



Species as units of analysis in ecology and biogeography: time to take the blinders off

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ABSTRACT

Species and their geographical distributions, tabulated either from regional faunal and floral monographs or directly from natural history collections, often are used as the basic units of analysis by ecologists and biogeographers. It has been argued that in order for species to be operationally useful units for evolutionary and ecological studies, they need to be recognizable and identifiable as distinct entities. A growing body of molecular phylogeographic studies demonstrates that currently recognized species often are unreliable in their approximation of fundamental evolutionary and geographical units, leading, for example, to proposed usage of molecular-based evolutionarily significant units in lieu of species in conservation biology. We argue that ecologists and biogeographers should likewise employ evolutionarily significant units as basic units of analysis

when evidence clearly indicates that a formally recognized species either fails to convey important evolutionary and geographical information (i.e. includes multiple geographically distinct evolutionary lineages) or fails to delineate a natural entity (i.e. does not represent a monophyletic set of populations). We demonstrate the limitations of current species as evolutionary, geographical, and conservation units within the ecologically well-studied North American desert rodent assemblage. We suggest that biotic surveys should be designed to allow the efficient assembly and dissemination of molecular phylogeographic data from ecologically and biogeographically representative systems.

Key words. Biogeography, conservation biology, ecology, evolutionarily significant units, macroecology, mammals, phylogeography, rodents.

INTRODUCTION

Species are widely used as fundamental units of analysis in several areas of ecology and biogeography (Brown, 1995; Brown *et al.*, 1996; Blackburn & Gaston, 1998). A pragmatic reason for doing so is that species historically have attained a role as primary entities in palaeontology, macroevolution, and conservation biology, thus providing a common currency between disciplines (Brown, 1995). However, a rapidly increasing number of biogeographers have begun to utilize a different currency: the geographically discreet evolutionary lineages revealed through analysis of molecular data, usually mitochondrial DNA (mtDNA) in animals. This discipline has been called *phylogeography*, and defined

as ‘... the study of the principles and processes governing the geographical distributions of genealogical lineages, including those at the intraspecific level’ (Avice, 1994, p. 233). Conservation biologists have proposed calling such lineages *evolutionarily significant units* (ESUs). While some controversy exists over the best recognition criteria for delineating evolutionarily significant units (ESUs) (e.g. Moritz *et al.*, 1995; Waples, 1995), Moritz and colleagues have defined the phylogeographically based ESU as consisting of ‘... historically isolated sets of populations for which a stringent and qualitative criterion is reciprocal monophyly for mitochondrial DNA (mtDNA) combined with significant divergence in frequencies of nuclear alleles’ (Moritz *et al.*, 1995 p. 249).

Our intention is to address three related issues, stemming from the remarkable growth in phylogeographic surveys of geographical population structure over recent years (Avice, 1998). First, we ask whether recent findings in phylogeography seriously challenge several assumptions underlying the use of currently recognized species as units of analysis in ecology and biogeography. Second, we briefly address the kinds of questions that most likely could be compromised by using species as primary units if they either subsume significant phylogenetic and geographical structure, or are not natural entities. Third, we offer suggestions for efficient implementation of biotic surveys that would develop representative phylogeographic information for use by ecologists and biogeographers. We recognize that a variety of questions in ecology and biogeography will not be affected appreciably by the issues we raise here (e.g. tabulation of species within local community assemblages for purposes of investigating local patterns and processes). Instead, we draw attention to areas of inquiry where distinct advantages should accrue from using phylogeographically based ESUs. Specifically, we recommend that ecologists and biogeographers make use of the most appropriate and informative phylogeographic information currently available by incorporating ESUs into species-level analysis.

SPECIES AS UNITS OF ANALYSIS

As used in ecological and many biogeographic analyses, species and their geographical distributions are most often extracted either from available monographs (e.g. Hall, 1981) or directly from natural history collections. We would not expect most practitioners in need of an operational unit for ecological and biogeographic analysis to have insight into the reliability of species tabulated in this way. Rather, they must rely on the taxonomies generated by systematists. Ecologists understand that recognition and delineation of species are not without error (Brown, 1995; FAUNMAP working group, 1996). Nevertheless, in well-studied groups (e.g. terrestrial vertebrates), currently recognized species are assumed to represent a sufficiently accurate and robust depiction of natural phylogenetic and geographical entities that subsequent revisions will result only in small changes in species-level taxonomy. As Brown, (1995, p. 27) states, 'All that is really necessary . . . is that species be operationally identifiable, that they represent relatively comparable

