Conservation Genetics at the Species Boundary

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Abstract: Conservation genetics has expanded its purview such that molecular techniques are now used routinely to prioritize populations for listing and protection and infer their historical relationships in addition to addressing more traditional questions of heterozygosity and inbreeding depression. Failure to specify whether molecular data are being used for diagnosis-related questions or for population viability questions, however, can lead either to misinterpretation of character data as adaptive information or to misinterpretation of frequency or distance data as diagnostic or historical information. Each of these misinterpretations will confound conservation programs. The character-based approach to delimiting phylogenetic species is both operationally and logically superior to “diagnostic” methods that involve distance- or frequency-based routines, which are unstable over time. Tree-based criteria for the diagnosis of conservation “units” are also inappropriate because they may depend on patterns inferred without reference to diagnostic characters. Intraspecific studies, conservation-related or otherwise, that adopt terminology and methods designed to infer nested hierarchic relationships confuse diagnosis with historical inferences by treating diagnoses as outcomes rather than as precursors to phylogeny reconstruction. A character-based diagnostic approach recognizes the analytical dichotomy between species hierarchies and population statistics and provides a framework for the understanding of each. No species concept, however, should be viewed as an absolute criterion for protecting populations, but as part of a framework from which identification of protection and management goals can be achieved effectively and defensively.

Genética de la Conservación en los Límites del Nivel de Especie

Resumen: La genética de la conservación ha expandido sus alcances a tal grado que las técnicas moleculares son utilizadas abierta de manera rutinaria para priorizar poblaciones a ser enlistadas y protegidas y para inferir sus relaciones históricas, además de abordar preguntas más tradicionales sobre heterocigocidad y depresión por inbreed. Sin embargo, fallos al especificar si los datos moleculares están siendo utilizados para resolviendo preguntas relacionadas con diagnósticos, o para resolver preguntas sobre viabilidad poblacional pueden conducir tanto a la mala interpretación de datos de caracteres como información adaptativa o a la mala interpretación de datos de frecuencia o distancia como información de diagnóstico o histórica, cualquiera de estas interpretaciones confundiría los programas de conservación. Las aproximaciones para delimitar especies filogenéticas basadas en caracteres es tanto operacional como lógicamente superior a los métodos de “diagnóstico” que involucran rutinas basadas en distancia o frecuencia, mismas que son inestables con el tiempo. Los criterios basados en árboles para el diagnóstico de “unidades” de conservación son también inapropiados puesto que pueden depender de patrones inferidos sin referencia a caracteres de diagnóstico. Los estudios intraespecíficos relacionados con la conservación o que bajo diferentes condiciones adoptan terminología o métodos designados para inferir relaciones jerárquicas anidadas confunden el diagnóstico con inferencias históricas al tratar los diagnósticos como productos y no como precursors para la reconstrucción filogenética. Una aproximación de diagnóstico basada
en caracteres reconoce la dicotomía entre jeraquías de especies y estadística poblacional y provee un marco de trabajo para el entendimiento entre ellas. Sin embargo, ningún concepto de especie deberá ser visto como un criterio absoluto para proteger poblaciones, sino como un marco de trabajo a partir del cual la identificación de metas de protección y manejo pueden ser alcanzadas efectiva y defensivamente.

**Introduction**

Scientists and land stewardship specialists have debated the relevance of genetic information to conservation planning in at least three contexts: interpreting population viability (Falk & Holsinger 1991; Loeschcke et al. 1994 and references therein), identifying biological “units” for protection (Ryder 1986; Waples 1991; Amato & Gatesy 1994; Moritz 1994b, 1995; Vogler & DeSalle 1994; Amato et al. 1995); and, most recently, inferring historical relationships (Avise 1992, 1995; Avise & Nelson 1989; Moritz 1995; Avise & Hamrick 1996). Initially, the utility of genetic information was realized at the population level, and debates focused on requisite genetic variability for long-term persistence (Lande 1988; Avise 1989a). More recently, molecular markers have been used for diagnostic purposes; that is, to identify unique groups of populations whose identity may have been masked by described taxonomic epithets.

