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THE IMPACT OF SPECIES CONCEPT ON BIODIVERSITY STUDIES

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Species are the currency of biology. In particular, reactions to the ongoing biodiversity crisis are ubiquitously phrased in terms of species. Areas of importance (e.g., biodiversity hotspots) are selected on the basis of the species they possess, conservation schemes are assessed on how many species are preserved, lists are compiled of endangered species and the factors that threaten them, and conservation legislation and politics are focused on species preservation (Mann and Plummer 1992; Collar et al. 1994; Baillie and Groombridge 1996; Karl and Bowen 1999; Soltis and Gitzendanner 1999).

Despite this importance, the very term "species" is deeply ambiguous. While biologists customarily treat species as tangible entities—at least more so than any other sub- or supraspecific group (Hendey 1964; Ereshefsky 1999)—there is nonetheless a vast spectrum of meanings attached to the word. The argument over how species should be defined is endless, with over twenty species concepts in circulation at present (Mayden 1997). These concepts encompass many operational and empirical definitions, often resulting in a given group of organisms being viewed in drastically different ways by different workers (Mallet and Willmott 2003).

The potential taxonomic conflicts posed by the use of different definitions for the term "species" are not just questions of semantics or miscommunication. Consensus on issues of species richness or biodiversity hotspots is difficult if no agreement can be reached on the actual identity of the species involved (Kartesz 1994). It is therefore necessary to survey the use of opposing concepts in the literature and, without promoting or deprecating any particular concept, determine the extent to which different methodologies will arrive at different boundaries and discuss the implications for the practice of biodiversity studies.

Nonphylogenetic Species Concepts

The concept of species has been well discussed in the literature; for recent reviews, see Claridge et al. 1997, Wheeler and Meier 2000, Hey 2001, and Mallet 2001. The main problem for biodiversity studies has been the gap between theory and practice. Driven by a desire for a universal and objective definition of species, a large number of ideal-centered concepts have been formulated and compete for acceptance (e.g., Van Valen 1976; Wiley 1978). The overwhelmingly dominant of these is the biological species concept (BSC) (Mayr 1942), in which species are defined as populations that cannot interbreed successfully. Species therefore are necessarily reproductively isolated, representing separate evolutionary lineages. A large part of the BSC’s appeal is that proposed species boundaries are falsifiable by the natural (and substantial) production of fertile hybrids across them.
The BSC is simple, obvious, and ultimately flawed.

Outside of ideals of the BSC, discerning potential reproductive barriers can be difficult, time consuming, expensive, and fraught with error. For example, the populations in question may be allopatric, the organisms may be both difficult to observe in the wild and difficult to raise in the laboratory (Taylor et al. 1999), or the genetic component unclear (Kullander 1999). The creatures may also be extinct or only characterized from preserved material (Claridge et al. 1997). For asexual organisms, the biological concept is simply inapplicable (Ghiselin 1987). Also, the BSC encounters difficulties where hybridization is taking place (e.g., in many plants) (Donoghue 1985). It is possible to stand by a strict interpretation of the BSC and argue that the above “exceptional” populations are, by definition, not species (Ghiselin 1987), but this leaves a vast number of organisms with a nebulous status. The BSC can illuminate only a small fragment of the Tree of Life.

Such problems are typical among the ideal-based definitions. In a conservation context, more operational methods (concerned with how a species may be delimited rather than what it represents) are a necessity (Sites and Crandall 1997). These have often employed the proxy of a phenotypic definition, where species are delineated by overall, usually morphological, similarity (“morpho-species”). Yet even this most basic of approaches has problems. There is a large element of subjectivity involved (e.g., what constitutes a reasonable character, what degree of difference equates to the species level). Morphological classification can be confounded by convergent evolution, morphological simplicity (Klautau et al. 1999), ring species (Mayr 1963), natural intraspecies variation (e.g., sexual dimorphism or polymorphism), morphologically cryptic species (Ameziane and Roux 1997), and phenotypic plasticity (Mishler 1985).