units of biological organization, and that the individuals and populations recognized as being conspecific be more closely related to each other than to other recognized species. The species of terrestrial vertebrates and many other well-studied groups meet these criteria.' Thus, terrestrial vertebrate species are considered to represent appropriate units for evolutionary, palaeontological, and ecological studies (Brown, 1995; Blackburn & Gaston, 1998). This would be an acceptable perspective if, as is commonly believed, the most contentious issue regarding species-designations revolves around the particular species concept being employed (e.g. biological, phylogenetic, or congruence species concepts; reviewed in Avice, 1994). A more insidious problem in using species as units of analysis would arise if the kinds of characters and criteria historically used by systematists frequently result in either overly coarse or inaccurate depictions of taxonomic species as evolutionary lineages. Below, we contrast information content of species vs. ESUs in a system that has been an ecological workhorse: the guild of North American desert rodents.

North American desert rodents

North American desert rodents make up one of the most intensively studied guilds of terrestrial vertebrates in the world and have been used as a paradigmatic system for testing hypotheses about ecological organization at population, community, and landscape scales (summarized by Reichman, 1991; Brown & Harney, 1993). In a seminal study of community composition, Brown & Kurzius (1987) compiled a large, geographically representative data set on desert rodent species distribution and coexistence in 202 local communities across four desert regions in North America (Great Basin, Mojave, Sonoran, Chihuahuan). Their study produced the core data set used in a series of recent papers in which the North American desert rodent guild has been contrasted with patterns of community assembly and organization in physically similar biomes across the globe (e.g. Morton *et al.*, 1994; Kelt *et al.*, 1996). It has become customary in these studies to combine local assemblage presence/absence data from large geographical areas into a single regional species pool for subsequent intercontinental comparisons. For example, Kelt *et al.*, (1996) concluded that the four major deserts in North America share a sufficiently large number of species to justify lumping all data into a single North American desert region for comparison with regional deserts on different

continents. Implicit in this procedure are several assumptions: (1) that individuals have been properly identified ('operationally identifiable'; criterion 1 of Brown, 1995); (2) that a species represents the same evolutionary entity (ESU) in each desert region where it occurs (criterion 2); and (3) that all populations of a species are more closely related to each other than to populations within a different species (criterion 3). A major conclusion that has been derived from this body of related ecological studies is that dispersal (historical or ongoing) across desert regions largely predominates over a history of isolation and divergence (vicariance) between populations in different regions. We contend that the implied assumptions are not valid, and so negate the conclusion that dispersal has predominated in the history of regional deserts. Further, we contend that these errors result from an unjustified and unnecessary reliance on the species level as the appropriate unit of analysis.

Data on molecular phylogeographic structure are becoming available for a number of the species in the North American desert rodent ecological studies. Although we have not yet rigorously analysed the generality of biogeographic patterns inferred from phylogeographic structure for each taxon, a preliminary compilation of available data (Table 1) provides an opportunity to address the extent to which a number of species of North American desert rodents are meaningful units for ecology, evolution, and biogeography. The North American species included by Kedd et al. (1996) in their comparison of desert small mammals across four continents can be partitioned qualitatively into those that are strongly desert-adapted or desert-distributed vs. those that are more characteristic of nondesert regions, with only peripheral distributions in desert regions. After doing so, phylogeographic data are available for 14 of 29 desert-adapted species. Do currently recognized species meet the three criteria stated by Brown (1995) in order to serve as reliable units of analysis?

Criterion 1: Operationally identifiable

Reliable identification appears to be the most trivial assumption underlying the use of species as units of analysis, particularly among the seemingly well-known terrestrial vertebrates, and most particularly those from parts of the world with extremely long histories of scrutiny, such as might be expected for North American mammals. Unfortunately, cryptic or sibling species abound among arid-adapted rodents and are common

in the pocket mice (*Chaetodipus* and *Perognathus*) and white-footed mice (*Peromyscus*). Often, field identification in areas of sympatry is only an approximation, and reliable identification must await detailed analysis of cranial and dental anatomy, bacular morphology, chromosomal complement, or molecular sequence data.