Several authors (e.g., Cracraft 1983, 1987, 1989; Donoghue 1985; Avise & Nelson 1989) have expressed concern that traditional taxonomic descriptions do not afford a means of examining taxonomic diversity with high resolution, and for this and other reasons the popularity of the biological species concept (BSC) continues to wane among practicing systematists. The BSC, however, is still championed by several population geneticists (e.g., Avise & Ball 1990; Avise & Wollenberg 1997) and retains adherents in the conservation community (e.g., Waples 1991, 1995). Fueled in large part by the advent of molecular techniques, there has been a call for intraspecific examination of biological diversity for the explicit purposes of identifying and prioritizing groups of organisms for conservation (Avise 1989a). A number of authors now routinely employ the paradigm of “intraspecific phyleogeography” (Avise et al. 1987) to recover historical connections among populations using mitochondrial DNA, with an eye toward putting conservation priorities in a more rigorous historical context. Debates now focus on criteria for diagnosing conservation “units” (Moritz 1994b, 1995; Vogler & DeSalle 1994; Vogler et al. 1993b) and on identifying “evolutionarily significant units” (sensu Ryder 1986).

Broadly speaking, each of these endeavors is laudable and merits the attention of the conservation community. We especially applaud the efforts of Avise, Moritz, and their colleagues to introduce a historical biogeographic component of understanding to conservation science. That emphasis followed from the observation that conservation decisions based solely on established taxonomy epithets, especially those involving captive breeding and reintroduction programs, can be misleading. There continues to be considerable confusion, however, over the appropriate utilization and relevance of most kinds of genetic data (Sites & Crandall 1997). We maintain that this confusion revolves around inferring the appropriate biological boundaries to which certain analytical methods can legitimately be applied. Specifically, some studies have confused character data intended for diagnostic purposes with adaptive information geared toward identifying “evolutionary significance” or “evolutionary potential” (Waples 1991; Dizon et al. 1992). Others have suggested applying hierarchic historical information to groups of organisms whose relationships are not necessarily hierarchic (Moritz 1994b; O’Brien et al. 1996). Following Moritz (1994a), we emphasize that there are fundamental differences between interpretations of genetic frequency data within populations and those of diagnostic genetic characters that are fixed within or among populations. This essay is intended both as a discussion of what we consider common misunderstandings of species concepts in the conservation literature and as a primer for conservationists contemplating the use of genetic information to address specific problems. No doubt much of our terminology will be new to an audience of nonsystematists. Given the number of studies devoted to molecular genetics of endangered species and the frequency with which terms such as monophyly now appear in the conservation literature, we attempt to clarify the least accessible terms.

**Pluralism and Mechanism versus Operationalism and Observation in Species Definitions**

One of the more vexing and fundamental issues in biology has been the quest for a widely applicable yet logically sound species concept. Definitions of species remain as hotly argued as ever, paralleled by equally ardent debates on the definition (Moritz 1994b), diagnosis (Vogler & DeSalle 1994), and relevance (Ryder 1986; Rojas 1990) of minimal “units” for conservation prioritization and management purposes. All biological conservation efforts require at least a rudimentary understanding of the boundaries of species and the management
needs of populations. Thus, having long plagued evolutionary biologists, the so-called species problem has now become a stumbling block in the design, implementation, and legislation of conservation programs (Rojas 1990). At issue are the disadvantages of using pluralistic or context-dependent species definitions in the formation of conservation programs and the worthiness of operational approaches as an alternative.

A logically defensible technique for identifying species enhances the scientific as well as the legislative defensibility of species-based conservation initiatives (Sites & Crandall 1997). Conservation demands a species concept that can be applied consistently to organisms with different taxonomic affinities, histories, and breeding and pollination syndromes, while enabling a framework from within which both population and supraspecific issues can be addressed. Any legitimate comparison of entities dubbed “species” requires at minimum that those be defined according to the same criteria. It is meaningless to compare the number of species in two different areas or the diversity of different groups of organisms in a single area if what constitutes a “species” varies from place to place and from taxon to taxon. Just as important, one would hardly wish to sample individuals of different species to determine inbreeding coefficients, levels of heterozygosity, or effective population size.

To the extent that conservation programs rely on species-based information, then, the mutability of species definitions is a problem for conservation biologists, and is chief among the pitfalls remedied by a strictly character-based approach. Suggestions that species be defined on pluralistic or context-dependent grounds have arisen most commonly in mechanistic conceptualizations of species, most of which rely on a suite of potential criteria for species status (Luckow 1995; Hull 1997). For example, the cohesion species concept focuses on “intrinsic cohesion mechanisms” (Templeton 1989). The recognition species concept focuses on “fertilization systems” (Paterson 1985). The traditional biological species concept of Mayr (1969) is limited to biparental sexually reproducing organisms, and its reliance on the potential to interbreed renders it inapplicable in many cases (Hull 1997; Otte & Endler 1989).

