Species, Characters, and Fuzziness in Taxonomy

CATHY WILLERMET
Department of Sociology, Anthropology, and Social Work, Central Michigan University, Mount Pleasant, MI 48859, USA; wille2cm@cmich.edu

ABSTRACT

Recognizing fossil species, and reconstructing their phylogenetic relationships, is dependent in part on our ability to accurately record and analyze continuously distributed data. We usually classify specimens into groups (whether species or populations) by using crisp set theory. Fuzzy set theory can aid analysis in situations where populations have indistinct boundaries. Two primary areas of cladistic research contain elements of fuzziness—the species concept itself, and the variables we use to analyze phylogenetic relationships among species. Analytical determination of species boundaries can be difficult due to hybridization as well as intra- and inter-specific variability. However, cladistic analysis requires that taxa are monophyletic, and unique in their morphological patterns. Variables used in cladistic analysis must be coded using discrete character states to determine polarity. But many morphological and metric variables are continuous or quasicontinuous in distribution, and are problematic for use in cladistic analyses without some type of non-overlapping dichotomization or breakpoint. The issue of how to utilize these continuously or quasicontinuously distributed variables, whether metric or nonmetric, is an ongoing issue in phylogenetic analysis. Fuzzy set theory is a method that circumvents two problematic assumptions implicit in phylogenetic analyses—crispness of taxa and crispness of traits. Using a fuzzy analysis, multiple character states are maintained through fuzzy variable sets that maintain the fuzziness of boundaries. Additionally, fuzzy analysis calculates a measure of the degree of group membership.

To illustrate this process, I analyzed nine multistate nonmetric cranial variables representing three regions of the skull on 14 Neandertals and 24 early moderns using a Mamdani Fuzzy Inference System to compare the relative performance of fuzzy and crisp variables and groups on group identification. The analysis that performed best contained both fuzzy trait groups and fuzzy taxon groups. Fuzzy analysis is useful to explore the degree to which fuzziness is present in trait variation and in taxa, and it can advance our understanding of species identification and phylogeny construction. Expanding our toolkit to include fuzzy set analysis can help us determine how crisp or fuzzy are our putative taxonomic groups.

> "[T]he cult of impressive technicalities or the cult of precision may get the better of us, and interfere with our search for clarity, simplicity, and truth" (Popper 1983: 60).

> "The closer one looks at a real-world problem, the fuzzier becomes its solution" (Zadeh 1973: 28).

INTRODUCTION

There are many areas in paleoanthropology where precision eludes us. It is uncertain how many fossil species existed in the past; fossil sample sizes are small, and the magnitude and pattern of character variation within fossil species is unknown. It is unclear to what degree many characters are correlated, or are selectively neutral. Nonmetric characters may present as a continuous distribution, yet not be easily described without partitioning that variation into graded, often dichotomous, categories. Metric characters may be measurable, but measurements have numerous sources of uncertainty and their taxonomic significance can be unclear. Yet paleoanthopological research relies heavily on these data to recognize species in the fossil record, and to reconstruct phylogenetic relationships. How important is intraspecific variation? How does it affect our ability to recognize fossil species? How does it impact cladistic analyses?

This lack of clarity is frustrating. In most phylogenetic analyses, there is an underlying assumption that only one historically "correct" phylogeny exists, and that species are "real" biological entities in some ontological, objective, systematic sense. But the nature of species is not as ontologically precise as we would wish. Species are sometimes organized into discrete, and sometimes semi-discrete, entities as an ordinary part of nature (Eldredge 1993; Jolly 1993). While synchronic species may be (more-or-less) discrete, it is sometimes difficult to determine whether a phenotypically distinct group should be identified as a subspecies or a separate species in its own right.

When constructing a scientific model, or describing a system, we strive to represent particular aspects of reality in some nonarbitrary way that allows prediction of behaviors or group membership (Popper 1959). We know that complex ecological, biological, and social systems interact in ways that can affect the evolution of species. Two major complications arise when we model real world systems in

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this way (Zimmerman 1996: 3):

1. Real situations are very often not crisp and deterministic, and they cannot be described precisely; and,
2. The complete description of a real system often requires far more detailed data than a human being could ever recognize, process, and understand simultaneously.

These complications can impact how we describe species in space and time, and make fuzzy distinctions between species artificially crisp. Are species ontologically fuzzy? Epistemologically fuzzy? Both? If species are fuzzy on both levels, this makes phylogenetic analysis problematic.

To examine these questions, we must think about how we organize specimens in our analyses. Fuzzy set theory may provide a way to deal with these complications; it is an alternative approach to classifying that accommodates imprecise or overlapping boundaries between groups. In this paper, I will first compare classic set theory and fuzzy set theory. I will then examine how fuzzy set theory can inform our thinking about the species concept and phylogenetic analyses.

WHAT ARE SETS?

We classify specimens into groups (whether species or populations) by using set theory. Traditionally, we model groups mathematically by using classic, or crisp, set theory. Crisp sets are collections of definite, distinguishable elements (or specimens) that could be conceptualized as forming a group. Any definition of a set defines its complement, which contains all specimens that are not members of the set. If two sets, *A* and *B*, share some common specimens, we use terms such as 'union' (the set of all specimens which are in *A* or in *B*) and 'intersection' (the set of all specimens which are both in *A* and in *B*). A subset is defined as a set whose specimens are all members of a second, larger set (Nanzetta and Strecker 1971; Zehna and Johnson 1962). Crisp set membership is either 1 or 0, meaning that a specimen is either in the set (1) or not (0). This is the way most of us normally classify things in our analyses, and most statistical methods have the concept of crisp sets as their foundation. Thinking about sets in this manner is adequate for many situations, including phylogenetic systematics involving unambiguously monophyletic groups.

However, when there is a significant amount of continuous variability, or questions about boundaries between categories, crisp set methodologies fall short. Interpretations of fossil specimens that fall in the intersection between two sets, for example, can be problematic (Willermet 2001; Willermet and Hill 1997). Using crisp sets, groups are required to be exhaustive and mutually exclusive (Bailey 1994). Researchers desiring to create crisp sets of specimens, using continuously or quasicontinuously distributed variables, must place specimens uniquely into sets by partitioning the continuous variation into predefined categories. These categories force precise character states for group inclusion. Organizing data into nominal or ordinal scales does this. Ordinal or ranked scales partition the "presence" category to include more degrees of expression of a trait. These categories might conform to some "natural" break in the distribution of data or draw upon previous knowledge about the data being collected. Researchers prefer dichotomous data (such as presence/absence) when they find it difficult to reliably score degrees of expression of a trait, or when choosing to score a trait as "present" at any discernable level of expression. Discriminant function analysis can often perform a similar role when using metric data to place individual specimens into groups.

