

# Species concepts in systematics and conservation biology – an ornithological viewpoint

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## ABSTRACT

The biological species concept (BSC) has dominated within ornithology since the 1930s, but the past decade has seen increased application of the phylogenetic species concept (PSC). The central role of species concepts is to delineate the units of nature and thus provide the essential framework for understanding biological diversity. The PSC does this more objectively than the BSC. Many conservation biologists, particularly those who manage *in situ* and *ex situ* breeding programmes, have recognized that the BSC is inappropriate for this task. Their solution, 'evolutionary significant units (ESUs)', has gained wide support within the conservation community, yet it has significant problems. There is no general support on how to define ESUs nor apply the concept objectively. Perhaps more important, ESUs have no status within formal taxonomy, hence they have no standing within those legal instruments designed to conserve and use sustainably biological diversity. Phylogenetic species, as basal diagnosable units, are effective functional equivalents of ESUs, have standing in formal taxonomy, and have many advantages over biological species when applied to conservation and management problems. It is suggested that the concept of ESU be abandoned and that the PSC become the taxonomic currency of conservation biology.

## 16.1 INTRODUCTION

The discipline of ornithology has had a large influence on the debates over species concepts. Ornithologists such as O. Kleinschmidt and E. Hartert,

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and later Erwin Stresemann and Bernard Rensch, were among the first to see the importance of species concepts and begin the shift toward the so-called polytypic, biological concept. In their midst was a young systematist, Ernst Mayr, who became the leading advocate for the biological species concept (BSC) and who remains an active partisan over 50 years later (Mayr, 1942, 1963, 1970, 1992, 1993). Since Mayr's influential work of 1942, many avian systematists whose primary interest was geographic variation and speciation analysis adopted the BSC (Short, 1969; Mayr and Short, 1970; Selander, 1971; Bock, 1987; Haffer, 1992).

In recent years support for the BSC within ornithology has waned as systematists have adopted a phylogenetic species concept (PSC; Cracraft, 1983, 1989; McKittrick and Zink, 1988). Although the latter is not strictly a cladistic concept – in fact, there has been debate within cladistics over species concepts – the notion of phylogenetic species has found strong support among those avian systematists who see hypotheses of the history of taxic differentiation as being at the conceptual centre of the analysis of geographic variation and speciation.

The purpose of this chapter is not to revisit the debates over species concepts within ornithology (see Haffer, 1992, for a review from the perspective of a supporter of the BSC). The reasons for adopting the phylogenetic species concept within ornithology are compelling and have been discussed elsewhere (Cracraft, 1983, 1989; McKittrick and Zink, 1988; see also many papers cited below). The first section, instead, touches on some conceptual and linguistic arguments that tend to obfuscate understanding of the differences and implications of adopting alternative species concepts, no matter which group of organisms might be considered. The second section attempts to dispel several myths about the phylogenetic species concept. Following this, a section is devoted to a brief comparison of the BSC and PSC to illustrate their different implications for systematic and evolutionary biology. Finally, the last section examines the role of species concepts within conservation biology. Biologists have begun to recognize the implications of alternative species concepts when considering the units underlying conservation action and sustainable development, yet systematists have played little role in shaping this discussion.

## 16.2 SPECIES IN THEORY AND PRACTICE

### 16.2.1 The language of discourse

One underlying reason for the ongoing debates over species concepts and definitions, and what they mean theoretically and empirically, is the structure of the discourse itself. How species might be recognized becomes confused with how species might be defined. The evidence used in recognizing species is often taken to be more or less equivalent to the definition of a species. Biologists speak of morphological species,

genetic species, genotypic species, or behavioural species as if they are conceptually on the same level as biological species, phylogenetic species, or evolutionary species. The latter, more theoretical, definitions are often conflated with the evidence perceived to be at the heart of applying those definitions. Thus, biological species are taken to be genetic whereas phylogenetic species are characterized as being morphological. Inasmuch as genetic, morphological, behavioural, or other kinds of character data can be used to delimit species boundaries within the context of any view of species, such language serves only to confuse the dialogue over alternative species concepts. Notions of genetic species, genotypic species, or morphological species are inherently confusing and often non-sensical.