Mechanistic conceptualizations of species are both circular and impossible to test empirically (Rieppel 1986; Luckow 1995), and the architects of management and recovery plans should bear these shortcomings in mind. It makes little sense to define species according to processes of speciation because an understanding of speciation relies fundamentally on identification of what species are in the first place. As Garland Allen stated (1980: 359, cited in Loevtrup 1987), “The view that a biologist holds about the nature of species will determine much of what he or she believes about the . . . means by which species arise.” Basing a species definition on observable features is desirable precisely because it obviates reliance on presumed microevolutionary mechanisms of speciation.

Furthermore, a species concept that is generalizable cannot rely on mechanisms of speciation identified a priori; any such criteria used to justify or falsify a species’ status vary too freely to be of use in either an empirical or an applied framework. The phylogenetic species concept allows for consistent applications across taxonomic boundaries because of an attribute that is often underemphasized (e.g., by Mallet 1995 and Hull 1997): it is strictly based on characters. Although many find it tempting to apply their understanding of the temporal behavior of genes within populations to the delimitation of species, systematists consider genetic character information no different logically from other kinds of character information (morphological, behavioral, and ecological; Wayne 1992; Legge et al. 1996). A species concept that relies on attributes of the organisms themselves, be they morphological, molecular, behavioral, or ecological traits, and not on assumptions of their mating dynamics carries the advantage of being applicable to any organism.

### History, Hierarchy, and Diagnosibility

Unfortunately, the phylogenetic species concept has been misinterpreted variously in the conservation and the systematics literature, so a brief review of its salient features is warranted before we explore its relevance to wildlife stewardship.

Introduced by Eldredge and Cracraft (1980) and subsequently expanded upon by Cracraft (1983), Nixon and Wheeler (1990), and Davis and Nixon (1992), the phylogenetic species concept (PSC) identifies the criterion of fixed character states as having the unique potential to distinguish populations or groups of populations. More generally, phylogenetic species represent minimal units that may be analyzed phylogenetically. Most critical to this essay, the PSC purports to identify the boundary separating reticulating and hierarchically related organisms from groups of organisms whose relationships can be represented as a nested hierarchy. In theory the PSC thus identifies the boundary above which nested hierarchies represent biological reality and below which hierarchy-generating “phylogenetic” operations are inappropriate.

It is valuable to explore the relationships between observable attributes of organisms, their distinction as species, and their prioritization in conservation programs. Our focus is thus the boundary between groups of organisms united through these two kinds of history: reticulating (or “tokogenetic”) genealogical connections (such as the individuals in a population of bi-parental organisms) and those whose relationships are best represented hierarchically. Although earlier authors have emphasized this distinction in the context of phylogenetic...
systematics (Davis & Nixon 1992; Luckow 1995; Brower et al. 1996) and conservation biology in particular (De-Salle & Vogler 1993), discussions of the PSC in the conservation literature remain largely confined to the importance of maximizing resolution among groups of organisms. Following Davis and Nixon (1992), Luckow (1995), and Brower et al. (1996), our emphasis is on the necessity of understanding the level below which a hierarchical resolution in the form of cladograms is no longer an appropriate portrayal of nature and will likely mislead conservation priorities. Our premise is that biological entities can be united through two kinds of history—reticulating genealogical connections and cladogenetic relationships that are most appropriately represented by nested hierarchies—and that these comprise complementary but logically distinct spheres from within which to approach conservation-related questions. The distinction of entities from one another, regardless of whether one wishes to bestow them with formal specific epithets, is a separate scientific operation from the investigation of variability within those entities, and such diagnoses must logically precede inferences of their historical relationships as well.

The relevance of Hennig’s (1966) original distinction between latticed networks of organismal connections and hierarchic networks derives from the twin observations that (1) cladistic analysis always retrieves a hierarchically depicted result (a cladogram), regardless of whether the units being analyzed are themselves related hierarchically (Davis & Nixon 1992), and (2) that relationships such as those among parents, children, and cousins in sexual populations cannot be depicted accurately as such nested hierarchies (Luckow 1995). It follows that there must be a level below which the interpretation of the results of cladistic analysis as “phylogenetic” is inappropriate. The PSC addresses that boundary, and phylogenetic species are the minimal aggregates of organisms for which phylogenetic analysis (sensu Davis & Nixon 1992) is legitimate. It is readily seen that when the underlying relationships among things are not hierarchal, a numerical procedure such as cladistic analysis that necessarily shoehorns those things into a hierarchical framework will lead to spurious results. Bremer and Wänntorp’s (1979:624-625) statement applies here: “A hierarchic description of a fishing net would be a kind of description indeed but it would certainly be a very poor one.” The phylogenetic species “concept,” then, is less of a definition than it is a criterion specifying that such a boundary exists.