The concept of fuzzy sets originates from the observation that objects, or groups of objects, are not always describable using crisp, discrete attributes. Fuzzy set theory applies to classes of objects where the classes have indistinct boundaries, and membership in the class is a matter of degree (Zadeh 1965). "Fuzzy" does not mean "muddled" or "unclear." It is a strict mathematical framework in which to study fuzzy conceptual phenomena (Zimmerman 1996). Often classes of objects do not have precisely defined criteria for group membership (Zadeh 1965). While it is assumed that a pattern of features belongs to only one class, this is often not true or realistic, particularly not mathematically (Bezdek and Pal 1992), but possibly also not biologically. When this assumption is violated, but the data are treated as though they are crisp, the analysis can lead to incorrect interpretations. If the crisp analysis is testing whether two closely related groups are one species or two, such as Neandertals and modern humans, then this assumption can bias the result. Fuzzy sets are therefore useful for classification problems in which the source of the imprecision is the absence of sharply defined definitional criteria for group membership (Zadeh 1965).

A fuzzy set *A* is defined as a set whose members each possess a membership function; the function $f_A(x)$ assigns to each member a number between 0 and 1 representing the degree of membership of that element in the set. A specimen, then, may belong to many sets to a degree, as represented by the membership function. The closer the membership function is to 1, the higher the grade of membership of that specimen in the set. The complement of a fuzzy set *A'* is simply $f_{A'}(x)=1 - f_A(x)$. The union of two fuzzy sets *A* and *B* is the smallest fuzzy set (minimum) containing both *A* and *B*. The intersection of two fuzzy sets is the largest fuzzy set (maximum) that is contained in both *A* and *B*.

Membership functions come from the same sources as probability density functions—from theory or data (Civanlar and Trussell 1986; Li and Yen 1995; Linden and Bhaya 2009; Novák 1989). They are a measure of how similar the object is to other objects in the set for a given set of variables (Bezdek and Pal 1992). Sets are characterized as more fuzzy if the membership values lie near the middle of the distribution between 0 and 1, and less fuzzy (crisper) if the values lie close to 0 or 1 (Smithson 1987). Crisp sets are, then, a special case of fuzzy sets, and are easily accommodated. The crossover point between sets (0.5) is the point of maximum ambiguity of group membership. Using fuzzy sets, we can assess how distinct two sets of specimens are. Thus, it may be easier to characterize hybrid populations

or samples for which the boundaries between two sets are not clear.

Fuzzy sets are useful when modeling complex systems. As the complexity of a system increases, the ability to make precise and yet significant statements about its behavior decreases (Zadeh 1984). This problem is pervasive throughout science; a complex event such as speciation is an excellent example of such a system. Fuzzy logic allows for a continuum of set membership, which reflects the biological reality of a continuum of gene expression present in many variables (Sokhansanj et al. 2009).

ARE SPECIES ONTOLOGICALLY FUZZY?

One of the assumptions of science is that the universe is real, objective, and knowable. In the past, animals were born, lived, had offspring, and died; their offspring lived or did not. Populations expanded, split, rejoined, and went extinct. That these things did in fact happen, and continue to happen, is not at issue. But can we group these living and past populations into real, crisply-bounded species?

The species concept is inherently fuzzy (Van Valen 1988). Darwin himself called the species concept "arbitrary" and "indefinable" (Ereshefsky 2011). Species can grade into each other through space (Jolly 1993; Jolly et al. 1995). As one moves further back in time from the present, the boundaries between species become less clear and more subjective (Bock 1986). Species that hybridize and produce offspring with reduced fitness (ranging anywhere from nearly 1 to nearly 0) can be seen as conspecific, separate species, or something in between (Holliday 2003).

While there may be objectively real biological entities called species, in many cases we are limited by our ability to directly observe them. The individual organism (or group of organisms) is relatively easy to observe; an abstract collective such as "species" is not (Hull 1970; Jolly 1993; Van Valen 1988). Linnaean categories are ranked; for example, definitions of the taxon names of species, genera, and families require a rank and a type (International Commission on Zoological Nomenclature 1999). In fact, Laurin (2010: 132) comments, "…ranking taxa into Linnaean categories is almost universally recognized as a fairly subjective exercise among taxonomists." Species are generally regarded as the lowest level and least inclusive taxonomic rank, vital for understanding variation, adaptation, and evolutionary lineages. Since species is such an important concept, it is necessary to define it in such a way as to apply to both contemporary and fossil species.

There are several strategies for defining species—the biological species concept (Dobzhansky 1937; Mayr 1942, 2000); the ecological species concept (Van Valen 1976); the evolutionary species concept (Simpson 1961; Wiley 1981); the phylogenetic species concept (Cracraft 1983, Kimbel and Rak 1993); the cohesion species concept (Templeton 1989); and many, many more (Hey 2001). Since directly observable data on behavior or soft tissue anatomy generally do not preserve in fossil material, paleontologists often utilize the phylogenetic species concept (although this practice has been sharply criticized, e.g., Hennig [1965]; Shea et al. [1993]; Szalay [1993]). Multiple lines of evidence are used to recognize species in the fossil record—morphological autapomorphies; analogies derived from ranges of variation seen in modern species; geographic range; ecology; and temporal period (Habgood 1989; Harrison 1993). Overlap in one or more of these evidentiary areas in closely related taxa tends to fuzzify the boundaries between them.

Jolly (1993) suggests that species can be defined such that two independent observers arrive at the same conclusions about its parameters, but only if there is advanced agreement on boundaries delineating the edges of the class (Jolly 1993: 69):

> "Although we can treat species as real, we must recognize that each of the… current species concepts depends upon criteria (reproductive isolation, homologous morphological distinctiveness, and mate recognition…) that in nature are continuously distributed and multifactorially determined. Such data can easily be expressed as a list of entities called species, and all taxonomists should agree on the number and limits of these, as long as they also agree upon the diagnostic cut-off point on the appropriate continuum: how absolutely isolated, how distinctive, how similar in the mate-recognition system, do two populations have to be, to be called different species?"

If one is dealing with populations that are "continuously distributed and multifactorially determined," then one can lose vital information about population variability by drawing arbitrary and crisp boundaries between them.

The problem of identifying boundaries within a continuum is crucial in efforts to model phylogenetic relationships. Creation and maintenance of species boundaries is at the heart of speciation models (Dobzhansky 1937; Mayr 1942). We do not yet understand the complex relationships between genetic changes, skeletal anatomy, fitness, reproductive isolation, reticulate evolution, and time needed to develop reproductive barriers, whether genetic, behavioral, or both (Arnold 2009; Arnold and Larson 2004; Curnoe and Thorne 2003; Holliday 2003; Howard 1998; Jolly 2009). This is particularly true of closely related, recently divergent species. Harris and Disotell (1998) report that intergeneric hybridization amongst papionins can create introgression of nuclear alleles or mtDNA haplotypes, creating misleading sister taxon relationships, a result echoed by Jolly (2001). Reticulate evolution has been posited for many hominin fossil species, making cladistic analyses problematic (Arnold 2009, and references therein; Holliday 2003; Jolly 2001).