Such confusion would seem to render the word “species” meaningless. In reality, most biologists hold a similar, intuitive idea of what a species represents: a population on an autonomous historical trajectory. The different methods of defining species will sometimes arrive at different answers, but if they are all measurements of essentially the same underlying entity, then comparison between studies is not unreasonable. Also, taxonomic arguments are usually concerned not with the number of species but whether organisms in a sample are or are not members of the same species (Mayden 1997). The preeminence in the field of the biological and morphological concepts makes comparison even easier, and within major groups there is often a commonality among working taxonomists about the degree of morphological difference that corresponds to a biological species boundary (Erwin and Anstey 1995; O’Keefe and Sander 1999).

The Phylogenetic Species Concept

With the advance of molecular phylogenetics and the increasing popularity of the phylogenetic species concept (PSC), the species debate has rekindled. Although the PSC has a spectrum of definitions (e.g., Mishler and Budd 1990; Nixon and Wheeler 1990; Davis and Nixon 1992), it is commonly taken to define a species as a group of organisms that share at least one uniquely derived character (Nixon and Wheeler 1990; for reviews see Wheeler and Meier 2000), perhaps with a shared pattern of ancestry and descent (Cracraft 1983) or monophyly (Donoghue 1985; de Quieroz and Donoghue 1988, 1990). The PSC is more widely applicable in practice than previous species concepts because it can be applied to asexual organisms and allopatric populations. Furthermore, it has been argued that the PSC is more objective, may reveal morphologically unremarkable but important populations, and is a better indicator of biodiversity and conservation worth of a population than other measures (Soltis and Gitzendanner 1999).

Thus, for the biodiversity researcher, the PSC is potentially useful. A more debatable point is to what extent species assessments under the PSC will concur with those made under other criteria. Species boundaries previously established from fossils are unlikely to change, as most fossil taxa are sampled too poorly for geographic variation to cause the inference of new species, and may be slightly inflated anyway due to the uncertainty of
how much intraspecific variation (e.g., sexual dimorphism) exists. In the case of contemporaneous taxa, it could be reasoned that the various definitions of species might be expected to more-or-less agree on actual species boundaries. The character-based interpretation of the PSC has some congruence with morpho-species and the history-based version with biological and evolutionary concepts. Indeed, it has been argued that the species boundaries defined by PSC should be similar to those found by other methods, on the basis that isolated populations should differ in at least the character responsible for sympatric isolation (Knowlton and Weigt 1997; Geiser et al. 1998; Avise and Walker 1999).

Conversely, there are reasons why different species concepts will arrive at different species. It has been argued that the BSC and PSC are detecting fundamentally different entities at different stages along the speciation trajectory (Harrison 1998). Furthermore, within the PSC there is no privileged phylogenetic level that corresponds to a species other than “the smallest aggregate” (Horvath 1997). This makes the degree of taxonomic resolution sensitive to sampling effort (Sites and Crandall 1997; Walsh 2000) and could cast subspecies or, in the extreme, even individual organisms as species (Amadon and Short 1992). In contrast to this “splitting,” it could be argued that the BSC overemphasizes potential gene flow between populations (Templeton 1989; Harrison 1998) and will “lump” species together. Finally, many phylogenies of species are in reality phylogenies of genes. The evolutionary history of a species and its genes may not match due to gene duplication or loss, horizontal transfer, or incomplete gene sorting (Slowinski and Page 1999; Mindell and Meyer 2001). Thus, it is widely recognized that the PSC will often split a species determined under nonphylogenetic criteria with two or more “new” species (Corbet 1997; Cracraft 1997; Knowlton and Weigt 1997). The increasing use of the PSC could thus lead to an apparent increase in extant species numbers, producing “new” groups with more restricted geographic ranges and decreased abundance. To what extent this will occur, and its potential impact on conservation biology and management decisions, is examined below.