Equally unhelpful is the use of pejorative language in characterizing some species concepts as being typological, non-populational, or non-biological as is sometimes done by advocates of the BSC (Mayr, 1992; Haffer, 1992). Proponents of all species concepts use populational thinking inasmuch as they would not knowingly consider placing different sexes, morphs, or different stages of a life-cycle in separate species. Mistakes can happen under the guise of any species concept, but the biological species concept, simply because the word 'biological' appears in its name, is not inherently more biological, populational, or genetic than is the phylogenetic species concept. Likewise, the latter is not more inherently morphological. It is also not useful to characterize some concepts as being purely theoretical, in contrast to others that might be said to be practical or empirical. All definitions, no matter how empirical they may sound, are theory laden and rely on some conceptual understanding of other terms.

### **16.2.2 The structure of species definitions**

Unless species concepts are used to individuate real, discrete entities in nature, they will have little or no relevance for advancing our understanding of the structure and function of biological phenomena involving those things we call species (Cracraft, 1987). Debates over species concepts rarely include much discussion about this. Perhaps systematists just take for granted that species are discrete entities, but this is not evident in some of the debates (nor has it been true in practice, especially within palaeontology where a nominalist-like view of species has long prevailed). If species are not considered to be discrete real entities – and holding this view does not mean that delimiting boundaries will always be straightforward or that the boundaries cannot be fuzzy depending on the spatiotemporal scale of the observer – then it implies that evolutionary and systematic biology would be based largely on units that are fictitious, whose boundaries, if drawn, are done so arbitrarily. It would also mean that most, if not all, of the processes that we ascribe to species are concoctions

of the mind and have no objective reality. Entities of postulated processes must be real and discrete if those processes are to have much meaning. Having a theory about the behaviour of electrons, for example, makes no sense if electrons do not exist as discrete entities; the same is true for species. The notion of discreteness, clearly, must be contextualized with respect to a certain spatiotemporal frame of reference, and different perceptions of the latter can lead biologists to see species as being discrete, real things, on the one hand, or as arbitrary segments of evolutionary continua, on the other (Cracraft, 1987).

Unless a species concept can be used to individuate real-world entities, that concept will have limited utility for systematists getting on with their task of sorting out and understanding biological diversity. Both the BSC and PSC are meant to be guides to the practice of recognizing species, but they do not do so in the same way or equally effectively. Some biologists think the primary task of species concepts is to understand process-level phenomena. Important though that task may be, the view taken here is that the central role of species concepts is to delineate the units of nature and thus provide the essential framework for understanding life's diversity.

Species definitions should have three key elements if they are going to be useful for systematic practice:

1. They need to mention or imply reproductive cohesion (be populational) in order to provide a conceptual basis for including males and females of the same population in the same species.
2. They must have some notion of diagnosability so that populations or groups of populations can be distinguished one from another.
3. They must include some criterion for ranking these populations at the species-level as opposed to some other level of the Linnean hierarchy.

The definition of biological species – a group of interbreeding natural populations that is reproductively isolated from other such groups (Mayr, 1963) – has the first two of these key elements. 'Interbreeding natural populations' implies reproductive cohesion, and the phrase 'reproductively isolated' provides for some basis of diagnosability (if one assumes there are character-based differences that lead to reproductive incompatibility). Yet the definition is inherently flawed because it does not provide any specific framework for ranking. Proponents would like to use the conjunction of 'interbreeding' and 'reproductively isolated' to rank an entity at the species-level. The definition, however, sets no bound on where species limits might be drawn, only that it will stop at some point of 'reproductive isolation'. Yet, few supporters of the BSC would claim that all populations capable of interbreeding should be included in the same biological species, and considerable difference of opinion exists among supporters of the BSC over how much (or little) interbreeding is necessary and/or sufficient to justify uniting populations in the same species. In fact,

it is the difficulty in reconciling these two components of the BSC that has led many biologists over the years to abandon it in practice.

In contrast, the definition of phylogenetic species – the smallest population or group of populations within which there is a parental pattern of ancestry and descent and which is diagnosable by unique combinations of character-states (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Cracraft, 1983; Nixon and Wheeler, 1990) – has all three key elements. The phrase 'parental pattern of ancestry and descent' implies reproductive cohesion over time; the element of diagnosability is specifically mentioned; and the statement referring to the smallest population establishes the basis for ranking (that is, the boundary to species limits is the smallest population or group of populations that is diagnosably distinct).

### 16.3 THE PHYLOGENETIC SPECIES CONCEPT: SOME MYTHS AND MISREPRESENTATIONS

Growing support for the PSC within systematics has resulted in various reactions from those – primarily non-systematists – whose traditional allegiance has been to the BSC. This reaction has included a significant amount of misunderstanding about the PSC: what it is, how it might be applied, and what might be the consequences of using it broadly within systematics and evolutionary biology. Several of the most important misunderstandings deserve discussion.