A major task in our analysis of molecular variation within some of the species of *Chaetodipus* and *Peromyscus* has been to reconcile molecular data with morphological identifications (i.e. traditional species designations). Although we purposely sample populations at previously sampled localities, and specimens that we collect match exomorphological and even cranial characteristics of described species, we continually discover that many of the morphological characters fail to match molecular data. We conclude that many of the morphological traits are unreliable and that a significant number of specimens in existing collections, upon which geographical distributions are based, are misidentified. This is particularly true for four species of *Peromyscus* (subgenus *Haplomyloms*): *P. eremicus*, *P. eva*, *P. merriami*, and *P. crinitus*; and four species of *Chaetodipus*: *C. arenarius*, *C. baileyi*, *C. formosus*, and *C. penicillatus*. Molecular analysis has allowed us to focus on those morphological traits that are consistent and reliable, and to re-evaluate the actual geographical ranges with increased confidence.

Criterion 2: Relatively comparable units of biological organization

An estimated minimum number of 31 geographically distinct ESUs are contained within the 14 desert-adapted species that thus far have been assayed (Table 1; Fig. 1). This large discrepancy between estimates of numbers of species vs. ESUs leads us to postulate that even more widespread species of desert-adapted rodents in North America will eventually be divisible into multiple geographically and evolutionarily separate entities. Additionally, the divisions generally tend to reflect in scale and distribution a high level of congruence with geomorphological features delineating boundaries between the major regional deserts (some not yet fully recognized in the literature, e.g. an evolutionary history of the Baja California Peninsular Desert biota that is separate from that of the mainland Sonoran Desert; Hafner & Riddle, 1997). Furthermore, the divisions tend to reflect high levels of sequence divergence between ESUs, indicating decidedly ancient times of

Table 1. Summary of currently recognized species or species-groups and minimum number of ESUs inferred from available mtDNA and supporting evidence for North American desert-adapted rodents. Inferred distributions according to the outline of regional deserts used by Brown & Kurzius (1987) and subsequent ecological studies of North American desert rodents, with additional arid regions added. Regional deserts: GB = Great Basin; MO = Mojave; SO = Sonoran; CH = Chihuahuan; PN = Peninsular Desert. Additional, peripheral regions: GP = Great Plains; CP = California chaparral; ST = Subtropical thornscrub

Currently-recognized species	Min. no. ESUs	mtDNA and supporting evidence for separate ESUs within a single taxonomic species	Inferred geographic distribution of ESUs across regional deserts	Sources
<i>Perognathus flavus</i>	2	Provisional congruence of exemplar mtDNA lineages with allozyme evidence for two ESUs representing nominate species <i>P. flavus</i> and <i>P. merriami</i> .	WEST (northwest CH) EAST (Tamaulipan section of CH)	Lee and Engstrom, 1991; Riddle, unpubl. data
<i>Perognathus flavescens</i>	3	Reciprocally-monophyletic mtDNA lineages defining three ESUs: two within previously-recognized species <i>P. apache</i> ; one representing <i>P. flavescens</i> . No supporting nuclear evidence available.	FAR WEST (Colorado Plateau section of GB) WEST (northwest CH) EAST (GP)	Nickle, 1994; Riddle, unpubl. data
<i>Perognathus longimembris</i> species-group	2	Congruence of reciprocally monophyletic mtDNA lineages and karyotypes for two ESUs defining the species <i>P. longimembris</i> and <i>P. amplius</i> .	WEST (GB, MO, PN, CP, SO west of Colorado River) EAST (SO east and GB south of Colorado River)	McKnight, 1995; McKnight and Lee, 1992
<i>Perognathus parvus</i>	3	Provisional congruence of reciprocally monophyletic mtDNA lineages and karyotypes defining very divergent ESUs.	SOUTH (southern section of GB) CENTRAL (southern Columbia Plateau section of GB) NORTH (Columbia Plateau section of GB) FAR WEST (MO and SO west of Colorado River) WEST (SO east of Colorado River and far northwest CH) EAST (most of CH) NORTH (northern PN) SOUTH (southern PN)	Ferrell, 1995; Riddle, unpubl. data; Williams, 1978 Lee <i>et al.</i> , 1996; Riddle and Hafner, unpubl. data; Patton <i>et al.</i> , 1981 Riddle and Hafner, unpubl. data
<i>Chaetodipus penicillatus</i>	3	Congruence of reciprocally monophyletic mtDNA lineages, allozymes, and karyotypes defining ESUs, recently identified as separate species, <i>C. penicillatus</i> and <i>C. eremicus</i> .		
<i>Chaetodipus arenarius</i>	2	Reciprocally monophyletic mtDNA lineages defining two very divergent ESUs. No supporting nuclear evidence available.		