Comparing Phylogenetic and Nonphylogenetic Species

We surveyed the primary literature, searching for instances of sets of organisms that had been classified by both the PSC and other means. Typically, these examples involved studies where researchers reevaluated the taxonomy of a group using a phylogenetic approach with either molecular and/or morphological data, whose species were formerly defined using either a biological species concept or a morphological surrogate of that concept. In total we reviewed 89 studies, examining changes both in the number of species and in the identity of groups; i.e., whether the “new” species nested within the boundaries of the old, fell across the old boundaries, or merged several “old” groups (Figure 1). The results are summarized in Table 1. A wide variety of taxa from many different environments were included in our survey, but it should be emphasized that the selection is limited by the availability of data that compare the status of the taxa under the competing concepts. Thus, despite their prevalence and conservation importance, there is a relative paucity of suitable studies on insects and amphibians.

In total, the studies covered between 1245 and 1282 non-PSC-based species, which on reanalysis gave rise to between 1912 and 2112 PSC-based species, an increase of 48.7%. (In this and all further analyses, if a span of species numbers is recorded, any change or difference is reported as the smallest possible within that range.) Across studies, the average number of species in a group increased by 121.0%. The increase in group size was assessed with a sign test to be significant, with \( p < .0001 \) (z value of 6.20). Given that a number of studies overlap in the taxa studied, notably the vertebrate-wide survey (Avise and Walker 1999) and the birds of paradise studies (Cracraft 1992; Collar 1997), these numbers might be distorted by a small number of atypical taxa. However, even if all such studies are excluded, the increase in species numbers is 60.3%, and the average increase per study is 118.3%. The increase was significant with
Figure 1. Reclassification of Phylogenetic Boundaries

Three types of changes in taxonomic identities are possible. In nested reclassifications, a single species is split into two or more. In non-nested reclassifications, a new species is formed containing members of previously distinct species. In reverse-nesting reclassification, species are "lumped" into a new larger species. In this figure phylogenetic species are represented as least inclusive monophyletic groups (i.e., history-based PSC).
TABLE 1

Comparing nonphylogenetic and phylogenetic species

<table>
<thead>
<tr>
<th>Organisms</th>
<th>Region</th>
<th>Species (non-PSC)</th>
<th>Species (PSC)</th>
<th>Nested?</th>
<th>Reference</th>
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<td>(Acalypha rhomboidea)</td>
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<td>Grass (Leptochloa)</td>
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<td>3</td>
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<td>(Ramulina americana)</td>
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<td><strong>Birds</strong></td>
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<td>Huæt-huets and turcas</td>
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<td>Kiwi</td>
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<td>Scaled woodcreepers</td>
<td>Brazil</td>
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<td>Sharp-beaked ground finch</td>
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### Mammals

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<th>Phylogenetic</th>
<th>Conformity</th>
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<td>Australian bats</td>
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<td>Bottlenose dolphin</td>
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<td>Brown lemur</td>
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<td>Deer mouse</td>
<td>Mexico</td>
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<td>Marten</td>
<td>North America</td>
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<td>Right whales (Eubalaena)</td>
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<td>Spiny rats</td>
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<td>Tiger</td>
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<td>Titi monkies (Callicebus)</td>
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### Arthropods

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<td>Bee family (Halictidae)</td>
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<td>Brown plant hoppers</td>
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<td>Ctenopoda beetles</td>
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<td>Pomace flies (Drosophila willistoni)</td>
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### Reptiles

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<tr>
<td>Pacific skinks</td>
<td>Southeast Asia &amp; Pacific</td>
<td>4</td>
<td>7</td>
<td>No</td>
</tr>
<tr>
<td>Pseudocera</td>
<td>Brazil</td>
<td>1</td>
<td>1</td>
<td>Equal</td>
</tr>
<tr>
<td>Short-necked turtles</td>
<td>Australia</td>
<td>3</td>
<td>10</td>
<td>Yes (7) / No (3)</td>
</tr>
<tr>
<td>Spiny lizard</td>
<td>Mexico</td>
<td>1</td>
<td>2</td>
<td>Yes</td>
</tr>
<tr>
<td>Spitting cobras</td>
<td>Indochina</td>
<td>2</td>
<td>3</td>
<td>Yes</td>
</tr>
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</table>

