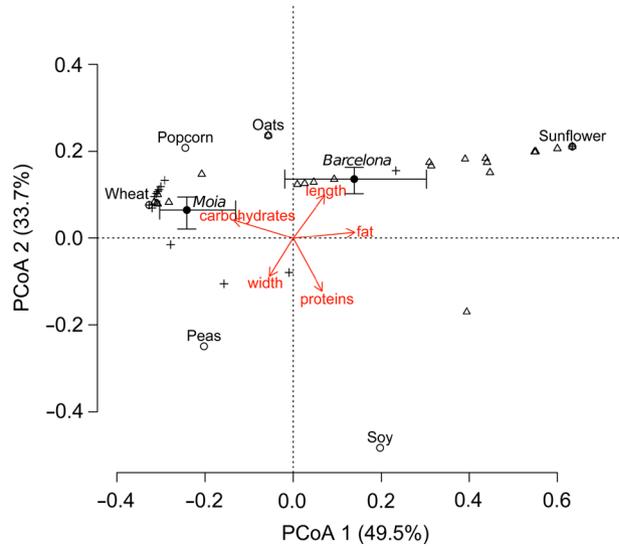


Figure 3. Resource space (i.e. principal coordinates analysis of matrix **D**) with arrows indicating the correlation between resource axes and original seed characteristics. Niche centres for the two Pigeon populations are displayed (black dots) along with the 95% confidence intervals in each resource dimension. Niche centres of individuals are also shown for Barcelona (triangles) and Moia (crosses) pigeons.

wheat seeds. For the benefit of interested readers, we include in Appendix A2 a small tutorial showing how the analyses of the feral pigeon data were conducted using R and the ‘resniche’ package.

Discussion

The niche concept is an important foundation for theories of ecological and evolutionary phenomena (Chase and Leibold 2003), but quantifying all dimensions of the niche is operationally impossible. The alternative is to measure one or a few dimensions of the realized niche that are particularly relevant for the question being asked (Devictor et al. 2009). The framework that we propose to quantify the species resource niche goes in that direction. Our framework of resource niche analysis resembles the one proposed by Colwell and Futuyama (1971) in that resources are not assumed to be equally distinct, but their degree of distinctiveness is incorporated in the estimation of niche metrics.

Table 3. Resource niche metrics (niche breadth and niche overlap) evaluated at the population level.

	Equal seed distances		Unequal seed distances	
	Niche breadth	95% CI	Niche breadth	95% CI
Barcelona population	0.297	(0.270, 0.337)	0.245	(0.232, 0.257)
Moia population	0.181	(0.102, 0.268)	0.085	(0.028, 0.177)
	Overlap	95% CI	Overlap	95% CI
Barcelona vs Moia	0.741	(0.436, 0.924)	0.791	(0.528, 0.938)

This has two main advantages. First, it allows researchers to obtain more accurate estimates of the resource niche of the species. The fact that some resources are more similar among them than when compared to others may lead to inaccurate estimates of the niche metrics if this unequal resemblance is ignored, entailing a loss of ecologically relevant information that may cause an underestimation of existing differences among the studied organisms. Our analysis of pigeons' diet illustrates well this problem. There were niche breadth differences between populations, but these differences would not have been detected if we had not taken into account the differences between resources. The second advantage of taking into account resource distinctiveness appears when the investigator him/herself has to define the niche categories. The advantage is that the niche metrics become less influenced by the way resources are defined by the researcher (Abrams 1980). That is, if the researcher defines two resource categories that are found to be equivalent, then the two categories will lie in the same position of the resource space and the resource metrics (centre, breadth, overlap and displacement) will not be affected (Appendix A1.2).

While our approach resembles in important aspects that proposed by Colwell and Futuyma (1971), it also shows notable differences, most of them already mentioned in the Introduction. The possibility of displaying the niche of species in the resource space is an important advantage of the framework presented here, because it helps address a number of ecological questions. For example, the resource space may be useful to track niche displacements in terms of both direction and intensity, a tool that may for instance be useful to study niche shifts during ontogeny or to describe how resource partitioning changes across seasons or environmental conditions (Bolnick et al. 2002, 2003). Regarding the resource space itself, we required above that \mathbf{D} should be a Euclidean distance matrix. If \mathbf{D} is non-Euclidean, negative eigenvalues will appear in the PCoA. In that case, one can still represent the real subspace of the relationships between resources in an ordination graph. The distance between niche centres can still be computed using the full resource space (Anderson 2006, Anderson et al. 2006), but negative niche displacements may occur. Incidentally, note that the resource niche can be complementarily studied using canonical ordinations, which allow one to relate the resource preferences of species to a set of explanatory factors. For example, Vitt and Pianka (2005) used canonical correspondence analysis to show the relationships between diet and phylogeny in squamate reptiles.