Although this distinction highlights the logical asymmetry between the PSC and other species concepts, the abstract condition of underlying hierarchy does not in itself provide a means of identifying hierarchically related groups themselves. To remedy this shortcoming, Davis and Nixon (1992) suggested the procedure of population aggregation analysis (PAA), which identifies the most inclusive groups of organisms united by fixed or diagnostic character states.

Unfortunately, unwillingness to rely on character-based diagnoses to interpret the limits of hierarchical inference has resulted in three related classes of data misinterpretation in the conservation literature: the interpretation of frequency data or lumped similarity (phenetic) data as species-diagnostic; the interpretation of raw character data or character frequency data as somehow adaptive or reflective of “evolutionary potential”; and the application of hierarchy-based concepts and terms to nonhierarchically related groups of organisms from which inference of biological or biogeographic history is spurious. We discuss these in turn.

**Diagnosibility versus Frequency and Distance Data**

Species diagnosibility is critical to conservation programs that claim a foundation in organismal information. Recognition of phylogenetic species is based exclusively on observable attributes of individual organisms. The kinds of molecular genetic character data that are capable of meeting these requirements are confined to DNA sequence data and the characterization of specific alleles. Unfortunately, methods of systematics that have fallen out of favor in that field retain adherents among conservation biologists. Ironically, they are precisely the methods most certain to mislead the design of conservation programs. Distance data and continuous or morphometric data are cases in point. Although the use of distance methods (including, for example, DNA-DNA hybridization and analysis of allele frequency data) to recover phylogenetic relationships has been rejected by systematists for more than a decade, recent contributions to the conservation literature have not taken the shortcomings of these techniques into account (e.g., Fjeldså 1994; Haig & Avise 1996; O’Brien et al. 1996). Continuous or lumped similarity data provide no unequivocal means of diagnosing species or conservation units. Under any distance measure, two entities may erroneously appear highly divergent from each other without either being characterized by a single feature. Two such entities may likewise appear as “sister taxa” without being united by a single shared character (Fig. 1). In fact, under certain species concepts that claim a foundation in phylogenetics, some individuals are unassignable to any species whatsoever (Nixon & Wheeler 1990).

**“Evolutionarily Significant Units” and “Evolutionary Potential”**

Various authors have proposed guidelines for management design based on notions of “evolutionary poten-
"evolutionary potential," hence the genesis of the "evolutionarily significant unit" (Ryder 1986). Ryder's discussion is explicitly tied to the use of genetic distances to infer "evolutionary potential"; suggestions that recognition criteria be based on various forms of continuous data (including morphometric, genetic distance, and allele frequency) have been grounded in that premise.

Ryder's (1986) coinage of the evolutionarily significant unit is also a reasonable attempt to provide conservationists with a means of sidestepping oversimplifications caused by taxonomic epithets believed too imprecise. But the stated appeal of this notion stemmed from the perceived need to protect "locally adapted gene pools." Ryder and Moritz both justified the use of character divergence by recourse to the evolutionary "significance" of character change, arguing alternatively that such change be interpreted as adaptive (Ryder 1986; Waples 1991), or that character change leads to novel evolutionary trajectories and, presumably, the potential for future adaptation and macroevolution (Moritz 1994b). This of course requires some arbitrary means of deciding how much character change is evolutionarily "significant."

Notions of "evolutionary potential" also have been used to justify the use of continuous data as diagnostic tools, and herein lies an additional flaw. If evolutionary potential refers to the prospects for evolutionary change, one may well wonder how that change will be achieved without causing a concomitant change in the allele frequencies that were themselves used to identify the units of protection in the first place. In this case the criteria by which two populations were "diagnosed" change as soon as allele frequencies diverge, leading to a shifting baseline syndrome of sorts. Although three hypothetical populations bearing different allele frequencies might each be in Hardy-Weinberg equilibrium, any frequency change in a bi-allelic system entails departure from that equilibrium. For evolutionary "potential" to be realized, the allele frequencies initially used to diagnose the populations in question must change, and thus the initial basis for distinguishing those populations must change as well, even if the populations remain distinct. This leads to a logical shell game wherein the justification for diagnostic criteria requires that the criteria themselves change.