### Fish

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>European freshwater fishes</td>
<td>Europe (exclusive of former USSR)</td>
<td>213</td>
<td>358</td>
<td>Unknown</td>
</tr>
<tr>
<td>Troglobitic catfish</td>
<td>Brazil</td>
<td>1</td>
<td>2</td>
<td>Yes</td>
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</tbody>
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### Molluscs

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep-sea snails</td>
<td>Global</td>
<td>2</td>
<td>1</td>
<td>Reverse</td>
</tr>
<tr>
<td>Hawaiian tree snails</td>
<td>Hawaii</td>
<td>2</td>
<td>1</td>
<td>Reverse</td>
</tr>
<tr>
<td>Intertidal snails</td>
<td>Ireland</td>
<td>2</td>
<td>1</td>
<td>Reverse</td>
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</table>

### Echinoderms

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linckia starfish</td>
<td>Indian and Pacific ocean</td>
<td>5</td>
<td>5</td>
<td>Yes</td>
</tr>
<tr>
<td>Sea urchins</td>
<td>Global</td>
<td>7</td>
<td>10</td>
<td>Yes (4) / No (3)</td>
</tr>
<tr>
<td>Six-rayed starfish</td>
<td>Eastern North Pacific</td>
<td>5</td>
<td>4</td>
<td>Reverse</td>
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### Corals

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hard-rayed coral (Montastraea annularis)</td>
<td>Caribbean</td>
<td>1–3</td>
<td>1</td>
<td>Yes</td>
</tr>
<tr>
<td>Reef-building corals</td>
<td>Caribbean</td>
<td>3</td>
<td>1</td>
<td>Reverse</td>
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### Annelids

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligochaete worm (Tubifex tubifex)</td>
<td>Global</td>
<td>1</td>
<td>2–5</td>
<td>Yes</td>
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<tr>
<td>Polychaete worm</td>
<td>North America and Europe</td>
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<td>3</td>
<td>Yes</td>
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### Miscellaneous

<table>
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<tr>
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<th>Geographic Distribution</th>
<th>Nonphylogenetic</th>
<th>Phylogenetic</th>
<th>Conformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frogs</td>
<td>Sub-Saharan Africa</td>
<td>1–3</td>
<td>10</td>
<td>Unknown</td>
</tr>
<tr>
<td>Malaria parasites</td>
<td>Caribbean Islands</td>
<td>2</td>
<td>2</td>
<td>Equal</td>
</tr>
<tr>
<td>Vertebrates</td>
<td>Global</td>
<td>252</td>
<td>252–592</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
$p < .0001$, $z$ value of 5.82. It is true these populations may, by their very nature, be a biased sample. Taxonomic reassessment will often focus on groups where there is dissatisfaction with current understanding. The wide variety of taxa studied, however, the consistent increase in species numbers, and its agreement with previous estimates (e.g., Zink and McKitrick 1995) imply that the trend is approximate but correct. This trend of increasing species counts appears to contradict a previous study based on fossil data (Alroy 2002) that postulated synonymous or otherwise invalid taxa were inflating the global species count by up to 50%. However, we feel that optimistic estimation of fossil coverage and ignoring the vastly different techniques used to delineate species in living and fossil taxa render such an extrapolation meaningless.

It is difficult to detect any trend across groups, and given the small sample size and how it was obtained, any putative trends should be treated with suspicion. With this in mind, the greatest increase in species numbers was seen in fungus, a 300% increase. This may in part reflect the confused taxonomy in the field (Hawksworth 1993). Similar comments could be made about lichens (259% increase) and plants (146% increase). Among animals, reptiles showed the greatest increase (259% increase) and plants (146% increase). The relatively small increase in echinoderm species (8%) can perhaps be explained by this group being conspicuous, species poor, and thoroughly investigated. The marked decrease in mollusc species (50%) is perplexing. Perhaps it is due to the past activities of amateur mollusc taxonomists, who may have been overenthusiastic in identifying new species.

