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CORRESPONDENCE

Species as units of analysis in ecology and biogeography: are the blind leading the blind?

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ABSTRACT

Riddle & Hafner (1999) suggest that genetically differentiated lineages should be formally recognized as evolutionary significant units (ESUs) and that ESUs should replace currently recognized species as units in quantitative ecological and biogeographic analyses. Riddle & Hafner imply that if comparisons of desert rodent communities across many localities in south-western North America by Brown & Kurzius (1987) and Kelt *et al.* (1996) had used ESUs rather than species, substantially different results and conclusions would have been obtained. Here we defend our use of species in these studies, and question the wisdom of formalizing the concept of ESU and applying it in most biogeographic, ecological and behavioural studies. Studies of genetic variation and description of ESUs are uneven across taxa of mammals and geographical regions, and those ESUs that have been described are often difficult or impossible to identify on the basis of the morphological traits used to distinguish currently recognized species. Consequently, most of the specimens in museum drawers, nearly all of the fossil remains, and most of the animals studied in the field or laboratory by ecologists, behaviourists and other biologists cannot be assigned to ESUs. The currently recognized species, usually described originally on the basis of morphological and biological species concepts, provide the only relatively consistent, operational taxonomic units. Results of our studies on the biogeography of desert small mammals are not seriously altered by recent subdivisions of some species into multiple ESUs.

Key words Biogeography, conservation biology, desert small mammals, evolutionary significant units, macroecology, North America, rodents, species as entities.

The application of new theoretical paradigms and molecular data are rapidly increasing our understanding of the history of biological evolution. Particularly noteworthy are advances in ‘phylogeography’, a research programme that endeavours to reconstruct the phylogenetic histories of different kinds of organisms and map them onto the past and present geography of the earth (e.g. Riddle, 1995; Dumolin-Lapegue *et al.*, 1997; Strange & Burr, 1997; Walker & Avise, 1998). We applaud the efforts of Riddle, Hafner, Lawlor, Sullivan and colleagues to reconstruct the evolutionary and biogeographic histories of populations of mammals in south-western North America, and to use this information to improve understanding of the climatic and geological history of the region.

Unfortunately, the zeal of some phylogenetic systematists and phylogeographers is leading to increasing demands that an explicitly phylogenetic framework be applied to all comparative biological studies. Efforts to impose such orthodoxy on concepts and methods are inimical to the spirit of creativity and the pluralism of approaches that are essential for scientific inquiry. Elsewhere, Brown (1999) has argued against the assertion that macroecological and other comparative biological studies should necessarily include phylogenetically independent comparisons or other explicitly phylogenetic analyses. Here we respond to another demand for phylogenetic orthodoxy. In a zealous polemic, Riddle & Hafner (1999; R&H) criticize recent comparative studies of desert rodent assemblages in south-western North America (Brown & Kurzius, 1987; Kelt *et al.*, 1996; hereafter B&K and K&A, respectively) for failure to use evolutionary significant units (ESUs) rather than currently recognized species. Claiming that K&A have 'perpetuated' the 'evident failure of implicit assumptions about species made by Brown & Kurzius (1987)', R&H claim that it is 'time to take the blinders off' and imply that substantially different results and interpretations would have been obtained had ESUs been used in our analyses.

In recent years, studies of molecular genetic variation have revealed new patterns of variation within and between currently recognized desert rodent species (see references cited in R&H). Several populations with distinct genotypes have either been described as new species or designated as ESUs. The geographical distributions of alternative genotypes have been interpreted to reflect the historical isolation and differentiation of populations in response to past climatic and geological events. Here, we do not question the genetic distinctiveness of the populations designated as ESUs, although we note that the sample sizes used in the molecular genetic analyses often were sufficiently small that rare genotypes might not have been detected. We also do not question the historical reconstructions, although we note that they should be regarded as hypotheses and subjected to rigorous independent testing before being widely accepted. For example, most of the ESUs have been described on the basis of haplotypes of mitochondrial DNA (mtDNA). Because the mitochondrial genome is maternally inherited and new variants appear as a result of point mutations, duplications, insertions and deletions, rather than as a result of recombination, the evolutionary dynamics of mtDNA differs from that of the nuclear genome. While this almost certainly influences the pattern of variation within and between populations, it is still unclear how the maternal clonal inheritance of mtDNA may affect historical reconstructions. It remains an open question how often and in what circumstances congruent patterns of variation, reflecting the pervasive influence of important historical events, are preserved in both mitochondrial and nuclear genomes.

While we agree that continued dissection of evolutionary lineages is important for understanding evolutionary and biogeographic histories, at issue here is whether the ESUs of desert rodent populations that have recently been characterized using mtDNA or other genetic attributes are more appropriate units than traditional species for comparative ecological and biogeographic studies. Additionally, an unstated implication of R&H is that research using conventional species is fatally flawed, and other scientists should cease their efforts until the phylogeographers of the world have completed theirs.