More generally, assumptions about adaptation serve only to confuse the relevance of character information to conservation priority setting. To the extent that the process of adaptation is not accompanied by fixed characters at a level discernible by scientists, we find it difficult to imagine how one might identify it at all, much less set about protecting it. Nonetheless, the protection of the evolutionary process or the potential for evolution in the broad sense is an important goal, much like the protection of "biodiversity" in the broad sense. But like biodiversity, evolutionary potential is not precise...
enough a term to be useful in specific conservation programs or at scales relevant to site-specific conservation. We concur with Moritz (1994a) that evolutionary “significance” is effectively arbitrary, that “potential” thus refers to an unknowable future and is thus too vaguely articulated a concept to be immediately useful. But a species concept must lend itself to recovering past historical relationships if it is to succeed in that context.

Species from Fixed Character Differences or from Trees

Avise (1989b) and Avise et al. (1987) have championed the notion that species fall along a continuum of biological entities, none of which is necessarily any more discrete than the others. This notion is the premise of Avise et al.’s “intraspesific phylogeography,” which uses hierarchical relationships among individuals inferred from mtDNA to examine micro-biogeographic questions. Mitochondrial genomes, being maternally inherited and essentially clonal, are necessarily related in a nested hierarchical fashion. But a problem arises when a cladogram representing that mitochondrial hierarchy is equated with the historical relationships among organisms. Following the lead of Avise and his colleagues, many conservationists now routinely use cladistic algorithms to assess the relatedness of organisms (that is, to make cladograms that are supposed to reflect the relative recency of common ancestry) by analyzing mtDNA sequences. The relevance of this phylogenetic approach to conservation is illustrated by the now-famous example of the Dusky Seaside Sparrow (Ammodramus maritimus nigrescens; Avise & Nelson 1989), whose last captive individuals were bred with individuals from a distinct lineage. The result was a hybrid of sorts whose relevance to the maintenance of the original Dusky Seaside Sparrow population is questionable. Avise correctly pointed out that an understanding of the historical connection among sparrow populations would have been useful in the captive breeding program by virtue of suggesting an appropriate source population.

Unfortunately, the paradigm of “intraspesific phylogeography,” taken alone, may be an inappropriate paradigm for introducing phylogenetic histories to conservation endeavors. Although Avise’s stated hope in generating such cladograms is to uncover phylogenetic history at the finest levels, that goal is compromised by interpreting the hierarchically depicted relationships among mitochondrial haplotypes as relationships among organisms that are not hierarchically related (Fig. 2). In our review of the literature on the conservation genetics of endangered organisms, none of the authors who have explicitly couched their analyses in the framework of intraspesific phylogeography discuss any of these issues. Some authors (e.g., Miththapala et al. 1996) even use phylogeography to resurrect and claim new relevance for the subspecies (“phylogeographic subspecies”), a concept regarded as empirically defunct since the 1950s.

Failing to recognize the appropriate lower boundaries of hierarchic inference has also confounded the use of hierarchic terms and concepts that are fundamentally necessary to interpret the relationship between the molecular characters of organisms and their histories. Avise and Moritz have both suggested that “monophyletic” or “reciprocally monophyletic” taxa are of use in prioritizing conservation efforts. In the topological (cladogram-based or “tree-based”) criterion of reciprocal monophyly, taxa are considered legitimate candidates for protection only when both they and the members of their sister “taxon” are united as separate “monophyletic” units arising from a single node (Fig. 3). Such usage perpetuates a notion dating to Donoghue’s (1985) coinage of the “monophyletic species concept” that is repeated by several authors in the systematics literature. But the use of “monophyly” at infraspesific levels is simply inappropriate. As Nixon and Wheeler (1990), and Luckow (1995) have all explained, the criterion of monophyly is neither desirable nor meaningful below the species level because the interpretation of monophyly depends fundamentally on an underlying hierarchy among the terminals being analyzed. Because there is a level below which representation of terminals as hierarchical is not accurate, that level also dictates where the identification of monophyletic groups is appropriate. Under a character-based approach (as opposed to a tree-based one), all individuals are assignable to species or “units” without it being necessary to determine their relationships to one another (Fig. 3).

Perhaps more critical than the connection between monophyly and underlying hierarchy is that between monophyly and characters themselves, an issue never discussed by the proponents of reciprocal monophyly in conservation. Monophyly, paraphyly, and polyphyly are, above all else, character-based terms. But in three papers devoted to the applicability of reciprocal monophyly to conservation, Moritz (1994a, 1994b; 1995) never critically discusses alternative methods for recovering such relationships. The use of distance methods that have only weak connections to character data is consistent with the use by Moritz and others of “monophyly,” but that use is incorrect. As Farris (1991:304) put it, “Without characters, paraphyly and polyphyly mean nothing.”