As already noted, linguistic characterization can go far in casting aspersions on a particular species concept without actually facilitating a rational dialogue about it. Describing the PSC as being purely morphological or non-populational (Mayr, 1992), and therefore typological, for example, does little to further scientific discourse about species concepts because the description is patently false. The PSC is defined in terms of populations and their diagnosability, and nowhere in the definition does the word morphological appear. Indeed, systematists will want to use all relevant data when determining species limits under the PSC. The fact remains that most of the information available to systematists – no matter what definition they adhere to – is morphological, yet this does not make a definition, including even the BSC, non-biological or non-populational. A strength of the PSC is that it can be applied using only morphological data. The PSC is centred around the notion of diagnosability, which can be inferred more or less directly from morphological data; the BSC, in contrast, relies on an understanding of reproductive isolation, which can be inferred only very indirectly from morphological data.

The PSC is sometimes mistakenly interpreted as being a cladistic concept (Haffer, 1992; Mallet, 1995), and although cladists have been among the strongest proponents of the PSC within systematics, over the years a number of species concepts have been used by cladists. One perception

that has arisen from the association of the PSC with cladism is that phylogenetic species are defined by apomorphies, or derived characters (Mallet, 1995), that they are (or must be) monophyletic (Haffer, 1992), or that they are somehow based on phylogeny (Mallet, 1995). Whereas it is true that some have supported defining phylogenetic species in terms of the smallest populations having apomorphic characters (Rosen, 1978, 1979) and that phylogenetic species should be monophyletic (McKittrick and Zink, 1988), others have argued that not all diagnosably distinct populations may have characters inferred to be derived yet those populations still deserve taxonomic recognition [Nelson and Platnick, 1980; Cracraft, 1983 (contra Mallet, 1995: 298), 1989]. Although the populations included within a phylogenetic species that is diagnosed only in terms of primitive characters may actually represent more than one phylogenetic species, such a mistake is simply a matter of available evidence. All designated species, whether delimited by apomorphic characters or not, are hypotheses subject to revision when new evidence arises. Inasmuch as phylogenetic species are basal, application of the concept of monophyly is superfluous and unnecessary. In addition, even though the PSC is the clear choice when the goal is to reconstruct phylogeny accurately, this does not imply that the definition of phylogenetic species is dependent upon any assumptions of cladistics or, contrary to Mallet (1995), is dependent on phylogeny. The PSC is a mechanism for sorting and interpreting character (broadly interpreted) variation within and among populations in order to recognize basal diagnosable taxa, and is largely independent of assumptions about process.

Critiques of the PSC have argued that a consequence of defining species as the smallest, diagnosably distinct population will be a proliferation of species taxa, since each small population can be found to be distinct for some character, particularly at the molecular level. This criticism can be carried to extremes when not thinking in terms of taxa: 'with detailed morphology or modern molecular techniques, one can find apomorphies for almost every individual' (Mallet, 1995: 298; see also Avise and Ball, 1990; Avise, 1994; among others).

Two misunderstandings are hidden in this criticism. First, it is argued that each individual organism is distinct, therefore the PSC is inapplicable. It may well be the case that each individual organism can be distinguished using one method or another – who would be surprised at this? – but such a finding is irrelevant because the PSC is not about the diagnosability of individuals but of populations. Such a criticism forgets that species concepts are populational concepts that are used to delimit basal taxa. The concept of apomorphy, moreover, has no meaning at the level of an individual but only at the level of taxa. Delimiting species taxa is a problem for systematics not population biology (Nixon and Wheeler, 1990; Wheeler and Nixon, 1990), although obviously population-level data are relevant.

Seeing species as taxa, and as being different from populations and individual organisms, is fundamental for describing and understanding biological diversity. Some critics of the PSC have seemingly not understood this distinction.

A second misunderstanding related to the first is the belief that the PSC will lead to an inordinate inflation of species names. The belief that having too many names would be inconvenient or pernicious has had a long history within systematics, and the consolidation of names was given as one reason why the BSC was a particularly useful innovation: with the introduction of the BSC the 'total number of [bird] species to be memorized by the taxonomist has thus been cut by two-thirds [from 27 000 to 8500; but see below]. The practical advantage of this simplification is so obvious that nothing more needs to be said' (Mayr, 1942: 127). One's memory capacity aside, such views have little scientific relevance for our attempts to describe taxic diversity accurately. It is essential – for many reasons – to individuate diagnosably distinct taxa in nature, including those that are basal (species) and if nature has a multitude of these, so be it.