Table 1. continued

Currently-recognized species	Min. no. ESUs	mtDNA and supporting evidence for separate ESUs within a single taxonomic species	Inferred geographic distribution of ESUs across regional deserts	Sources
<i>Chaetodipus baileyi</i>	3	Congruence of reciprocally monophyletic mtDNA lineages, allozymes, and karyotypes for two ESUs.	WEST (SO west of Colorado River and PN) EAST (SO east of Colorado River, far western CH, and ST)	Riddle and Hafner, unpubl. data; Patton <i>et al.</i> , 1981
<i>Peromyscus eremicus</i>	3	Congruence of reciprocally monophyletic mtDNA lineages and allozymes for distinct Peninsular (<i>P. eremicus</i> plus <i>P. eva</i>) versus mainland ESUs; mtDNA lineages defining eastern and western mainland ESUs, but no supporting nuclear evidence available.	FAR WEST (PN, CP) WEST (MO, SO, ST, northwest section of CH) EAST (CH)	Walpole <i>et al.</i> , 1997; Riddle and Hafner, unpubl. data; Avise <i>et al.</i> , 1974)
<i>Onychomys leucogaster</i>	3	Congruence of reciprocally monophyletic mtDNA lineages and morphology for three ESUs.	CENTRAL (GP, Colorado Plateau section of GB) SOUTHEAST (CH)	Riddle and Honeycutt, 1990; Riddle, 1995;
<i>Onychomys torridus</i>	2	Congruence of reciprocally monophyletic mtDNA lineages, morphology, allozymes, and karyotypes for two ESUs defining species <i>O. torridus</i> and <i>O. arenicola</i> .	WEST (most of GB) WEST (MO, SO, ST, CP, far western CH) EAST (CH)	Riddle and Choate, 1986 Riddle and Honeycutt, 1990; Riddle, 1995; Hinesely, 1979; Sullivan <i>et al.</i> 1986
<i>Neotoma albigula</i>	2	Congruence of reciprocally monophyletic mtDNA lineages, morphology, and allozymes for separate ESUs.	WEST (SO, southeast GB, CH west Rio Grande, Rio Conchos)	Planz <i>et al.</i> , 1996; Planz, 1992
<i>Neotoma lepida</i>	3	Congruence of reciprocally monophyletic mtDNA lineages, morphology, allozymes, and karyotypes for three ESUs defining separate species <i>N. intermedia</i> , <i>N. lepida</i> and <i>N. devia</i>	EAST (CH and GP east Rio Grande, Rio Conchos) FAR WEST (PN, CP, SO west of Colorado River) WEST (SO west of Colorado River, MO, GB) EAST (SO, MO, and GB east of Colorado River)	Planz, 1992; Mascarello, 1978