Another important consideration for conservation is how changes in the classification and number of species under the PSC map onto the previous species distributions. With conflicting species identifications, the newly defined species may either nest within the previously recognized species (“nested redefinition”), cross the boundaries of two or more of the former species (“non-nested redefinition”), or represent the fusion of several species (“reverse nesting”) (Figure 1). Only fifteen of the studies examined (17.0%) showed a definite non-nesting of the PSC-defined species. However, this fact should be tempered with the knowledge that another six showed reverse nesting (i.e., merging of two or more non-PSC-based species into a single entity) and boundaries changes were not available for eleven studies. Again, it is difficult to draw trends across groups, but non-nested redefinitions may be more prevalent in the birds, possibly by increased taxonomic attention.

Consequences

From the above analysis it can be seen that recategorization via use of the PSC leads to an increase in echinoderm species (8%) can perhaps be explained by this group being conspicuous, species poor, and thoroughly investigated. The marked decrease in mollusc species (50%) is perplexing. Perhaps it is due to the past activities of amateur mollusc taxonomists, who may have been overenthusiastic in identifying new species.

apparent increase in the number of species and a more modest remapping of species across previous taxonomic boundaries. As far as biodiversity studies are concerned, the consequences of this fall into a number of categories: the change in the number of endangered species, the economic and political fallout, and conservation practice.

Reclassification under the PSC will lead to an apparent rise in the number of endangered species. This is due not only to the detection of “new” species but also to an increase in the proportion that are endangered due to a reduction in the distributional area of the inferred species range. Because the new species tend to arise through the splitting of previous entities, the abundance of and area occupied by each can at best be a subset of the previous values. Both measures can therefore be expected to decline on average. Formal classifications of endangered species like the IUCN Red List (Baillie and Groombridge 1996) use both number of individuals and geographic range as diagnostics. We can therefore expect at least a proportionate or greater increase in the number of threatened species.

It is possible to estimate the impact of these decreases on formal threat classifications. For example, the IUCN category “Vulnerable” identifies species that are at a high risk of extinction based on (among other criteria) the species having fewer than 1000 mature individuals. The threat category above, “Endangered,” defines those species at a very high risk of extinction by having fewer than 250 mature individuals. The 48.7% increase in species number that we observed infers an average decrease in mature individuals per species of 32.8%. If we assume the number of mature individuals in “Vulnerable” species are distributed evenly throughout the band of possible values (250 to 1000), a 32.8% drop will cause 10.9% of these species to have less than 250 mature individuals and so be reclassified as “Endangered.” This is a conservative estimate as it assumes that the new species are of equal size, whereas unequal splitting will produce more small groups in the “Vulnerable” category.

The impact on species range is more difficult to formalize. For example, a 50% drop in the number of adult individuals does not necessarily imply a 50% drop in range. Nonetheless, as use of the PSC splits and therefore shrinks species, the new entities will tend to have reduced ranges. By virtue of this, the proportion of species formally classified as endangered will increase.