If two species are very closely related, sharing a recent common ancestor, they will hold many traits in common. Even when a cladistic autapomorphy is identified for one of these species, there may be variable expression of the character, or it may not appear in all members of the group. In modern human origins research, it is clear that Neandertals and modern humans are very close to one another genetically and behaviorally. The similarities between them are more than expected of most other groups of hominids—they could be two populations within a highly variable spe-

cies (e.g., Wolpoff et al. 2001), or two subspecies (Wolpoff 2009), or two species that share a very recent common ancestor (e.g., Rak et al. 2002). The recent work on sequencing the Neandertal genome (Green et al. 2010) documents some Neandertal-modern human gene flow, yet researchers cannot agree on whether (or where) to draw the species boundaries (Gibbons 2011). A critical implication of the Neandertal genome is that the boundary between Neandertals and modern humans is fuzzy.

ARE SPECIES EPISTEOMOLOGICALLY FUZZY?

Whether one might ontologically *define* species as fuzzy or crisp, it may not be possible to *model* species as crisp. And if species are in fact ontologically fuzzy, then the use of analytical methods that assume they are crisp can lead to a false sense of precision. Examples of fuzziness can appear at the variable, individual, population, species, and lineage levels, making boundary determinations difficult. How do we deal with fuzziness in our data? How do we reconstruct phylogenetic relationships with these data?

Cladistics has become increasingly popular in paleoanthropology as a method to test competing phylogenetic hypotheses of hominin origins (Argue et al. 2009; Bjarnason et al. 2011; Hammer and Zegura 2002; Lieberman et al. 1996; Strait 2001; Stringer et al. 1997; Wood and Collard 1999). Cladistic classification requires that all taxa be crisp sets, monophyletic and mutually exclusive in their morphological patterns (Eldredge and Cracraft 1980; Hennig 1966; Mayr 1981; Olsen 1978; Wiley 1981). The characters used to compare taxa are features identifiable on the skeleton either as qualitative features or quantitative measurements/ratios (Lockwood and Fleagle 1999). Cladists trace evolutionary relationships between taxa through the identification and comparison of synapomorphies, avoiding character similarity due to sympleisomorphy or homoplasy (Delson et al. 1977; Forey et al. 1992; Grande and Rieppel 1994; Hennig 1966; Quicke 1993).

Cladists argue that a cladistic methodology provides a meaningful, testable, rigorous, and precise method for reconstructing phylogenetic relationships among taxa. However, two problematic assumptions underlie cladistic phylogenetic analyses: 1) species are crisp; and, 2) traits are crisp. These assumptions are explored below.

ASSUMPTION 1: SPECIES SHOULD BE MODELED AS CRISP SETS

The validity of cladistic analyses can vary with taxonomic level; some contend that cladistic analyses are more robust at higher taxonomic levels than at lower levels such as genus and species (e.g., Wiley 1981). Many researchers use the results of cladistic analyses to justify species-level distinctions between groups (González-José et al. 2008; Groves 1991; Halter 2001; Lieberman 1995; Rak 1998; Wiley 1981) and even subspecies or population distinctions (Hammer and Zegura 2002; Haneji et al. 2007; Rosenblum et al. 1997).

Considerable criticism has been leveled regarding the appropriateness of using the cladistic approach to phylogenetic analysis at the species level (Harrison 1993; Trinkaus 1995; Wolpoff and Crummett 1995). For example, it is difficult to determine, in closely related taxa, whether shared characters are due to homology or homoplasy (Lockwood and Fleagle 1999; Wood 1999), or to what degree apomorphies are affected by sample size or inter- or intrapopulation variation (Hawks 2004). A more problematic issue when using cladistic analyses in modern human origins research is that groups must be separated *a priori* into discrete taxa as a requirement of the methodology. Autapomorphies are often used to uniquely define new taxa (Hammer and Zegura 2002; Rak et al. 2002; Tattersall and Schwartz 2008), although species are not diagnosable in terms of autapomorphies alone (Nelson and Platnick 1981). A cladistic approach therefore *cannot* be used to examine the question of whether two populations are distinct at the species level; as species groupings are created as a prerequisite to cladistic analysis, the anaylsis is circular and the answer will always be "yes" (Clark 2001; Hennig 1966). Harris and Disotell (1998) argue that choosing between competing phylogenies is very difficult when there is a short divergence time between species.

ASSUMPTION 2: CONTINUOUS TRAITS SHOULD BE PARSED INTO CRISP CATEGORIES

Most cladists argue that characters considered autapomorphic for phylogenetic analyses cannot vary within a species (Masters and Brothers 2002; Wiley 1981; Wolpoff et al. 2004). This implies, then, that any character used must be discrete and fixed in the population. Characters are typically coded into discrete categories (or states) for determination of polarity (primitive or derived) as compared to an outgroup. One major problem affecting the determination of character polarity is that many characters of interest are continuous or quasicontinuous in their expression across populations and/or taxa. This is a hurdle for cladistics, which requires discrete polarity states for all variables used in the analysis (Farris et al. 1970; González-José et al 2008).

Continuously distributed characters, metric or nonmetric, routinely present intraspecific variation (Rae 1998). Some cladists object to the use of continuous characters in phylogenetic analyses either on principle or on method (MacLeod and Forey 2002; Rae 1998). Some, for instance, question the cladistic significance of mathematical concepts such as a mean or ratio (Pimentel and Riggins 1987). Others object to perceived arbitrariness of the determination of discrete character states. Quicke states (1993: 13):

> "Continuously variable characters may be employed for cladistic analysis but then they need to be subdivided into two or more non-overlapping ranges (discrete character states). Unfortunately, very little is known about what is the best way to convert continuously variable characters into discrete ones despite the frequency with which taxonomists need to do this. Consequently it is a source of considerable disagreement and there may in fact be no one best way of coding continuously variable data."

González-José and colleagues (2008) point out that creating discrete data from continuously distributed data can be done explicitly or implicitly. Examples of techniques to code quantitative continuous data explicitly into discrete states include gap-coding (Archie 1985; Bjarnason 2011), segment-coding (Chappill 1989), finite-mixture coding (Strait et al. 1996), quantitative statistical methods (Felsenstein 2002; Rae 1988); and a step-matrix approach (Wiens 2001). An example of a more implicit model is the Arizona State University Dental Anthropology System. This system was created to standardize dental morphological traits, coded as ordinal categories based on degree of expression of characters, with breakpoints defined to provide subsequent dichotomization of data for statistical analysis, if desired (Scott and Turner 1997; Turner et al. 1991). Many other craniodental nonmetrics also have been used in phylogenetic analyses (e.g., Matthews and Rosenberger 2008).