Avise and colleagues made the interesting observation that cladistic analyses of successive generations within a population tend to show a progression from polyphyly through paraphyly to monophyly (Avise 1994; Avise & Ball 1990). Those authors do not point out that two groups of organisms may achieve “monophyly” with respect to a given gene system—even reciprocal mono-
phyly—without having achieved character fixation. With respect to another putative species, then, the “achievement” of monophyly is not necessarily coincident with character fixation, but this is irrelevant under Avise’s or Moritz’s scenarios because even after character fixation has happened, the topology of sampled individuals will almost certainly be polyphyletic or paraphyletic with respect to other (unsampled) individuals in their respective population. Sampling is thus no less a problem for tree-based approaches than for character-based approaches, and mutually exclusive character fixation is clearly distinct from reciprocal monophyly. If one adheres strictly to the PSC, then whether or not some individuals within a particular phylogenetic species are

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**Figure 2.** Example of the problem of enforcing hierarchic depictions of relationships among nonhierarchically related entities. Each figure (a–e) depicts the relationships of haplotypes in the same population of 10 individuals in a sexual diploid population for eight generations: (a) the reticulating network for a nuclear gene system and (b) the maternal mtDNA system. Position of one individual in (a) is the same as in (b). Star above the column of males represents a series of direct male-line descendants. Generations are numbered in reverse, and arrows identify three generations in which the maternal haplotypes indicate that the male in generation “D” is not part of the same mtDNA “clade” as his son or his father. Arrows in generations C, D, and E correspond to the males in mitochondrial cladograms in (c), (d), and (e), and the position of the male line shifts clades from one generation to the next when the cladogram is constructed exclusively on the basis of mitochondrial data. No genealogies are drawn for the reticulating bisexual diploid system because of the reticulating nature of the nuclear marker. The male indicated by the arrow in (c) is the father of the male indicated by the arrow in (d), and the male indicated by the arrow in (d) is the father of the male indicated by the arrow in (e). Although males indicated by arrows are direct descendants of one another, they are obviously not all members of the same mtDNA clade.
more or less closely related to each other than to mem-
bers of their own is simply irrelevant to the reconstruc-
tion of relationships among species.

The glib application of cladistic analysis to nondiag-
nosible entities and the interpretation of resultant group-
ings as “monophyletic” are manifestations of a common
failure to recognize the limits of applying phylogenetic
analysis to conservation. Phylogenetic interpretations of
cladistic analysis depend fundamentally on the presence
of an underlying hierarchy to begin with. Yet a common
conception of the relevance of phylogenetic informa-
tion to the diagnosis of natural entities generally and to
the PSC in particular is that diagnosis is itself somehow
cladogram- or topology-dependent (i.e., that it follows
cladistic analysis). Mallet (1995), for example, while not-
ing the desirable aspect of enhanced resolution inherent
in the PSC, expresses confusion as to what he perceives
as circularity in the delineation of phylogenetic species.
Mallet raises the question of how one might base a spe-
cies definition on topology when the relationship
among terminals in that topology is inherently depen-
dent on those terminals having been identified accu-
rately prior to the analysis (Cracraft 1997). Mallet (also
Dizon et al. 1992; Haffer 1992) simply conflates the diag-
nosis of phylogenetic species with the hierarchic repre-
sentation of their relationships. Although Mallet’s point—
that species definitions should not be tree-based—is
analogous to our indictment of reciprocal monophyly, in
no way does it pertain to the PSC, as Mallet suggests,
because the PSC relies on a strictly character-based operation.

Moritz (1994a) suggests that diagnoses based on mito-
chondrial characters be corroborated by other charac-
ters (nuclear ones, for example), and that “units” thus
corroborated bear the highest priority for protection. Al-
though we endorse the view that species delineations
should be as robust as possible and should be supported
by as many fixed characters as are available, the require-
ment that topologies generated from separate analyses
of different character sets be congruent is flawed. This is
especially so when terminals are inappropriately chosen. Rather than rely on tree-based species definitions, we suggest that pooled population aggregation analyses of mitochondrial and nuclear data precede any tree-
based diagnoses.