Any increase in the number of endangered species requires a corresponding increase in resources and money devoted toward conserving those species. For example, it has been estimated that the complete recovery of any of the species listed by the U.S. Endangered Species Act will require about $2.76 million (USFWS 1994). Thus, recovering all species listed currently would cost around $4.6 billion. With widespread adoption of the PSC, this already formidable amount could increase to $7.6 billion, or the entire annual budget for the administering agency (U.S. Fisheries and Wildlife Services) for the next 120 years. The per-species cost is admittedly high—being based on the costs to save what are sometimes subspecies or already critical populations—but given that species size and range will fall on average, and that cost of rescue rises with the degree of threat, total costs might actually reach far beyond this point. Resurveying taxa of importance for consistent species recognition would involve less money, but still requires amounts that are nontrivial considering the disagreement over species concepts. An evaluation of the threat status of 120,000 potentially threatened tropical taxa has been proposed, conservatively valued at $100 per species, summing to a relatively modest $12.1 million (Pitman and Jorgenson 2002). A higher figure of $135 million can be calculated by assuming Platnick’s figures for a dedicated taxonomic team (Platnick 1999). If this resurvey were to reveal only 10% of these taxa as endangered, the rescue bill could amount to $33.1 trillion. Even just formally listing these taxa as endangered would, by USFWS figures, cost $816 million. These figures are arguably acceptable to industrial nations, but frankly impossible for many impoverished and biodiverse countries. It has been said that the economic cost of current conservation strategies are already unacceptable (Mann and Plummer 1995). The impact of the PSC serves only to reinforce this
point, and may require a rethinking of poli-

cies that seek to preserve every species (Moul-
ton and Sanderson 1999).

If more resources are needed, then there
is also a need for more education and mobi-
lization of opinion. Unfortunately, disagree-

ment between species concepts may present
problems. Public concern has a great influ-

ence over the allocation of conservation
resources, it being easier to find money for
the preservation of charismatic, easily recog-
nized organisms than for more obscure and
less appealing ones, independent of their evo-

lutionary or ecological significance or con-
servation status (Ando 1999; Gittleman et al.
2001). Changing species identities and a
flood of threatened species may create con-

fusion and apathy in the public’s mind. Fur-

thermore, consistent application of the PSC
may make this task more difficult by identi-

fying morphologically disparate entities as
members of the same species and superfi-
cially similar entities as members of different
species (Wayne and Gittleman 1995; Bruna et
al. 1996). This is not to say that only easily
“marketable” species should be saved, but
conservation biologists should prepare for
the difficulties caused by a change in species
identity and numbers. Taxonomy may be
seen as the enemy of conservation due to
these unpalatable implications (for example,
see Collar 1997). Complex ideas of species
identity under the PSC may also thwart the
use of parataxonists, who have proven so
useful in covering remote biodiverse areas.
Conversely, application of the BSC in the field
can also be difficult. If the application of the
PSC reveals more species and increases the
threat status of those groups, more taxo-
nomic and conservation attention may be
drawn to groups neglected under previous
regimes.

Changing species boundaries may also cast
doubt on the efficacy of current conservation
schemes, leading to arguments about
whether conservation efforts are being cor-

crectly allocated and prioritized. This is exac-
erbated by the tendency of conservation
schemes to focus on reserves and protected
regions. The endemic birds of Mexico pro-
vide an excellent illustration of this point
(Peterson and Navarro-Siguéenza 1999).

Under the BSC there are 101 species, concen-
trated in the mountains of southern and west-
ern Mexico. Under the PSC, however, the
number of species increases to 249, with a
general concentration in the west of Mexico.
Any effort directed at widespread preserva-
tion of Mexico’s avian biodiversity based on
either classification would, from the point of
view of the other, be preserving many of the
“wrong” regions (Figure 2); for further exam-

ples, see Daugherty et al. 1990, O’Brien and
Mayr 1991, Soltis and Gitzendanner 1999,
and Bates and Demos 2001. Shifts in species
concept effectively change the importance of
different taxonomic groups for identifying
regions of biodiversity. The question changes
from one of where the biodiversity is to one
of which species concept is more appropriate.

The redefinition of species, where new
entities cross the boundaries of the old, also
casts doubt on the efficacy of conservation
schemes. Even with a consistent species con-
cept this may happen, but changing concepts
may exacerbate this problem. Where redefi-
nition of species is reverse nested, we should
expect few problems. Schemes directed at sav-
ing the old species should be suitable, and
perhaps even excessive, for saving the new
species. Nested and non-nested redefinitions
pose a greater problem, as anything less than
total preservation of the old species may leave
some of the new species uncovered. Given the
sample size of this survey and the relatively
small number of clades that demonstrate
non-nested rearrangements, it is not clear if
this problem will be widespread. Nonetheless,
the examples unearthed should serve as
grounds for caution. If a mix of concepts is
used to define species in a survey of species
abundance, disagreement over critical areas
of biodiversity could result.