Habgood (1989) argued that a cladistic approach that does not allow for morphological variation would take too narrow a view of evolutionary relationships. In fact, dichotomizing continuous or quasicontinuous variation results in a loss of information (González-José et al. 2008; Hawks 2004; Willermet 2001). Pleijel (1995) identified four distinct methods for coding data using dichotomous or multistate methods, each with distinct advantages and disadvantages, and with implications for the resulting cladistic analysis. Strait et al. (1997) analyzed the effect of utilizing variable characters as data on cladistic analysis. If a species expressed variation in a particular character, they coded it as "intermediate," "present" (if a majority of specimens exhibited it), or as "missing data." They found that utilizing intermediate character states resulted in more parsimonious trees. In fact, reticulate patterns caused by genetic introgression are often identified by presentation of intermediate character states (Wanntorp 1983). Removal of these intermediate states during data collection or analysis can mask evidence of reticulate patterns.

The decision must be made by the researcher, then, as to whether to remove from the analysis all variables that vary continuously or to partition the variability. If variability is partitioned, one must consider how and why it should be done. The most common approach is to dichotomize data into two discrete categories, usually presence/absence using a threshold point or breakpoint. All the grades above the breakpoint are collapsed into "present" and those below into "absent." This makes certain analyses such as biodistance possible, as traits can be transformed into frequency data to compare populations (Khamis et al. 2006, Irish and Konigsberg 2007). However, the richness of the multiple character state data is not analyzed.

THE FUZZY INFERENCE SYSTEM

The fuzzy inference system (FIS) is alternative way of coding and analyzing multiple character state data. The central idea behind an FIS is to map an analysis from input to output using fuzzy logic. There are different types of inference systems; the most commonly used is Mamdani (Kruse et al. 1994; Rutkowska 2002). The FIS approach has been used in many scientific disciplines for data analysis and classification, and software toolboxes are now available through MathWorks (The MathWorks 2011) and Mathematica (Wolfram Research 2010). The FIS combines membership functions, fuzzy logic operators, and *if-then* rules of set membership.

The Mamdani-type FIS has five basic steps:

1. "Fuzzify" the input variables. The data are converted to a degree of membership based on predefined fuzzy membership functions. Membership functions can be inferred through examination of data, inductive reasoning, rank ordering, and/or prior knowledge.
2. Apply a fuzzy operator to link the rules (*if* statements). Decision rules are created, and fuzzy operators are applied that link the fuzzy variables together, such as AND or OR.
3. Apply the implication method (*then* statements). The variables can be weighted equally or otherwise. The rules are evaluated in parallel.
4. Aggregate all outputs. The output is a degree of membership in each fuzzy set.
5. "Defuzzify" the output (optional). The resultant fuzzy set is translated into a crisp output value.

This FIS provides a method for linking several traits together to get one output that is influenced by several variables, like integrating features for phylogenetic complexes. By putting multistate character data through the FIS, nuances of degree of expression should be retained, providing finer-grained analysis of relationships between populations. This method avoids two problematic assumptions implicit in phylogenetic analyses—crispness of taxa and crispness of traits. Continuous traits can be divided into fuzzy categories, and populations compared. Defuzzified results could also be used to define "discrete" character polarity, and help us better identify breakpoints between character states.

METHODS AND MATERIALS

To illustrate this process, I analyzed nine multistate nonmetric cranial variables representing three regions of the skull on 14 Neandertals and 24 early moderns (Tables 1 and 2) using a Mamdani FIS in order to compare the relative performance of fuzzy and crisp variables and groups on group identification (Willermet 2011). Nonmetric variables were limited to those having three or more character states; variable definitions and data collection procedures followed the coding described in Lahr (1996).

I collected nonmetric data over a five-week period on original specimens and casts from the British Museum of Natural History, Tel Aviv University, the Rockefeller Museum, and the Institute of Human Origins, as part of a larger study. I performed an intraobserver error test of nonmetric data collection on a subset of 10 casts at Arizona State University over the course of three weeks prior to formal data collection. I calculated intraobserver error by comparing the three trial means, by variable, using ANOVA through SPSS 17.0.0 (SPSS 2008); the results were not significant

TABLE 1. SPECIMENS USED IN THE ANALYSIS.

Neandertals	Moderns	
Amud 1	Cro Magnon 1	Předmostí 4
Gibraltar 1	Dolní Věstonice 3	Předmostí 814
Krapina C	Fish Hoek	Qafzeh 6
La Chapelle	Gamble's Cave 4	Qafzeh 9
La Ferrassie	Gough's Cave 1	Singa
La Quina 5	Hotu 2	Skhūl 4
Monte Circeo	Iwo Eleru	Skhūl 5
Saccopastore	Jebel Irhoud 1	Skhūl 9
Shanidar 1	Jebel Irhoud 2	Wadjak 1
Shanidar 5	Kanjera	Zhoukoudian 101
Spy 1	Liujiang	Zhoukoudian 102
Spy 2	Ohalo 2	Zhoukoudian 103
Tabūn C1		
Zuttiyeh		

($p \geq 0.875$ to $p = 1.00$).

If, for these variables, the character states are discrete for Neandertals and early moderns, then the analysis should reflect low levels of fuzziness. If these two groups are best modeled as crisp taxa, then the analysis should also reflect this. In short, Neandertals and moderns should be distinctly different. If there is a great deal of intraspecific variation, and both groups share many of these character states in common, then the analysis should reflect a higher degree of fuzziness.

I performed a Mamdani analysis using the MATLAB R2011b Fuzzy Logic Toolbox software platform (The MathWorks 2011). Mamdani-type fuzzy inference rules provide contextual information for the variables. These rules use linguistic variables to assign statements using antecedents and consequents (IF—THEN). I delimited antecedent-consequent relationships based on a reading of Lahr's trait descriptions (1996), published accounts (Ahern 2006; Manzi et al. 2000; Weaver 2009), and personal observation as to what was considered a Neandertal or modern feature. Fuzzy inference rules can use these rules in aggregate to calculate membership into "Neandertal" and "Modern" sets.

For example, the variable "canine fossa" has three possible states—CF1 (absent) through CF3 (pronounced). Generally, the presence of a canine fossa, particularly a pronounced one, is considered a modern, not a Neandertal, trait. One could write the following linguistic variables for analysis of the canine fossa in the sample:

IF canine fossa is CF1 THEN group is Neandertal;

IF canine fossa is CF2 THEN group is Modern;

IF canine fossa is CF3 THEN group is Modern.

This would essentially define a breakpoint between CF1 and CF2 for this trait. If only one trait is used, then a crisp analysis would sort specimens crisply into two groups based on the specimen's canine fossa bivalent character state (absent/present). Since we know, however, that the canine fossa actually presents a continuous or quasi-continuous degree of expression, the above analysis is unsatisfactory. A fuzzy approach would "soften" the boundary at the breakpoint.