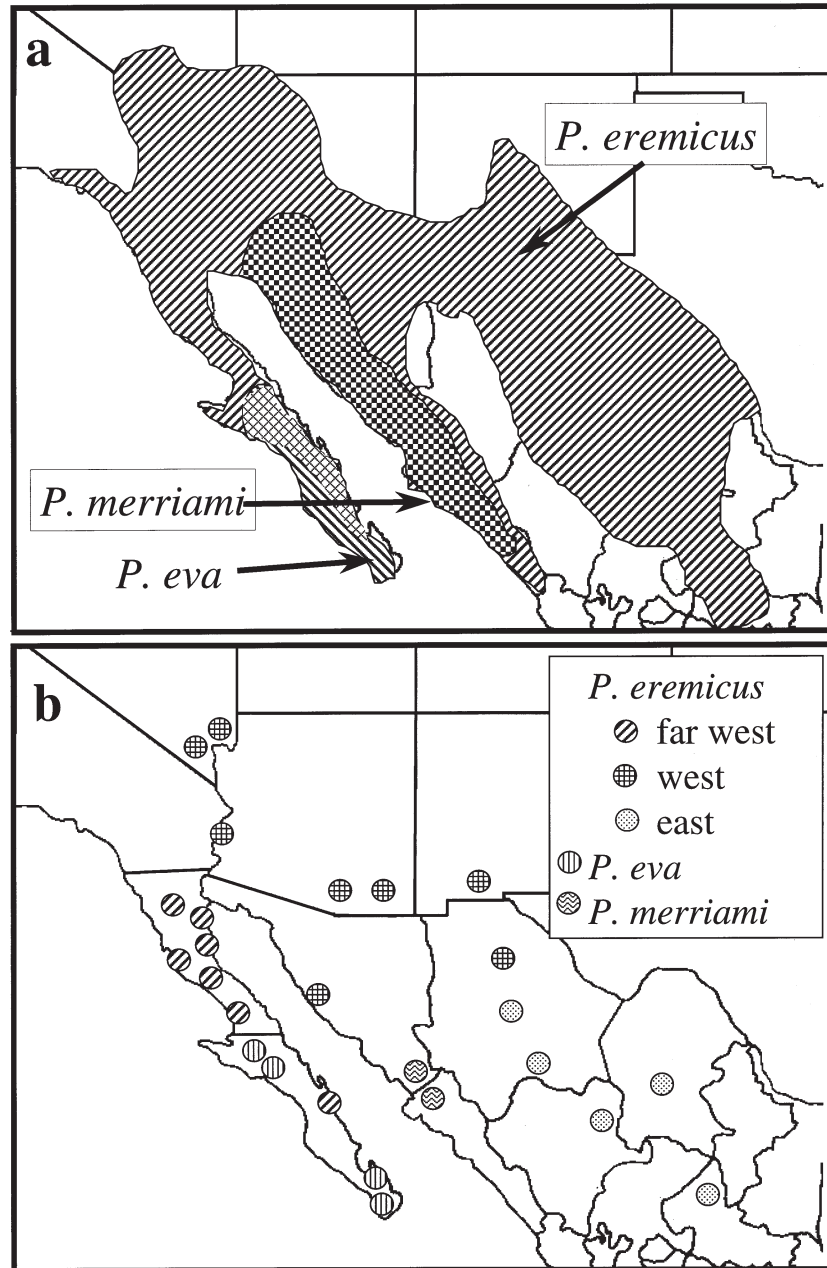


Fig. 1. (a) distribution of three currently recognized species in the *Peromyscus eremicus* species-group (redrawn from Hall, 1981); (b) distribution of mtDNA haplotype lineages (Table 1), with proposed ESUs as listed in Table 1. See text for discussion.

separation, falling within a late Miocene to early Pleistocene time frame (Riddle, 1995). The picture that is emerging suggests that many of the currently recognized species in the North American desert rodent

guild generally do not represent single phylogeographic lineages or ESUs. This pattern of cryptic, intraspecific evolutionary and geographical structure is far from unique to the desert rodent guild, and in fact is

becoming a common feature of phylogeographic assays in many parts of the world and across many kinds of organisms (e.g. da Silva & Patton, 1998; Schneider *et al.*, 1998; Walker & Avise, 1998). Clearly, it seems increasingly dangerous to assume that currently recognized species capture the evolutionary and geographical information critical for evaluating a variety of patterns and processes in ecology and biogeography.

Why restrict biogeographic analyses to species that have been described, for the most part, solely on the basis of morphological characters and are assumed to be reproductively isolated from related species? As stated by Futuyma (1986 p. 222), '... there is nothing mystical or intangible in the difference between species; their differences are amenable to the same analyses as variations within species, and prove to have the same kinds of genetic foundations.' Numerous studies have demonstrated that there is little correlation between levels of genetic differentiation and reproductive isolation among species (e.g. Ayala, 1975; Avise & Aquadro, 1982; Patton & Smith, 1990). We suggest that the time has come to take the blinkers off, and to include as much appropriate information as is available. As a hypothetical example: if any two species that co-occur continuously throughout an area simultaneously experience a single vicariant event, it is certainly possible for only one of the two divided taxa to speciate. Subsequent secondary contact of populations from the two formerly isolated regions would result in three species being recognized based on the biological species concept: one continuously distributed and two sister taxa in the formerly isolated regions. (In the absence of morphological differentiation, it is also possible that the speciation event would remain cryptic). In contrast, ESUs would probably reflect correctly the simultaneous vicariance of both ancestral taxa. If the goal is to reconstruct the historical biogeography of these taxa, ESUs clearly convey more of the appropriate information.