Remedies

What, then, are we to do? Rejecting the
PSC solely because of (apparently) unpleas-
ant biodiversity implications smacks of expe-
dience. Reverting to the BSC ignores its oper-
ational problems. Indeed, it is perhaps not a
question of which species concept is best.
There may be no one solution to the species
concept issue, with particular concepts being
more apt in different circumstances (Hey
Figure 2. Endemism and Species Concept.

The shaded areas represent the top 20% for richness of endemic avian species in Mexico under (A) non-phylogenetic and (B) phylogenetic species classification. Adapted from Peterson and Navarro-Sigüenza 1999.
A plurality of species definitions is likely to remain part of biology and the conservation landscape. Conservation biologists will remain trading in a variety of "currencies," and concern for what is lost will be conflated by confusion over how much is lost (Rojas 1992).

A few broad remedies can be suggested. Where species lists are being used in conservation, it is necessary to be clear about how the species involved were defined. In this way, one can move toward consistency and replicability of any conclusions, or at least clarity about how the conclusions can be flawed. The BSC should be used only where it can be robustly diagnosed and the grounds for this inference made clear. Species inferred from morphology should always be treated as tentative. Where the PSC is used, sufficient individuals and characters should be sampled to ensure an adequate and even resolution of the species status across clades (Walsh 2000).

However, even consistent use of a single concept does not guarantee consistent species boundaries. As stated above, ring and hybrid populations present an intractable problem for the BSC. A strict interpretation of the concept in these cases is uninformative, while more relaxed interpretations are subjective and possibly inconsistent. The PSC has been implemented under a wide variety of methodologies—e.g., population aggregation analysis (Davis and Nixon 1992), cladistic haplotype aggregation (Brower 1999), genealogical concordance (Baum and Shaw 1995), and gene trees with geographical concordance (Wiens and Penkrot 2002)—and it has been shown that these need not agree (Wiens and Penkrot 2002). It may be possible that different species concepts and methods can be used to reinforce each other, so as to reach consistent if conservative conclusions on species boundaries (e.g., Jarman and Elliott 2000). Any move toward greater consistency in classifying species will also require an increase in the resources devoted toward unifying taxonomy and making it more accessible (Godfray 2002).

Much of the problem may rest in the implicit assumption that species are distinct entities. In reality, species are probably not groups with rigid borders but "fuzzy sets" (Hey 2001; Mallet 2001b; Hendry et al. 2002), their boundaries blurred by horizontal gene transfer, hybridization, and recent isolation. Furthermore, species can arise by a variety of mechanisms, and different concepts consider different characteristics of a population. It is thus little wonder that each concept diagnoses a different sort of "species." Obviously, a single morpho-species can contain multiple species (sensu BSC or PSC) where morphology is cryptic or a limited number of characters are studied (Kasuga et al. 1999; Taylor et al. 2000). More subtly, the diagnostic form of the BSC emphasizes potential gene flow, conflating it with the actual lack of gene flow that may be both the cause and result of a species boundary (Templeton 1989). Species recognized as separate by the PSC may be lumped into a single species by the BSC, even if they are genetically and geographically separated (Vilgalys and Sun 1994). Given that interbreeding is still possible, at some point in the future the separate species (sensu PSC) may reticulate back into a single entity. Conversely, as genetic isolation precedes the loss of shared polymorphisms, shortly after the separation of two biological species the PSC may only recognize a single species (Doyle 1997). Thus we do not even have the certainty that PSC-based species will fall within biological species and biological species within morpho-species. The problem is not in any particular species concept, but in the nature of species.