There are several reasons for thinking that the PSC will not lead to an extraordinary proliferation of names. First, though they may not specifically acknowledge the use of a PSC, most systematists already apply the notion of a basal diagnosable taxon when delimiting species. This is true within most of entomology and those disciplines concerned with the highly speciose groups of non-vertebrates. As a consequence, extending the PSC to all groups of organisms, most of which are far less diverse, will not make a significant difference in global species numbers.

Second, even in those groups such as birds in which the BSC has had considerable influence, virtually all diagnosable taxa have already been described – as subspecies – and thus application of the PSC will not greatly affect the number of names, just potentially their ranking. Within the birds-of-paradise (Paradisaeidae), for example, applying the PSC to a group whose taxonomy has been dominated by the BSC increased the number of recognized species by only about two-fold (Cracraft, 1992). These results can possibly be generalized across all birds. When one randomly samples the world's biological species of birds, evaluates those species and their included subspecies as to whether they are basal diagnosable taxa, the estimated number of phylogenetic species in the world is again only about twice that of the current number (9000 or so) of putative biological species (G. F. Barrowclough, J. Cracraft and R. M. Zink, unpublished data).

There is no question that improved methods of resolving variation will increase our ability to recognize more diagnosably distinct taxa. Critics of the BSC seem to bemoan this fact; biologists interested in seeing nature described and interpreted with accuracy and precision will, in fact, applaud the use of the PSC.

## 16.4 TWO SPECIES CONCEPTS: A COMPARISON

The BSC and PSC provide very different lenses with which to see the world of systematic and evolutionary biology. How species are defined influences one's interpretations of patterns and processes (Table 16.1; see Cracraft, 1989, for additional discussion). Under the BSC, diagnosably distinct populations will sometimes be recognized as separate, monotypic species, but often those populations are united together under a single species name if the diagnosable differences are not judged to be significant. Within the context of the PSC, on the other hand, diagnosably distinct populations would always be accorded specific status. As a consequence, some biological species, those consisting of multiple diagnosable taxa of uncertain relationships to one another, will confound an accurate reconstruction of history if used as terminal taxa in a phylogenetic or biogeographic analysis (Rosen, 1978, 1979; Cracraft, 1983, 1989; Frost and Hillis, 1990; among many others). Phylogenetic species, in contrast, are appropriate terminal taxa for such analyses and cannot, in and of themselves, lead to a misrepresentation of history.

In principle, there is no gene flow among biological species because they are assumed to be reproductively isolated. In practice, however, proponents of the BSC will recognize two entities as biological species, even though there may be gene flow, as long as it is judged to be minor. Because phylogenetic species are defined in terms of diagnosability and not reproductive isolation, it is not uncommon, especially in plants, for there to be extensive gene flow across species borders. If the two entities are diagnosably distinct, they will be recognized as phylogenetic species even though there may be a hybrid zone within which gene flow might be extensive. In almost all cases the latter situation would result in the recognition of a single biological species. Under both concepts, however, populations that are reproductively isolated will also be distinct taxonomic entities.

Finally, the two concepts have markedly different implications for biogeography. If species are taken to be the units of analysis for recognizing areas of endemism, the use of biological species unless they are all monotypic and thus equivalent to phylogenetic species will always lead to a less precise classification of those areas than will be the case with the use of phylogenetic species. Furthermore, adoption of the BSC can sometimes confound the reconstruction of history and consequently lead to inaccurate depictions of the relationships among areas of endemism.