To illustrate the differences between a fuzzy analysis and a crisp one, I analyzed the sample dataset four ways: 1) both the variables and the groups are modeled as crisp; 2) the variables are modeled as fuzzy but the groups are modeled as crisp; 3) the variables are modeled as crisp but the groups are modeled as fuzzy; and, 4) both the variables and the groups are modeled as fuzzy. For all four analyses, the FIS rules are as follows:

IF infraglabellar notch = small THEN group = Modern;

IF infraglabellar notch = large THEN group = Neandertal;

IF orbits = sharp THEN group = Modern;

IF orbits = rounded THEN group = Neandertal;

IF supraorbital ridges = small THEN group = Modern;

IF supraorbital ridges = large THEN group = Neandertal;

IF zygomaxillary tuberosity = absent THEN group = Neandertal;

IF zygomaxillary tuberosity = present THEN group = Modern;

IF canine fossa = absent THEN group = Neandertal;

TABLE 2. VARIABLES USED IN THE ANALYSIS, INCLUDING CHARACTER STATES AND THEIR DESCRIPTIONS (adapted from Lahr [1996]).

Upper Face Region

Profile of the infraglabellar notch	IN1	Non-projecting glabella and flat nasion; both landmarks on approximately the same level
	IN2	Slightly or non-projecting glabella, but angled nasals, forming a slight curve in profile
	IN3	Prominent glabella and relatively deep and wide nasion angle
	IN4	Very prominent glabella, with very deep and narrow nasion angle
Rounding of the inferolateral margin of the orbits	RO1	Sharp, high line dividing the floor of the orbit from the facial portion of the malar
	RO2	Relatively rounded orbital margin, but raised in relation to the floor of orbit
	RO3	Pronounced rounding of the inferior lateral border, which is leveled with the floor of the orbit
Supraorbital ridges/torus	ST1	Flat or very slightly projecting superciliary ridges and glabella
	ST2	Superciliary ridges well-defined as two distinct units, separated medially by a flat glabella
	ST3	Superciliary ridges ranging from visible to well-developed, prolonged medially to form a prominent glabella
	ST4	Superciliary ridges very pronounced, joined medially by a very pronounced and projecting glabella, clearly separated from the rest of the frontal bone
	ST5	Continuous ridge formation composed of the three superciliary elements, although the superciliary ridges and lateral trigone can still be identified, but not separated, as different elements

Midface Region

Zygomaxillary (malar) tuberosity	ZT1	The surface of the malar bone is smooth and flat
	ZT2	Presence of a tubercle of small dimensions
	ZT3	Tubercle present, more pronounced and horizontally extended
	ZT4	Very large tubercle, forming a ridge along the surface of the malar, parallel to the lower free margin of the bone
Canine fossa	CF1	Absent
	CF2	Moderate
	CF3	Pronounced

TABLE 2. (continued).

Midface Region (cont.)

Zygomatic trigone	TR1	Completely smooth trigone, or very slightly salient, if at all; generally very thin
	TR2	Formation of a raised surface just adjacent to the fronto-malar suture, and extending anteriorly or posteriorly along the orbital margin or the temporal line, for up to 5mm
	TR3	The whole area of the trigone is inflated and widened, but retains a smooth surface
	TR4	Pronounced development of the trigone area, very salient, with or without a rugged surface; the frontal region adjacent to the zygomatico-malar suture may be considerably larger than its relative malar portion

Occipital Region

Occipital crest	OCR1	The occipital crest is only visible as a line or very slightly raised surface
	OCR2	Either the superior or the inferior occipital crest visible as a sagittal ridge
	OCR3	Clearly raised ridge or crest along the whole course between the tuberculum linearum and the foramen magnum
Occipital torus	OT1	Supreme nuchal lines not visible
	OT2	All that is visible of supreme nuchal lines is the external occipital protuberance
	OT3	Supreme nuchal lines visible, separated medially from the superior nuchal lines, i.e. the external occipital protuberance and tuberculum linearum are separate
	OT4	Supreme and superior nuchal lines visible and joined medially by the external occipital protuberance
	OT5	Same configuration as Grade 4, but superimposed on a torus, forming a 'Supranuchal Tubercle' of Hasebe
	OT6	Occipital torus, with a supratoral sulcus visible, but with a medial 'indent' caused by the presence of an external occipital protuberance along the superior toral margin
	OT7	Occipital torus present, with no visible external occipital protuberance
External occipital protuberance	EOP1	Absent
	EOP2	Slight
	EOP3	Medium
	EOP4	Marked

IF canine fossa = present THEN group = Modern;

IF zygomatic trigone = small THEN group = Modern;

IF zygomatic trigone = large THEN group = Neandertal;

IF occipital crest = small THEN group = Neandertal;

IF occipital crest = large THEN group = Modern;

IF occipital torus = not visible THEN group = Neandertal;

IF occipital torus = visible THEN group = Modern;

IF external occipital protuberance = absent THEN group = Neandertal;

IF external occipital protuberance = present THEN group = Modern.

In all cases, the FIS rules above were aggregated and equally weighted. The output provided membership identification in the sets of Neandertal and of Modern.

ANALYSIS 1: BOTH VARIABLES AND GROUP MEMBERSHIP ARE CRISP

In this analysis, the variables were converted into two crisp sets. Using breakpoints, variable states were collapsed into two states, usually describable as absence/presence or small/large (Table 3 and Figure 1). Breakpoints were identified through personal observation and published reports on Neandertal and modern human nonmetric characteristics (Ahern 2006; Manzi et al. 2000; Weaver 2009). Each variable was treated as crisply determining group membership. The analysis classified specimens crisply, as either Neandertals or moderns (Figure 2); results would indicate correct or incorrect classification, as compared to prior knowledge (see Table 1). As crisp sets are a special case of fuzzy sets, crisp analysis can also be performed using the Fuzzy Logic Toolbox software platform.

ANALYSIS 2: VARIABLES ARE FUZZY, BUT GROUP MEMBERSHIP IS CRISP

In this analysis, I defined fuzzy membership functions for each variable from their graded categories—for each variable, a fuzzy set was created for each character state. The underlying distribution for each multistate variable was assumed to be either continuous or quasi-continuous. For example, the variable "canine fossa," has three predefined recordable states ("absent," "moderate," and "pronounced"). An observer needs to choose one of these three character states for data collection. If the canine fossa is not present, the observer will choose "absent," if there is a canine fossa observable, but not very large, the observer will need to decide if it is expressed to the level of "moderate," or to score it as "absent" instead; if the canine fossa is bigger, the choice is between recording "moderate" or "pronounced." For each character state, then, there is some degree of fuzziness. The membership functions are designed to represent this fuzziness.