Criterion 3: Monophyletic lineages

It might be argued that the problem with restricted use of the traditional species is only one of scale: that for the most part, species-level taxa do generally reflect natural (i.e. monophyletic) entities. This assumption seems to be a false hope as well. In the desert-rodent system, several examples of paraphyletic or polyphyletic taxonomic species are available. First, *Onychomys arenicola*, formerly part of *O. torridus*, is

actually the sister-taxon to *O. leucogaster* (Sullivan *et al.*, 1986; Riddle, 1995). Second, although rigorous phylogenetic relationships have yet to be established, *Peromyscus eremicus* is clearly not a monophyletic group (Table 1, Fig. 1): the 'far west' ESU is a sister-taxon to *P. eva*; the 'west' and 'east' ESUs are sister-taxa; and *P. merriami* is the sister-taxon to either the 'far west' or the 'west + east' ESUs, making *P. eremicus* a polyphyletic species (Avise *et al.*, 1974; Riddle and Hafner, unpublished data). Third, although additional work is needed to establish phylogenetic relationships, current evidence indicates a paraphyletic relationship between *Neotoma albigula* and *N. micropus* (Planz *et al.*, 1996).

RELEVANCE FOR ECOLOGY AND BIOGEOGRAPHY

The previously stated hope, that revisions in well-studied groups will usually result in only minor changes in species-level taxonomy, is demonstrated here to be a false hope for North American desert rodents, and is unlikely to be true in a wide range of other terrestrial vertebrates. The relevant question for ecologists is: to what extent does it matter that species-level taxa across a wide array of ecologically and biogeographically important assemblages may be unreliable in identifying some taxa correctly, are not natural entities, and often fail to capture significant biogeographic and evolutionary structure? Studies most likely to be compromised by using species as units of analysis if they do not accurately reflect existing ESU structure include: (1) examination of macroecological patterns and processes (e.g. geographical range sizes, shapes, stability); (2) quantification of species and community attributes as they change across a landscape (e.g. diversity gradients, beta-diversity calculations; sizes and geographical ranges of regional species pools); and (3) inferences of historical evolutionary processes, including the evolution of regional biotas, vicariance in response to geotectonic events, dispersal vs. vicariance, range-shifting response to climatic oscillations, and origination of ecological traits. For example, the evident failure of implicit assumptions about species made by Brown & Kurzius (1987) and perpetuated by Kelt *et al.* (1996) seriously call into question their conclusions regarding the predominance of dispersal over vicariant events. If their chosen unit of analysis (species) failed to capture information about regional differentiation, they would necessarily, but incorrectly, have concluded that such differentiation did not exist.

It has been suggested (Mayden & Wood, 1995) that an ESU concept might not really be needed because ESUs do in fact qualify as species under a variety of species concepts. We do not intend to open that contentious argument here; indeed, we are not fully in agreement with each other about species concepts. The more immediate problem is how best to build an operational bridge between the accumulating store of phylogeographic information and the employment of that information by ecologists, biogeographers, and conservation biologists. Given the dramatic nature of changes in our abilities to estimate evolutionary and geographical patterns, every effort should be made to make the use of these data operational by the most efficient means possible. Formal taxonomic revisions based on rigorous molecular phylogeographic information can take years to produce (not to mention the time delay in which those revisions subsequently become incorporated into faunal and floral monographs). As such, researchers in need of the best-available estimates of evolutionary and geographical structure in widespread taxa will generally have inadequate information available by relying solely or primarily on species lists and museum catalogues. We believe it possible to improve on these practical constraints in several ways. We would encourage funding agencies to facilitate projects that seek to develop biotically representative phylogeographic databases (i.e. molecular biotic surveys) for target systems that are prioritized for their intrinsic ecological, biogeographic, and conservation value. For example, a 'North American mammal phylogeographic survey' could combine several objectives of traditional biotic inventory surveys with the logistical efficiency of networking several multi-investigator research laboratories (e.g. as accomplished by the human genome sequencing project). A tangible product of such a programme would be the development of a GIS database of phylogeographic information, perhaps analogous to FAUNMAP (FAUNMAP working group, 1996). In addition to its utility for ecologists and biogeographers in general, we believe that such a database would be extremely useful to conservation biologists, who are called upon to inform decision-makers on issues ranging from the 'importance' of populations and species, to the prioritization of areas as possible biodiversity reserves. The first, critical step, however, is to begin a productive dialogue regarding species vs. ESUs as units of analysis in ecology, biogeography, and conservation biology.

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