## 16.5 TAXONOMIC UNITS AND CONSERVATION BIOLOGY

### 16.5.1 The concept of evolutionary significant unit should be abandoned

As already noted, there is a growing awareness on the part of conservation biologists that species concepts have relevance for determining what to protect, how to protect it, and how to facilitate the sustainable use of

Table 16.1 Criteria for recognition and some comparisons between the biological and phylogenetic species concepts

<i>Criterion</i>	<i>Biological species concept</i>	<i>Phylogenetic species concept</i>
Diagnosably distinct populations recognized as separate species	Sometimes	Always
Species unit often includes diagnosable allopatric populations	Yes (subspecies concept widely applied)	Never (subspecies concept not relevant)
Species represent terminal taxa that can be used in phylogenetic and biogeographic analysis	Sometimes	Always
Inherently capable of misleading historical analysis	Yes	No
Gene flow among species	Rarely	Sometimes
Reproductively isolated populations recognized as separate species	Always	Always
Extensively hybridizing, diagnosably distinct populations recognized as separate species	Rarely	Almost always
'Potential' interbreeding of allopatric populations important for establishing species status	Yes	Never
Delimitation of areas of endemism	Coarse, less precise	Fine, more precise

biodiversity (Ryder, 1986; Avise, 1989, 1994; Rojas, 1992; Moritz, 1994a,b, 1995; Vogler and DeSalle, 1994; Grant, 1995; Barrowclough and Flesness, 1996). Many of these discussions, however, have not taken into account the full implications of the debates about species concepts within the systematic literature over the past 10 or 15 years. Instead, much of the dialogue has centred on the relevance of 'evolutionary significant units' (ESUs) and their use in conservation studies.

Discussion at the 1985 meeting of the American Association of Zoological Parks and Aquariums (AAZPA) sharpened the debate over the issue of the units of conservation (Ryder, 1986). With the introduction of the term ESU for those taxonomic entities having a distinct evolutionary history, the AAZPA aimed to identify groups that were most in need of conservation action, particularly those in captive breeding programs. Subsequent writers have given tacit support to the importance of ESUs in

conservation (Dizon *et al.*, 1992; Moritz, 1994a,b, 1995; Vogler and DeSalle, 1994; Barrowclough and Flesness, 1996).

The theoretical and practical goals of the ESU concept are important: to provide an objective basis for the definition and recognition of management units in conservation activities. A primary difficulty is that no clear agreement has been reached on what constitutes an ESU. Thus, Vogler and DeSalle (1994: 356) see ESUs as 'clusters of organisms that are evolutionarily distinct and hence merit separate protection'. And, Moritz (1994b: 373; see also 1994a, 1995) argues that to be an evolutionarily 'significant' unit implies that 'the set of populations has been historically isolated and, accordingly, is likely to have a distinct potential'. Moritz goes on to note (1994b: 373) that '*ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci*' [*italics in original*]. The confusion and ambiguity over how to define an ESU is so great – ranging from populations that are significantly differentiated, to biological species, to phylogenetic species – that its objective use is virtually precluded (see Grant, 1995, for a description of the confusion).

Both Vogler and DeSalle (1994) and Moritz (1994a,b, 1995) recognize earlier arguments [Cracraft, 1991; Barrowclough and Flesness, 1996 (in a paper circulated since 1993)] that ESUs are essentially equivalent to phylogenetic species. Despite this acceptance, Vogler and DeSalle (1994) and Moritz (1994a,b) would maintain the concept of ESU, even though the criteria used to recognize historically distinct and significant units are largely those that individuate phylogenetic species. Yet, the ambiguities implied by the various definitions of the ESU remain, thus leading one to conclude that it should be abandoned by conservation biologists.

Such a solution is also strongly supported by another consideration. The use of ESUs within conservation biology undercuts the scientific foundation and results of that discipline. ESUs have no scientific status within systematics, and it is systematics that provides the linguistic and historical framework for the study of biodiversity. The results of formal taxonomy – as reflected in species-level taxa – are now codified in an enormous series of national and international legal instruments. As Geist (1992: 274) remarks: 'courts and solicitors' offices are allowed to rule on taxonomy. Judges may now decide on matters such as the definition of species or subspecies, the criteria for establishing taxa, which taxa are valid, and which populations can be legally protected. The implications for conservation, but also for biology in general, are profound and worrying'.

Because ESUs have no formal systematic status, they will rarely have any legal status. The Convention on Biological Diversity will be the chief international legal instrument affecting the conservation and sustainable use of biodiversity for the foreseeable future. The use of ESUs in meeting the goals of the Convention would be difficult at best because of the lack of international standards of scholarship and formal nomenclatural rules

over those units. Despite the fact that there may be arguments over species concepts, species-level taxonomy and its rules of nomenclature have broad acceptance within the systematic community and among those biodiversity sciences that use taxonomic information. No such framework exists for ESUs.

### 16.5.2 Phylogenetic species are the most relevant units for conservation biology

A comprehensive programme of conservation and sustainable use of biological diversity will depend upon having all taxonomically distinct, diagnosable populations identified and named. A comparison of the BSC with the PSC demonstrates that phylogenetic species, not polytypic biological species, are the most appropriate units for conservation (Table 16.2).