Even if species could somehow be unambiguously defined, there are problems. If biological species are used, it is unclear how hybrid populations should be treated (see below). Also, while it has been argued that under the PSC species come closer to being ESUs (evolutionary significant units) (Ryder 1986) than any other defined entity (Cracraft 1997), this advantage is lost in the apparent lack of applicability of ESUs in the real world (Grannell et al. 2000; Hendry et al. 2002). Finally, while current conservation measures are often biased toward charismatic taxa (Metrick and Weitzman 1998; Gittleman et al. 2001), diagnosing biodiversity by counting species errs in the other direction by insisting that all species are equally important (May 1990). A large number of species does cor-
SPECIES CONCEPT AND BIODIVERSITY STUDIES

respond to general ecosystem stability (Naeem 1998), but the identification of a species as such does not say anything about its evolutionary distinctiveness or ecological importance. Species-centered conservation necessarily neglects the conservation-worthy diversity found within and between species, i.e., subspecies and hybrids (Balharry et al. 1994; Rieseberg and Gerber 1995; García-Moreno et al. 1996). Thus, species counts, however derived, are only the first step of diagnosing biodiversity.

Would it therefore be best to avoid the use of species? If so, the conservation worth of a population must be appraised in another currency, such as economic value, aesthetic appeal, or unique genetic and evolutionary information. Examples of this last type include phylogenetic diversity (Faith 1994), genetic diversity (Crozier 1997), phenotypic diversity (Owens and Bennett 2000), or taxonomic units based solely on evolutionary time (Avis and Johns 1999). In this way, biodiversity value can be measured in information: diversity measured as millions of years, allelic distance, or character richness. Conservation schemes can be designed so as to maximize the amount of information preserved. Highly diverse but putative species could be given the benefit of the doubt. In some cases, it might be proper for a divergent subspecific entity to be valued over a more conserved species. Such measures do not entirely obviate the need for identifying species, however. Comparing the biodiversity value of, for example, species of cetaceans and woodchucks is at least plausible if not always meaningful. Doing the same via information measures of cetacean and woodchuck populations introduces more possibilities for ambiguity and argument. Information measures can be sensitive to sampling effects, monotonically increasing with every organism examined. The use of measures other than species counts also forces us to ask what it is that we are trying to preserve. Phylogenetic and genetic diversity may be easy to measure, but it is far from clear that they are precisely what needs saving. Also, any attempt to abolish the use of species sacrifices the usefulness of discrete, identifiable units of conservation important for raising public sympathies.

At the opposite end of the scale, the species problem could be avoided by working to conserve higher taxa, supraspecific groups. These at least can usually be identified without controversy, and the broad outline of biodiversity preserved (Williams and Gaston 1994). This preservation is bought, however, at the possible expense of the fine detail of diversity and ecosystem stability. Furthermore, even if higher taxa are the focus of conservation, management plans must still consider species boundaries and whether groups of individuals are genetically and ecologically distinct (Crandall et al. 2000). Given that many species identities may remain ambiguous, or even undiscovered, for a long time, perhaps planning should concentrate on preserving areas where new species are likely to be uncovered. For example, the preservation of "Endemic Bird Areas" have been proposed (ICBP 1992; Jepson and Whittaker 2002), based on the idea that areas known to be endemic for some species are likely to be endemic for unknown species as well (Balmford and Long 1995). This is a more palatable solution than waiting for a perfect understanding of species boundaries that may never arrive.

While there is much to be said for de-emphasizing the importance of species in conservation decisions, they are far from dispensable. Indeed, the species problem is emblematic of conservation and the gulfs between science policy and practice. We would do the right thing, if only we knew what the right thing was. The best response to the terrible ambiguity of species may be for scientists not to work to reduce it nor to fear making conservation mistakes, but to learn how to work with it. "One size fits all" solutions based on identifying the "right" species may have to be abandoned for a flexible spectrum of methodologies that either employ a range of species concepts or dispense with species altogether. Most difficult of all may be the task of translating ambiguous species boundaries into workable guidelines for legislators, decision makers, and the layperson. Without action, we risk losing much time, much money, and much biodiversity.

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