To provide the clearest comparison between analyses, I retained the two membership functions corresponding to the dichotomized data. This time, however, I transformed the functions into fuzzy membership functions, represented by a trapezoidal function (Figure 3). Trapezoids are a common shape describing membership functions (Xu 2005); in this case, the functions allow for full membership in the set above or below a certain value. I defined the fuzzy membership functions by creating a one-half grade overlap at the breakpoint boundary. The intersection between the two functions represents the area of maximum fuzziness.

The FIS rules were aggregated, and the specimen data analyzed. As before, the analysis classified specimens crisply, as either Neandertals or moderns (see Figure 2); results would indicate correct or incorrect classification, as compared to prior knowledge (see Table 1).

ANALYSIS 3: VARIABLES ARE CRISP, BUT GROUP MEMBERSHIP IS FUZZY

In this analysis, the dichotomized data were again used. Each variable was treated as crisply determining group

TABLE 3. CONVERSION OF VARIABLES[1] INTO BIVALENT, CRISP SETS, USING BREAKPOINTS DESCRIBED AS LINGUISTIC VARIABLES.

Profile of the infraglabellar notch	Small: IN1, IN2	Large: IN3, IN4
Rounding of the inferolateral margin of the orbits	Sharp: RO1	Rounded: RO2, RO3
Supraorbital ridges/torus	Small: ST1, ST2, ST3	Large: ST4, ST5
Zygomaxillary (malar) tuberosity	Absent: ZT1	Present: ZT2, ZT3, ZT4
Canine fossa	Absent: CF1	Present: CF2, CF3
Zygomatic trigone	Small: TR1, TR2	Large: TR3, TR4
Occipital crest	Small: OCR1	Large: OCR2, OCR3
Occipital torus	Not visible: OT1, OT2	Visible: OT3, OT4, OT5, OT6, OT7
External occipital protuberance	Absent: EOP1	Present: EOP2, EOP3, EOP4

[1]Descriptions of variable states are given in Table 2.

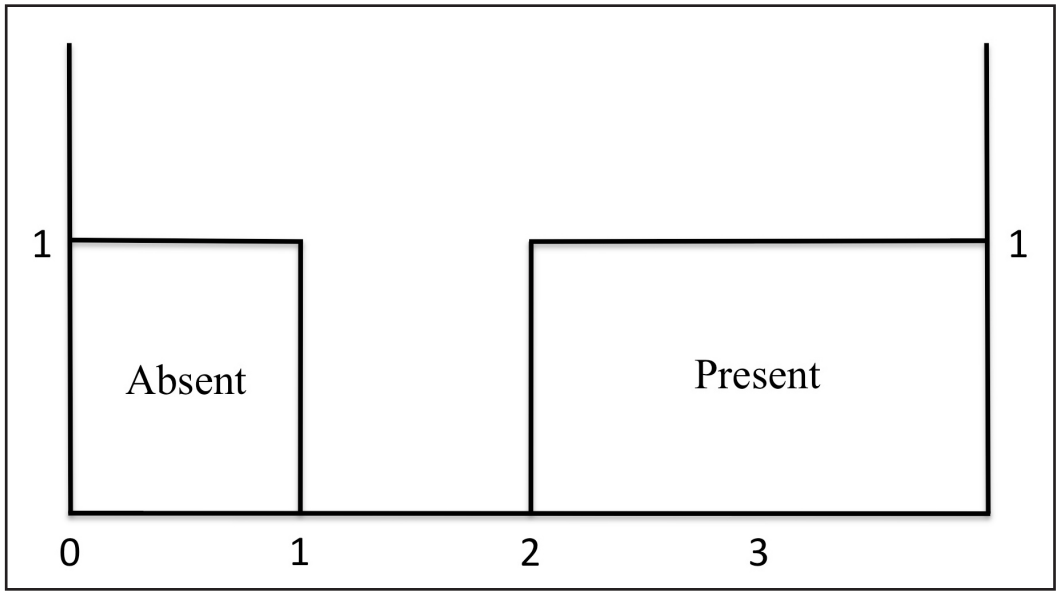

Figure 1. Dichotomization of grades, and corresponding crisp membership functions, of the variable "canine fossa."

membership. In this analysis, however, specimens were allowed to have partial set membership into Neandertals and Moderns, so the output sets were defined as fuzzy. Since the analyses are designed to compare methods, I created the two fuzzy sets as complements of each other. Trapezoidal membership functions were also defined for these two sets (Figure 4). The intersection between the two sets, the area of maximum ambiguity, was set at 0.5.

The FIS rules were aggregated by MATLAB, and the specimen data analyzed. However, the output was now a fuzzy set. To obtain the group membership value, I defuzzified the output using the smallest absolute value of maximum method. This defuzzification method selects the lowest value at which membership in the primary set is attained (Mahabir et al. 2003). The resulting output provided a degree of membership value for each specimen in each of the two fuzzy sets of Neandertal and Modern.

ANALYSIS 4: BOTH VARIABLES AND GROUP MEMBERSHIP ARE FUZZY

In this analysis, I used the fuzzy membership functions created for each variable from their graded categories, as in Analysis 2, and the outputs were again the fuzzy sets, as in Analysis 3. The FIS rules were aggregated, and the group membership values calculated. I again defuzzified the results using the smallest absolute value of maximum method, in order to provide a single output score. The resulting output provided a degree of membership value for each specimen in each of the two fuzzy sets of Neandertal and Modern.

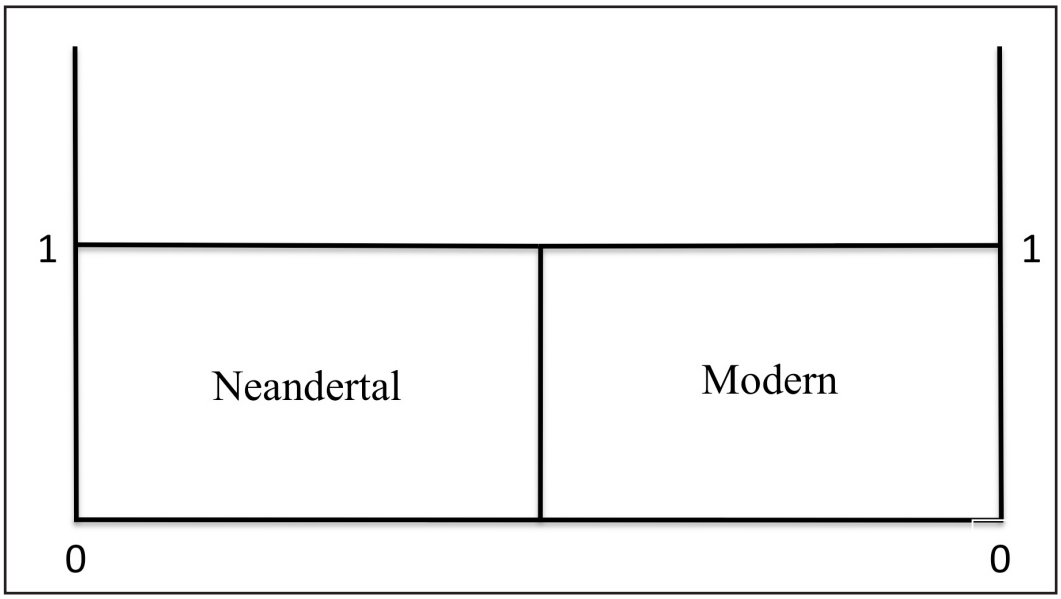

Figure 2. Crisp sets of Neandertals and Moderns.