Some scientists may object to the methodological par-
titioning of the schools of systematics and population
genetics. Indeed, Avise et al. (1987:490) referred to “the
stream of heredity that is phylogeny” and stated, further,
that “[T]oo many systematists and population geneticists
continue to operate in largely separate realms, employ-
ing different languages and concepts to address issues
that should be of importance to all.” We concur that the
two endeavors of evolutionary biology complement one
another, but simply combining desirable aspects of each
field into a philosophical patchwork does not engender
a more powerful form of inquiry. Explanatory power is
not additive when logical frameworks are confounded,
and the donning of this philosophical motley cannot en-
hance the conservationist’s ability to provide sound an-
wers to logically different types of questions. In our
view, the conclusions of systematics and population ge-
netics complement each other best—and are most suc-
cessfully realized—when it is recognized that the meth-
ods of each field are designed to address different kinds
of questions and are applied appropriately as such. Per-
haps the most rewarding investigations will be those
aimed at understanding the differences between the two
fields of inference, rather than arguing for their amal-
gamation.

**Diagnosibility and Setting Priorities**

Although conservation programs routinely develop re-
cov r y programs for species across their ranges, in situ
management is necessarily conducted at the population
level. Conservation biologists have sometimes assumed
that, to justify protection of an individual population or

![Figure 3. Three (of many possible) sce-
narios illustrating the distinction between
character-based species concepts and tree-
based species concepts. Hash marks indi-
cate diagnostic characters. Letters a–d
represent individual members of two pu-
tative species. Taxon O is an outgroup
used to root the tree. Lines drawn above
the terminals indicate where species des-
ignations would be made under both
tree- and character-based frameworks.
Only under the scenario of “reciprocal
monophyly” with character support do
tree- and character-based operations con-
cur on the delimitation of species.](image)
specific group of populations, they must demonstrate that the populations being managed, or management units, are diagnosibly distinct. The term management unit, however, has been used inconsistently in the literature. We refer to the management unit as an individually managed population rather than a group of populations managed collectively by virtue of collective management goals.

It should go without saying that a requirement of distinctness to warrant protection is overly restrictive. Under such a requirement, if two disjunct populations are biologically "equivalent" (to the best of available information), there is less scientific (and legal) justification for protecting either of them. To take this approach to its logical extreme would be to implement a Noah's Ark strategy in which organisms are protected in zoos, gardens, and gamete collections without regard for their habitats, life histories, and co-occurring species. Rojas (1990) called attention to various risks of protecting groups of organisms based on typological criteria alone. Primary among these is the certainty that protection based on established taxonomy alone will fail to account for the range of variability, a warning reminiscent of Avise's points to the same effect. The limitations of typology-based conservation decisions reside not just in the application of typology (or diagnosibility), but in the fact that such applications are not explicitly tied to any philosophy of area-based conservation. The PSC, in approaching the population more closely than traditional species concepts, allows for more precise phylogenetic inference and potentially for the identification of biogeographically unique areas at scales more directly relevant to conservation programs.

The importance of fixed character information is evident from Vogler (1994), who described a common biological scenario wherein a series of populations exhibits clinal geographic variation, with no single population characterized by fixed, unique character states. There are compelling reasons, both scientific and legal, to promote parochial conservation programs (Lesica & Allendorf 1995), and Vogler pointed out that failure to protect even undiagnosible populations (so called linker populations) can result in character fixation in other populations that become isolated. In other words, inadequate range-wide protection measures for a single species can potentially result in more unique, threatened entities that are themselves more urgently in need of protection.

In cases where ex situ captive breeding and reintroduction programs become necessary, consistent guidelines are required to direct independent management programs. The PSC has the potential to inform such programs. Proponents of captive breeding programs designed to facilitate biological restoration and management through reintroduction must still decide for themselves which paradigm best suits the goals of the program in question; more specifically, whether to approach the problem as one of recreating historical pattern or as one of reenacting historical process (Moritz 1995).

To understand this point, it is useful to consider again the data set of Vogler and DeSalle (1994) and Vogler et al. (1993a) for the Northeastern Beach Tiger Beetles (Cicindela d. dorsalis), which comprises one of three subspecies found on beaches along the eastern and southern United States. Having declined precipitously from its former range as a result of widespread use of recreational off-road vehicles, it was recently (1990) listed as threatened under the U.S. Endangered Species Act. The DNA sequence variation in this species may be characterized as clinal, with only one population diagnosable by fixed character data (a single base pair on the cytochrome oxidase III gene). That population is currently at the northern limit of the species' range, and one of the questions facing the recovery team is where to draw stock for restoration in both the northerly and southerly parts of the organism's range. Drawing from the disjunct Massachusetts population to restore the species to nearby historical sites makes sense from the standpoint of retaining the distribution of characters that distinguish the remnant population(s). But it is also clear that C. d. dorsalis is southern in origin, and one could argue (we do not) that drawing livestock from the south simulates the dispersal events that actually occurred when the species was originally expanding its range.