**Table 16.2** Possible implications of different species concepts for conservation and sustainable development

<i>Implication</i>	<i>Biological species concept</i>	<i>Phylogenetic species concept</i>
Equivalent to 'evolutionary significant units' of conservation biology	Sometimes	Essentially always
Estimates of diversity	Underestimates numbers of differentiated taxa	Yields accurate estimates of basal taxa given available data
Delineation of areas of endemism	Broadly defined; underestimates numbers of areas; confounds their historical relationships	Narrowly defined on basis of basal taxa; more finely resolved; historical relationships not confounded
Demographic analysis	May tend to overestimate population sizes of endangered taxa	Accurately estimates population sizes of basal taxa
Apportionment of genetic variation	Confounded	Accurately apportioned
Captive breeding of endangered taxa (and reintroductions)	Units of programme ambiguous; increased danger of mixing distinct evolutionary units	Units of programme are basal taxa; less risk of mixing distinct evolutionary units
Trade in endangered taxa	Enforcement loosely interpreted; fewer taxa protected; higher risk due to trade	Enforcement stringently interpreted; more taxa protected; lower risk due to trade
Political impact for endangered taxa	Less	More

Phylogenetic species meet the objectives envisioned for evolutionary significant units. The desire of conservation biologists to have a unit that is relevant for management purposes is fulfilled by the PSC but not the BSC. As numerous authors have noted, many biological species are composites of diagnosably distinct as well as arbitrarily demarcated races or subspecies. As judged by the managers of captive breeding programmes, this inconsistency will lead to innumerable problems in assigning conservation priorities (Ryder, 1986).

Different species concepts can result in different estimates of species diversity. The use of the BSC will underestimate the numbers of diagnosably (evolutionarily) distinct units as compared with the PSC. Comparisons of diversity are important for countries in setting conservation priorities and are of interest to funding agencies that support activities to implement those priorities.

Many countries and conservation organizations are currently concerned with creating protected areas and ecosystem management zones using measures of endemism to set priorities. If species limits are drawn differently under different species concepts, then so too will their areas of endemism. The use of biological species results in an underestimate of the numbers of areas of endemism, tends to overestimate their size, and confounds the analysis of their historical interrelationships. All these problems are avoided by the use of the PSC.

Species concepts have important implications for demographic analyses. Inasmuch as different concepts can allocate populations to species taxa in opposing ways, numbers of individuals within populations of those species will be estimated differently. Many decisions about conservation priorities and actions depend on demographic information. Phylogenetic species allow for an accurate count of individuals within basal taxa, whereas biological species do not necessarily identify basal taxa and can lead to inappropriate or inaccurate estimates. If all the populations of a polytypic biological species are included in a demographic assessment of that species, the numbers of individuals within endangered basal taxa may be overestimated or ignored altogether.

For the same reasons, the use of phylogenetic species will allow genetic variation to be apportioned within and between taxa more accurately than will biological species. If diagnosably distinct basal taxa are united into a single biological species, there is a risk of ignoring the levels of genetic variation within those distinct taxa in favour of creating an estimate of variation within the biological species as a whole, a situation that is likely to compromise effective management of biodiversity.

The concept of the ESU grew out of attempts by conservation biologists to provide an effective framework for managing *in situ* and *ex situ* breeding programmes for endangered taxa. The ESU was born because the BSC failed to provide that framework. The PSC, in contrast, provides the formal taxonomic context for managing breeding programmes.

The BSC also does not provide an effective basis on which to manage trade in endangered taxa. To be effective, management programmes will need to monitor and regulate trade of all distinct taxa. If distinct and endangered basal taxa are lumped with more common forms under the BSC, the danger is that sufficient protection will not be extended to the former. This problem is avoided with the PSC because each distinct basal taxon would be ranked at the species-level and therefore assume a heightened legal status over unnamed populations or subspecies.

Finally, although some national and international legal instruments extend protection to taxonomic units below the level of species, many do not. Taxa of species rank are still the primary currency for conserving and managing biological diversity. Endangered, distinct populations ranked at subspecies, or not given formal rank at all, will generally carry less political and conservation significance than those ranked at the level of species. Because the PSC provides for specific rank for all diagnosable populations, the importance of the latter is magnified relative to lumping those populations into a larger biological species.

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