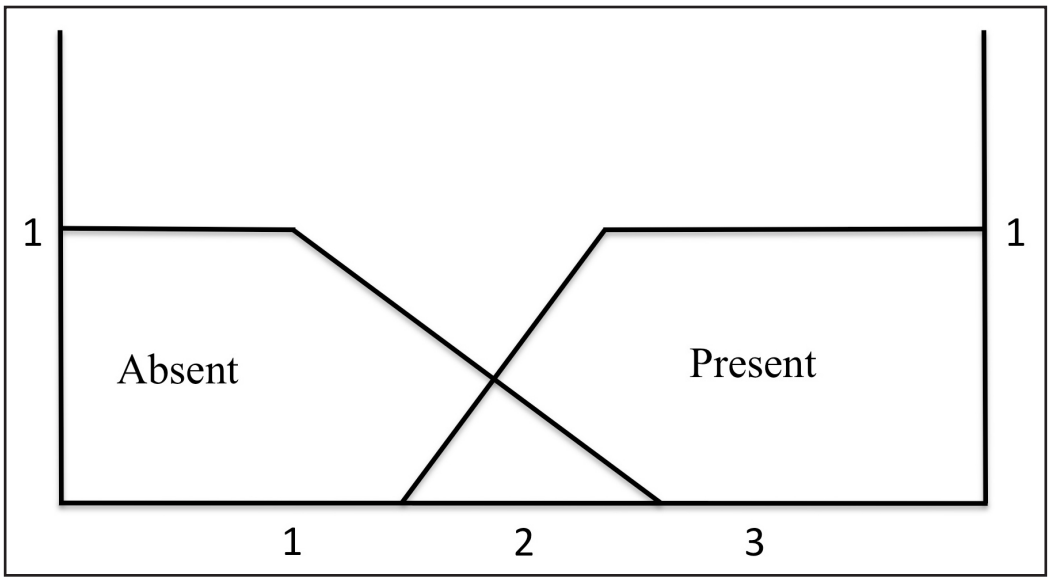

Figure 3. Fuzzy grades, and corresponding fuzzy membership functions, of the variable "canine fossa."

RESULTS

I considered specimens "correctly assigned" when their resultant membership matched previous identified group membership, as listed in Table 1. Results for all four analyses are listed in Table 4.

ANALYSIS 1: BOTH VARIABLES AND GROUP MEMBERSHIP ARE CRISP

A total of six of 14 Neandertals and 21 of 24 moderns were correctly assigned using a crisp analysis using these nonmetric traits. The results are given as crisp set membership, as in the set (membership = 1) or not (membership = 0). One Neandertal showed an equal number of Neandertal and modern features, and so was not assigned to either category. There is no information in the results that helps us understand how far the incorrectly assigned specimens were from the boundary.

ANALYSIS 2: VARIABLES ARE FUZZY, BUT GROUP MEMBERSHIP IS CRISP

In this analysis, ten of 14 Neandertals, and 19 of 24 moderns were correctly assigned using these nonmetric traits. Again, the results are given as crisp set membership. Using fuzzy variables, which retained multistate grade information, provided results that better matched the prior knowledge of group membership. However, there is still no information in the results that help us understand how far the incorrectly assigned specimens were from the boundary.

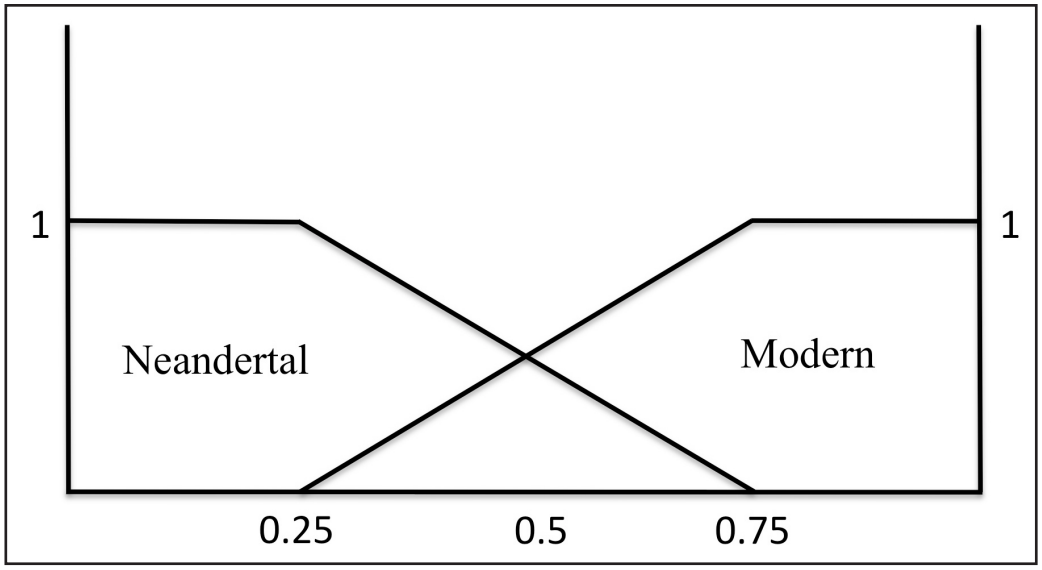

Figure 4. Fuzzy sets of Neandertals and Moderns.