We start by considering the narrow issue of whether it would have been scientifically justified — or even possible — for ESUs to have been used in the two studies criticized by R&H (Brown & Kurzius, 1987; Kelt *et al.*, 1996). We then take up the more general issue of the wisdom of describing as formal species or ESUs populations that can be diagnostically recognized only on the basis of molecular genetic traits.

Our first point is that it would have been impossible for either of the two studies criticized by R&H to have incorporated many of the ESUs reported by them. R&H present data (their Table 1) indicating that what were formally recognized as 13 species have been subdivided into at least 30 ESUs. Much of this information, however, was not available when the papers criticized by R&H (Brown & Kurzius, 1987; Kelt *et al.*, 1996) were published, and several of the ESUs are still unpublished. In fact, only 13 of the 30 ESUs (and only five of the 17 papers, including one unpublished Master's thesis) had been published when the paper by B&K was written. Even in 1995, when the paper by K&A was written, six of these 17 papers (as well as seven references to unpublished data and two unpublished theses) had not been published. How can we be faulted for not including information that was not available to the scientific community?

A related issue is which genetically distinct populations should be classified as ESUs. The authors cited in R&H described genetically differentiated populations, but R&H do not suggest that we should have considered them as ESUs and used them in our analyses. The formal criteria that biologists should follow in formally recognizing ESUs is a complicated issue that R&H conveniently avoid. Finally, not all of the papers cited by R&H distinguished new lineages. For example, McKnight & Lee (1992) pointed out that *Perognathus amplus* and *P. longimembris* were ring species, but did not change their taxonomic status.

Our second point is that it is still premature to use the desert rodent ESUs that have so far been described in broad, comparative ecological and biogeographic analyses, such as B&K and K&A. The former is a comparison of the composition of 201 desert rodent assemblages distributed across the entire arid region of the south-western United States, while the latter compares the composition of North American desert rodent communities as reflected in the 201 sites in the B&K dataset with similar data for desert rodent communities on other continents. What would be the result if the B&K dataset were updated, incorporating the ESUs that have been published to date? The result would still be a very incomplete and inconsistent incorporation of molecular genetic information. Compared to the collective taxonomic and geographical coverage of the museum collections that have been used to describe traditional species and map their geographical distributions, the coverage of molecular genetic studies is still very spotty. Only a fraction of the species of North American desert rodents have been subjected to detailed analyses of molecular genetic variation. For those species that have been studied, the geographical coverage includes only a small fraction of the localities where the species have historically been documented to have occurred. Furthermore different genetic traits, including mtDNA haplotypes, allozymes and karyotypes, have been used to describe different populations as ESUs (see e.g. Table 1 of R&H). Therefore, it is impossible to apply uniformly any criterion for designation of ESUs, and it is impossible to assign with confidence the rodent populations at many of the localities in the B&K dataset to published ESUs. The problems are compounded when comparisons are made between communities of North American desert rodents and those of other continents in K&A. While some genetic studies have been performed on desert rodents outside North America, the coverage of taxa and geographical areas is much sparser, and the variants have usually not been formally described as ESUs. So, had K&A used the known ESUs for North America, they would have introduced a major uncontrolled variable, degree of molecular genetic differentiation, into their analysis. Owing to the widely varying use of molecular genetic data in systematic practice, traditional species are much more comparable units for intercontinental geographical analyses than are ESUs. In order to perform comparative studies, it is necessary that the basic units of analysis are, in fact, comparable. ESUs do not yet meet this essential criterion.

We now address the question of whether our comparative geographical studies would have given materially different results if ESUs had been used instead of traditional species. R&H imply that this is the case but provide no direct evidence. The main effect of the recently described ESUs has been to subdivide previously recognized species into genetically — putatively historically — distinct, geographically isolated populations. The most closely related ESUs are almost invariably allopatric (although they may occur in close geographical proximity). Most of the analyses in B&K and K&A concerned the number and characteristics of the species that co-exist in local ecological communities; these results would not have been altered by using ESUs as units of analysis. Other analyses, however, concerned the frequencies of occurrence and co-occurrence of species across the South-west (in the entire dataset). These results would indeed be altered by the subdivision of traditional species into multiple ESUs. As noted above, however, analyses based on ESUs would only be valid if the ESUs represent consistent and comparable units across both taxa and geography. R&H correctly point out that the most serious errors would occur if the traditional species were not monophyletic units. B&A note three genera for which this might be a concern: *Onychomys* (*O. arenicola*, *O. torridus*, and *O. leucogaster*), *Peromyscus* (*P. eremicus*, *P. eva*, and *P. merriami*) and *Neotoma* (*N. albigula* and *N. lepida*). However, they make no attempt to show how recent identification of new, putatively monophyletic

ESUs would change the results of B&K or K&A. Inspection of the B&K dataset reveals only a few localities where misidentification of only two pairs of genetically defined ESUs (*O. arenicola*/*O. torridus* and *P. eremicus*/*P. merriami*) may have altered the analyses. Additionally, the updated dataset used by K&A may have misidentified a small number of samples of *Neotoma lepida*/*N. devia*. So, we conclude that the results of B&K, K&A and other studies that have used the B&K or similar datasets (e.g. Patterson & Brown, 1991; Fox & Brown, 1993; Kelt, 1999; Kelt *et al.*, 1999; Kelt & Brown, 1999; Brown *et al.*, in press) are robust to current applications of phylogeographic approaches, at least as reflected in emphasis on ESUs rather than traditional species.