While our approach may have broad applications in ecology and evolution, it may prove particularly useful in those areas where the resemblance between resources is expected to influence the results. One of these areas is the study of resource niche partitioning and individual specialization (Bolnick et al. 2002, 2003). Given that different organisms may have morphological (Herrel et al. 2009), physiological and behavioural constrictions that limit their ability to exploit certain resources (Werner and Sherry 1986, Bolnick et al. 2003), not taking into account the resemblance between resources may cause an underestimation of the differences among the studied organisms. Our analysis of the dietary niche of feral pigeons illustrates this point well. Another area that can benefit from our approach is macroecology, where

it is common to compare species with very distinct ecological requirements and where the resemblances between resources are unlikely to be equivalent. As highlighted by Chase and Leibold (2003), current niche theory is often too narrowly focused on explaining species interactions at local scale, where population dynamics is the only process present. However, many fundamental ecological questions occur at larger scales, where colonization and extinction dynamics play a dominant role (Owens and Bennett 2000, Cassey et al. 2004). To conclude, if we want to fully understand the forces that shape the ecological niche of organisms and that affect almost all aspects of their lives, we need to start improving the accuracy and precision of the resource niche metrics. By extending the classical resource niche metric approaches, we hope that the proposed framework will help addressing a variety of questions concerning the ecological niche in novel and promising ways.

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Appendix A1

Mathematical proofs

A1.1 O_D equals O for maximally distinct resources

A demonstration can be found in Shimatani (2001) for the relationship between Rao's diversity coefficient and the Simpson index when species are equivalent in species diversity assessments. We include here a similar proof that applies to O_D in the current context. For maximally distinct resources, the matrix of resource distances \mathbf{D} is defined as:

$$d_{jk} = \begin{cases} 1 & \text{if } j \neq k \\ 0 & \text{if } j = k \end{cases} \quad (\text{A1})$$

In that case the sums of distances weighted by species preferences are:

$$\begin{aligned} \sum_{j=1}^r \sum_{k=1}^r f_j f_k d_{jk}^2 &= \sum_{j=1}^r f_j \sum_{k \neq j}^r f_k \\ &= \sum_{j=1}^r f_j (1 - f_j) = 1 - \sum_{j=1}^r f_j^2 \end{aligned} \quad (\text{A2})$$

$$\text{and } \sum_{j=1}^r \sum_{k=1}^r f_{1j} f_{2k} (1 - d_{jk}^2) = \sum_{j=1}^r f_{1j} f_{2j} \quad (\text{A3})$$

Using Eq. A2 and A3 is easy to see that O_D becomes:

$$O_D = \frac{\sum_{j=1}^r f_{1j} f_{2j}}{\sqrt{\sum_{j=1}^r f_{1j}^2 \times \sum_{j=1}^r f_{2j}^2}} \quad (\text{A4})$$

A1.2 Proof of invariance of B_D and O_D to the subdivision of resources

Say a given resource j is split into two resources j' and j'' . In that case the observed preference values should be additive:

$$f_{j'} + f_{j''} = f_j \quad (\text{A5})$$

If two resources are considered of equal characteristics, then they should lie in the same point of the resource space, and we should have for any resource k :

$$d_{j'k} = d_{j''k} = d_{jk} \quad (\text{A6})$$

Therefore, again for any resource k , we should have:

$$\begin{aligned} f_{j'} f_k d_{j'k}^2 + f_{j''} f_k d_{j''k}^2 &\stackrel{(\text{A.6})}{=} f_{j'} f_k d_{jk}^2 + f_{j''} f_k d_{jk}^2 \\ &= (f_{j'} + f_{j''}) f_k d_{jk}^2 \stackrel{(\text{A.5})}{=} f_j f_k d_{jk}^2 \end{aligned} \quad (\text{A7})$$

$$\text{and similarly } f_{1j'} f_{2k} (1 - d_{j'k}^2) + f_{1j''} f_{2k} (1 - d_{j''k}^2) \quad (\text{A8})$$

$$\stackrel{(\text{A.6})}{=} \dots \stackrel{(\text{A.5})}{=} f_{1j} f_{2k} (1 - d_{jk}^2)$$

We have shown that splitting a resource into two does not have any effect on the sums of distances weighted by species preferences.

Reference

Shimatani, K. 2001. On the measurement of species diversity incorporating species differences. - *Oikos* 93: 135–147.