Objections to the Phylogenetic Species Concept in Conservation

Although some authors (e.g., Mayden & Wood 1995; Mayden 1997) concur that a single, consistently applicable species concept is desirable, they conclude that the PSC is inferior to the evolutionary species concept as a conservation tool. This resistance to the PSC appears to rest on the conflation of macro- and micro-evolutionary paradigms for interpreting genetic data, a point we hope to clarify.

Some authors (e.g., Avise 1989a; Moritz 1994a) appear to have abandoned the PSC for conservation purposes on the grounds that it will require protecting too much. Still other authors (e.g., Waples 1995) have criticized the PSC on precisely the opposite grounds, arguing that the PSC will not suffice to protect genetically “distinct”—but not diagnosible—populations under the U.S. Endangered Species Act (Waples 1991). That last argument fails by trying to apply identical criteria to the delineation of populations and species, and Waples concludes that the PSC is insufficient to address population-level questions. In point of fact, the ability of the PSC to delimit the boundary between populations and species
is precisely its strength and in no way obviates the usefulness of methods employed by Waples to evaluate subspecific stocks for conservation. Diagnosibility is just the beginning of understanding conservation priority, and incorporation of the PSC does not—either scientifically or legislatively—detract from the broader mission of protecting either particular populations or, more broadly, intraspecific diversity.

Moritz (1994a, 1994b) as well as Avise and Ball (1990) suggested that mtDNA alone is not sufficient to diagnose species because theory predicts that mitochondrial characters will become fixed more rapidly than nuclear ones; hence, they will not reflect “true” species boundaries. Their suggestion that nuclear data be used to “corroborate” mtDNA data once again illustrates the discrepancy between their approach and ours. Moritz and Avise simultaneously view species as parts of a continuum and as “real” objects of empirical discovery in nature. Again, we view species as elements that form the groundwork for understanding the hierarchy of life and that do not necessarily correspond to “real” entities that are validated or invalidated by competing sources of character data. Whereas Avise and Moritz view mitochondrial and nuclear DNA as independent “tests” of a species’s identity as a species, we view them simply as separate sources of character data. In our view, therefore, the fact that mitochondrial characters become fixed more quickly than nuclear characters is not a drawback. To the contrary, that fixation may occur more readily is, if anything, a boon to understanding the more recent history of speciation events and microbiogeography.

Finally, some critics of the PSC argue that it is “static” or unstable either to the sampling of additional individuals and character data or to the erasure of existing character data (by introgression, for example). In contrast, we view all scientific hypotheses as tentative, pending availability of more data. The availability of more data. The potential for extinction is no reason to abandon the endeavor of recovering historical pattern, and the possibility that available data (in this case, sampling of characters or individuals) might be “wrong” is not a sufficient reason to ignore them. Again to the contrary, the likelihood that such pattern might one day be erased is all the more reason to explore it.

Conclusion

Conservation requires a criterion for delineating species that is not only consistent across taxa but that also frees us to explore intraspecific variation without having to worry about our species suffering from shifting boundaries due to inconsistent definitions. The PSC and its operational precursor, population aggregation analysis (Davis & Nixon 1992), approach these requirements. In addition, the PSC provides a means whereby the definition of species more closely approximates that of the population, thus linking species-based protection to an explicitly area-based philosophy. In this way, biogeographic information may become useful at scales relevant to conservation programs. The PSC is thus a solution to competing definitions and to the problem of definitional pluralism; it reflects the logical asymmetry between species and other taxa that gets confused by other “phylogenetic” applications (Mayden 1997).

Diagnosibility should not be viewed as a minimum requirement for justifying protection. A complete understanding of the finest level of resolvable hierarchy is not feasible, nor should it be necessary to justifying and implementing management; a given population should not be excluded from protection simply because it does not constitute a phylogenetic species. The extent to which individual populations are to be protected is necessarily subject to other criteria, and species-limited efforts will likely diminish as the effectiveness of protecting natural areas and ecosystems is realized. On this point we agree with Moritz (1995) that molecular data may help to identify and prioritize regions that support cryptic, recently evolved organisms. Given that conservationists rarely have the luxury of choosing large areas to protect, it is likely that such data will prove useful primarily through the identification of smaller areas that support populations of phylogenetically distinct organisms (Vogler & DeSalle 1993b, 1994a), an endeavor that we argue is best served by adherence to the PSC.

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