R&H accuse us of adopting a 'dispersalist' and rejecting a 'vicariant' approach to biogeography; but nowhere in either B&K or K&A does either of these terms appear. In fact, we have deliberately avoided adopting either of these assumption-laden approaches. While neither dispersal nor *in situ* differentiation is central to B&K or K&A, our view of biogeography recognizes the importance of both processes. Such a balanced perspective is required to understand the effects of biological, climatic and geological processes on the expansion and contraction of geographical ranges and on build-up and breakdown of genetic differences among closely related populations. Unlike some doctrinaire 'dispersalist' and 'vicariant' biogeographers, we believe in using all reliable evidence and rigorous methods in the effort to explain how phylogenetic history and past and present environments have interacted to affect the distribution and diversity of organisms (see also Brown & Lomolino, 1998).

Finally, we end with an expression of some concern about the influence of new phylogenetic approaches on concepts of species or other genetically defined units such as ESUs. R&H's zeal for describing ESUs and using them as units of biogeographic analysis parallels efforts of others to define and apply new concepts of 'phylogenetic species' and 'evolutionary species' based on patterns of genetic differentiation (e.g. Wiley, 1981; Cracraft, 1989). Many of the new species of birds and mammals being described in the United States and other taxonomically well-surveyed areas represent subdivisions of previously recognized species into genetically distinct allopatric populations. These units differ from the traditional species, which were described based on a combination of morphological and biological species concepts. There is no question that the patterns of genetic variation reveal valuable information about the isolation and differentiation of populations and the influence of historical climatic and geological events.

We question, however, whether anything more is to be gained by giving these units formal designation with a scientific name or ESU. Many authors who advocate some such fundamental unit want to make an implicit or explicit link between phylogenetic and geographical patterns of genetic differentiation and the process of speciation. We question whether there is any single process of speciation that operates uniformly and universally in all organisms in all environmental settings. We also question whether there is any single level of genetic differentiation that leads inevitably to speciation and permanent splitting of lineages.

One problem with most of the recently described species or ESUs is that they can be identified with certainty only by means of technologically sophisticated, expensive molecular genetic diagnoses. This means that the vast majority of individuals and many populations cannot presently be identified to ESU, because they have not been diagnosed genetically and they cannot be diagnosed morphologically. We question the wisdom of having a concept of species or ESU that cannot be applied to identify specimens in museum drawers and bottles, remains preserved as fossils and individuals observed in ecological and behavioural studies. Most of the units designated as traditional species are valuable to a wide range of biologists because they indicate distinctiveness, not only genetically, but also morphologically, physiologically, ecologically and behaviourally.

The mismatch between the 'evolutionary significant units' recognized by phylogenetic systematists and molecular geneticists and the morphological species recognizable in the fossil record is especially troubling. How are hypotheses about evolutionary and biogeographic history to be evaluated rigorously if the units of phylogeographic analysis do not correspond to the distinctive units that can be recognized in the fossil record? Staunch phylogeographers might argue that such discrepancies underscore their concern that use of conventional species may reveal 'ghost patterns' that actually do not correspond to real evolutionary lineages. We do not have an answer to this dilemma. Nor, we believe, do R&H. We do believe, however, that zealous insistence that other scientists use certain concepts, terms and approaches that may have proven valuable in phylogenetic studies will ultimately hinder, rather than promote, the use of phylogenetic information in other disciplines, such as biogeography, ecology and behaviour.

We conclude that R&H is more a polemic than a substantive criticism of B&K, K&A and similar comparative biogeographic studies. Phylogeographic studies and analyses of genetic differentiation of populations are contributing importantly to efforts to understand the histories of lineages and places. However, we question the wisdom of recognizing ESUs formally and using them to replace species as units of biogeographic analysis. Such a course would be, at best, premature, because ESUs are not sufficiently and consistently characterized across taxa and regions, even for the relatively well-studied desert rodents of south-western North America. Furthermore, despite R&H's claims to the contrary, using currently recognized ESUs instead of species would not materially change the results or interpretations of our previous studies. R&H suggest that it is time for comparative and ecological biogeographers 'to take the blinders off', follow the lead of phylogeographers and start using ESUs in their studies; but that would indeed be a case of the blind leading the blind, at least until ESUs are as consistently characterized as traditional species.

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