Appendix A2

Using R and the 'resniche' package for the dietary analysis of feral pigeons

In this Appendix we give a few tips on how to use the "resniche" R package (ver. 1.3.0). As an example, we reproduce the calculations and plots carried out for the analysis of the dietary niche of the two feral pigeon populations (see main text). After installing the "resniche" package (it can be downloaded from <http://sites.google.com/site/miqueldecaceres/>), we start by loading it onto our workspace:

```
> library(resniche)
```

For our example, we also need three data items in our R console workspace: two 'dataframe' objects containing the seed consumption of each of the two pigeon populations – called `diet.barcelona` and `diet.moia` – and a 'dist' object containing the distance between resources – called `dfood`. Users will need to import their own data sets, but we provide the data for this example within the library. We load the three data sets using:

```
> data(pigeons)
```

Resource use data must be non-negative and columns represent resource types. With this information, we are prepared to start calculating niche metrics for individual pigeons and for whole populations.

A2.1 Dietary niche analysis at the individual level

The following lines yield individual niche breadths:

```
> nichevar(P = diet.barcelona)
> nichevar(P = diet.moia)
```

Since we do not specify any distance matrix for resource resemblance, the 'nichevar' function (and all the other functions for niche metrics) will assume equal resource resemblance. In order to provide this information, we need to add 'D = dfood' to our call:

```
> nichevar(P = diet.barcelona, D = dfood)
> nichevar(P = diet.moia, D = dfood)
```

Another niche feature we may want to calculate is the niche center of each individual in the resource space:

```
> centr.b <- nichecentroid(P = diet.barcelona, D = dfood)
```

```
> centr.m < -nichecentroid (P = diet.moia, D = dfood)
```

A2.2 Dietary niche analysis at the population level

In order to calculate niche metrics at the population level, we need to use `mode = "single"` when calling niche metric functions. This indicates that our niche analysis targets a single entity (e.g. a population or a species) from which several observations (i.e. rows of the resource use table) have been taken. Bootstrap confidence intervals are automatically produced in this mode. The following lines produce the niche breadth for the two populations, either including resource distances or not:

```
> nichevar (P = diet.barcelona, mode = "single")
> nichevar (P = diet.moia, mode = "single")
> nichevar (P = diet.barcelona, D = dfood, mode = "single")
> nichevar (P = diet.moia, D = dfood, mode = "single")
```

And the following two lines are used to calculate the overlap between the two pigeon populations, again with or without equal resource distances:

```
> nicheoverlap (P1 = diet.barcelona, P2 = diet.moia, mode = "single")
> nicheoverlap (P1 = diet.barcelona, P2 = diet.moia, mode = "single", D = dfood)
```

A2.3 Producing plots of the resource niche

In order to draw the qualitative resource niche, we first need to produce the axes of the resource space, which are obtained using the function `'cmdscale'` (called metric multidimensional scaling or principal coordinates analysis):

```
> cmd < -cmdscale (dfood, eig = TRUE, k = 5)
> eigp = 100 *cmd$eig/sum (cmd$eig)
```

We then start our plot by drawing the first two resource axes and the location of seed types within the resource space:

```
> plot (cmd$points[, c(1,2)], xlab = paste ("PCoA 1 (", format (eigp[1], digits = 3), "%)", sep = ""), ylab = paste ("PCoA 2 (", format (eigp[2], digits = 3), "%)", sep = ""), cex = 1, axes = FALSE, ylim = c(-0.5,0.5), xlim = c(-0.4,0.7))
> axis (1)
> axis (2)
> abline (h = 0, lty = 3)
> abline (v = 0, lty = 3)
```

We also add the name of the resources (seed types):

```
> text (cmd$points[,c(1,2)], labels = names (diet.barcelona), cex = 1, pos = 3, offset = 0.3)
```

After that, we may place the niche centroid of each individual that we calculated above. We used here different symbols for the two populations.

```
> points (centr.b, pch = 2, cex = 0.8)
> points (centr.m, pch = 3, cex = 0.8)
```

Finally, we can draw the niche centroid of the two populations, along with the 95% confidence interval. In this case we use the function `'plotniche'`, which facilitates the task for us:

```
> plotniche (P = diet.barcelona, D = dfood, mode = "single", add = TRUE, bubbles = FALSE, chull = FALSE, writeName = TRUE, species = "Barcelona")
> plotniche (P = diet.moia, D = dfood, mode = "single", add = TRUE, bubbles = FALSE, chull = FALSE, writeName = TRUE, species = "Moia")
```

The option `'add = TRUE'` specifies the niche centroid and confidence interval to be drawn in the current plot, instead of starting a new plot. We also have told the function not to draw convex hulls (these delimit the area of the niche) or bubbles (used to indicate the preference for each resource).