TABLE 4. RESULTS OF THE FOUR ANALYSES.[1]

	ANALYSIS 1		ANALYSIS 2		ANALYSIS 3		ANALYSIS 4	
Specimen name	Membership Neandertal	Membership Modern	Membership Neandertal	Membership Modern	Membership Neandertal	Membership Modern	Membership Neandertal	Membership Modern
Amud 1	1	0	1	0	0.55	0.45	0.62	0.38
Gibraltar 1	0	1	1	0	0.47	0.53	0.51	0.49
Krapina C	0	1	0	1	0.48	0.52	0.38	0.62
La Chapelle	1	0	1	0	0.58	0.42	0.99	0.01
La Ferrassie			1	0	0.50	0.50	0.58	0.42
La Quina 5	0	1	0	1	0.48	0.52	0.25	0.75
Monte Circeo 1	1	0	1	0	0.53	0.47	0.58	0.42
Saccopastore	0	1	0	1	0.45	0.55	0.42	0.58
Shanidar 1	1	0	1	0	0.55	0.45	0.74	0.26
Shanidar 5	1	0	1	0	0.58	0.42	0.99	0.01
Spy 1	0	1	1	0	0.48	0.52	0.58	0.42
Spy 2	0	1	1	0	0.47	0.53	0.57	0.43
Tabun C1	1	0	1	0	0.52	0.48	0.62	0.38
Zuttiyeh	0	1	0	1	0.48	0.52	0.38	0.62
Cro Magnon 1	0	1	0	1	0.32	0.68	0.37	0.63
Dolni Vestonice 3	0	1	0	1	0.27	0.73	0.25	0.75
Fish Hoek	0	1	0	1	0.32	0.68	0.25	0.75
Gambles Cave 4	0	1	0	1	0.27	0.73	0.25	0.75
Goughs Cave 1	0	1	0	1	0.36	0.64	0.41	0.59
Hotu 2	1	0	1	0	0.58	0.42	0.62	0.38
Iwo Eleru	0	1	0	1	0.45	0.55	0.42	0.58
Jebel Irhoud 1	1	0	1	0	0.52	0.48	0.49	0.51
Jebel Irhoud 2	0	1	0	1	0.48	0.52	0.37	0.63
Kanjera	0	1	0	1	0.47	0.53	0.28	0.72
Liujiang	0	1	0	1	0.32	0.68	0.37	0.63
Ohalu 2	0	1	0	1	0.27	0.73	0.25	0.75
Predmosti 4	0	1	0	1	0.47	0.53	0.38	0.62
Predmosti 814	0	1	0	1	0.42	0.58	0.41	0.59
Qafzeh 6	0	1	0	1	0.42	0.58	0.40	0.60
Qafzeh 9	0	1	0	1	0.39	0.61	0.40	0.60
Singa	0	1	1	0	0.52	0.48	0.58	0.42
Skhul 4	0	1	0	1	0.47	0.53	0.41	0.59
Skhul 5	1	0	1	0	0.53	0.47	0.59	0.41
Skhul 9	0	1	0	1	0.46	0.54	0.41	0.59
Wadjak 1	0	1	0	1	0.44	0.56	0.37	0.63
Zhoukoudian 101	0	1	1	0	0.47	0.53	0.42	0.58
Zhoukoudian 102	0	1	0	1	0.32	0.68	0.37	0.63
Zhoukoudian 103	0	1	0	1	0.32	0.68	0.25	0.75

[1]Shaded cells indicate "correct" or "incorrect" placement; that is, when the placement results match previous identification, as listed in Table 1.
Green = correct placement; red = incorrect placement; yellow = inconclusive result.

ANALYSIS 3: VARIABLES ARE CRISP, BUT GROUP MEMBERSHIP IS FUZZY

In this analysis, six of 14 Neandertals, and 20 of 24 moderns were correctly assigned using these nonmetric traits. These results are similar to Analysis 1. The results, however, now indicate degree of membership into the set of Neandertal and Modern. This degree of membership provides a measure of to what degree each specimen fits into the two fuzzy sets of Neandertal and Modern. Recall that the crossover point between sets (0.5) is the point of maximum ambiguity of group membership. Therefore, we can observe that nearly all of the misclassified specimens of Neandertals and moderns fall near this value in their fuzzy set memberships. One Neandertal again showed an equal membership in the Neandertal and Modern sets, with a defuzzified membership of 0.5 in both sets, and so was not assigned to either.

ANALYSIS 4: BOTH VARIABLES AND GROUP MEMBERSHIP ARE FUZZY

In Analysis 4, ten of 14 Neandertals, and 21 of 24 moderns were correctly assigned using these nonmetric traits. This analysis provided results that best fit that of prior specimen identification. The results again indicate degree of membership into the set of Neandertal and Modern. This degree of membership provides a measure of to what degree each specimen fits into the two fuzzy sets of Neandertal and Modern. In this analysis, the fuzzy gradations of the data provided information that pulled specimens away from the boundary between the sets. No specimens expressed maximum ambiguity (membership of 0.5); all specimens with membership near 0.5 in both sets had an assigned membership that matched previous assignment.

DISCUSSION

If, for these nonmetric cranial variables, the character states are discrete for Neandertals and early moderns, then the analysis should reflect low levels of fuzziness. In other words, the crisp analyses, particularly Analysis 1 and 3, should be sufficient to correctly place most of the specimens. In fact, the best results (as measured by correct specimen placement) were obtained in Analyses 2 and 4, where the variables were fuzzy. This suggests that retaining character state data, rather than dichotomizing data, provided additional information important to the analysis.

If, for these nonmetric cranial variables, Neandertals and moderns were distinctly different, and are best modeled as crisp taxa, then the analyses modeling crisp groups (Analyses 1 and 2) should be sufficient. If there is a great deal of intraspecific variation, and both groups share many of these character states in common, then the analysis should reflect a higher degree of fuzziness. While Analysis 2 provided good results, Analysis 4, when both variables and groups were both modeled as fuzzy, performed the best.

None of the nonmetric cranial variables analyzed showed a clear, unambiguous distinction between the two groups. Rather, differences between the two groups are seen more subtly through frequencies of expression of the different character states. All of the variables showed considerable overlap in multistate expression in the two samples. The fuzzy analysis example shown here can provide a nuanced understanding of the underlying variation in the samples. These results imply that the better model for comparing Neandertals and moderns is as fuzzy, overlapping groups, such as subspecies, rather than crisp ones.

CONCLUSIONS

One of the big issues in taxonomy today is how to best utilize the vast stores of continuously distributed data, both qualitative and quantitative, that has been, and is being, collected. Character coding for continuous or quasicontinuous variables is clearly an important area of research. Determining ways to find natural breaks in otherwise continuous data is essential if these data are to be utilized in phylogenetics. I think it will prove fruitful to explore ways to analyze nonmetric data that retain the information about underlying variation, as well as determine if, and where, breakpoints are appropriate to create multistate characters. Artificially dichotomizing the data can provide a false view of the variation seen in the data, and could obscure the distribution and pattern of variation expressed in multistate nonmetric variables. When many such variables are involved in the analysis, the effect can be large. Fuzzy set analysis is one way to do just that. It is a method that avoids two problematic assumptions implicit in phylogenetic analyses—crispness of taxa and crispness of traits.

We need to acknowledge the reality of intra- and interspecies variability and set overlap in a way that explicitly recognizes and addresses it, not as a statistical annoyance, but as a variable and informative part of the data. Fuzzy analysis is a useful tool to tease out the fuzziness underlying these distributions, to better advance their use for species identification and phylogeny construction. Expanding our toolkit to include fuzzy set analysis can help us determine how crisp and distinct, or fuzzy, our putative taxonomic groups are.

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