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S23-2 Species concepts versus species categories versus species taxa

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Abstract A clear distinction must be made between concept, category and taxon when discussing ideas of species, and it is best to always use the term "species concept" rather than "species" alone in that context. The species concept is part of basic biological theory, and evolutionary theory in particular, and bound up with the evolution of sexual reproduction in living organisms. The biological species concept, that a "species is a group of actually or potentially interbreeding populations of organisms which are actually or potentially genetically isolated in nature from other such species", fits neatly within currently accepted evolutionary theory. Species concepts which define the phyletic lineage instead should be rejected. A species taxon possesses genetic, reproductive and ecological properties that separate it from other species taxa and which are commonly expressed in phenotypic features that evolve during speciation. Recognition of narrowly delimited species taxa in sexually reproducing organisms such that geographical replacing populations are treated as species is often inappropriate and should be rejected as a rule. To do otherwise would raise several or more populations of humans to species level. No particular species concept or approach to recognizing species taxa is intrinsically better than another in conservation because the term "species" in conservation law and regulation is defined legally, and is not commensurate with species definitions or species taxa within biology.

Key words Species concept, Species category, BSC, Phyletic lineage, Species properties, Conservation

1 Introduction

The species concept has always been part of basic biological theory, not just systematics, and used to the present day as the theoretical base for delimiting groups of organisms living at the same time. Over the last 200 years, moreover, it has evolved to apply only to sexually reproducing organisms. Yet today one commonly reads such statements in taxonomic papers, both theoretical and practical, as: "I am unable to apply the biological species concept to the organisms under study". True, but it is equally impossible to apply any species concept directly to such biological organisms. A series of steps stands between the theoretical concept and the empirical recognition of actual species taxa.

A major source of misunderstanding concerning the 'definition' of species stems from the confusion among a series of related terms, including the term "species" itself which is commonly used indistinguishably for four different ideas and phenomena. These ideas are the species concept, the species category, the species taxon (the actual unit of biodiversity in nature), and the phyletic lineage. Species taxa are based on the species category which in turn stems from the species concept; each is sharply distinct from the others. It must be emphasized here that the recognition of species taxa requires considerable inference. Additional difficulties arise because of failure to distinguish between horizontal and vertical comparisons in space and time, because it is commonly assumed that the two are effectively one and the same. Herein I examine these different ideas and explain the relationships between them. For further discussion, see Bock (1967, 1979, 1986, 1995, 2000) and Mayr (1942, 1963, 1969, 1995, 1996).

2 The species concept

Under the currently accepted Biological Species Concept (BSC), species exist only in sexually reproducing organisms as a consequence of the mechanisms of genetic shuffling and recombination during meiosis and in zygote formation. Species do not exist in asexually reproducing organisms except as an artificial classificatory convenience. The BSC is usually defined as: *groups of actually or potentially interbreeding populations in nature which are reproductively isolated from other such groups* (Mayr, 1942, 1963:19, 1969:26). As such it is a core idea in the Synthetic Theory of Evolution, and altogether different from morphological, phylogenetic, and evolutionary species concepts which either take no account of gene flow within species (and barriers to it without) or confuse the species in space with the phyletic lineage in time.

By reproductive isolation, evolutionists mean that no gene flow exists between different species, not necessarily that members of different species cannot interbreed and produce hybrids. It is unfortunate that the adverb "reproductively" has been used in definitions of the BSC because it does not explicitly state the property of no gene flow between species as the defining criterion for species. Evolu-

tionists actually use the criterion of lack of gene flow between different species, rather than lack of reproduction, as the theoretical base for practical taxonomic work on them. Thus I advocated (Bock, 1986:33) a modified definition of the BSC, namely: *a species is a group of actually or potentially interbreeding populations of organisms which are genetically isolated in nature from other such groups*. This definition conveys the same intention as the conventional definition, but is more precise and appropriate in its wording.

The distinction between these two definitions is clarified in the classification of intrinsic isolating mechanisms (Mayr, 1963:92), as follows:

1. Mechanisms that prevent interspecific crosses (premating mechanisms)

(a) Potential mates do not meet (seasonal and habitat isolation)

(b) Potential mates meet but do not mate (ethological isolation)

(c) Copulation attempted but no transfer of sperm takes place (mechanical isolation)

2. * Mechanisms that reduce full success of interspecific crosses (postmating mechanisms)

(a)* Sperm transfer takes place but egg is not fertilized (gametic mortality)

(b)* Egg is fertilized but zygote dies (zygote mortality)

(c)* Zygote produces an F_1 hybrid of reduced viability (hybrid inviability)

(d)* F_1 hybrid zygote is fully viable but partially or completely sterile, or produces deficient F_2 (hybrid sterility)

All of these intrinsic isolating mechanisms serve to prevent exchange of genetic material between members of different species taxa and achieve genetic isolation. However, mechanisms marked with an asterisk do not reflect reproductive isolation between species, indicating shortcomings with that criterion in the definition of the BSC.

Species possess three individual sets of properties that separate them from one another:

1. Genetic coherence: the members of a species form a genetic community which is genetically isolated from other species. Genetic material from reproduction thus will flow between members of a single species, but not from one species to another under natural conditions. Genetic isolation is maintained by the possession of intrinsic genetic isolating mechanisms (see asterisked mechanisms above).

2. Reproductive coherence: the members of a species form a breeding community which is reproductively isolated from other species. Members of one species do not interbreed or attempt to interbreed with members of another species under natural conditions, regardless of the barriers to gene flow between them. Interbreeding between members of different species would be prevented by particular intrinsic reproductive isolating mechanisms. It must be stressed that reproductive isolation between species is not the same as genetic isolation, and that it is possible for two species to be genetically isolated without being reproductively isolated.

3. Ecological coherence: the members of a species have similar ecological requirements that differ from those of other species. Competition between sympatric members of different species is thus greatly reduced. Ecological properties common to the members of a species are enabled by shared phenotypic features which differ from those of other species. The phenotypic features must be integrated coadaptively into whole organisms. Mechanisms of meiosis and of zygote formation during reproduction have the potential to disrupt the genetic basis underlying phenotypic co-adaptation. Such disruption is prevented by maintenance of individual variation in the interbreeding population (and hence the species) within acceptable bounds, as advocated by a number of evolutionists (Mayr, 1963).

In fully evolved species, all three sets of properties are developed such that the species are completely genetically isolated, completely reproductively isolated and largely ecologically separated from other sympatric species. Although species taxa must be genetically isolated to maintain themselves sympatrically, not all species taxa have these properties fully or equally well developed; indeed in some species taxa, reproductive isolation or ecological separation may not be developed at all. These three properties of species rarely evolve at the same rate and the same time, and not as a result of the same evolutionary causes during the speciation process. Moreover, the evolution of all three basic properties are not absolutely irreversible; species taxa are not necessarily immortal, and can merge as a consequence of future evolutionary events. Depending on the nature of the features underlying each of these properties, functionally sympatric species taxa can again become a single genetic unit, reproductive unit and/or ecological unit, as shown by two former species of towhees (*Pipilo erythrophthalmus*, *P. ocaci*). Living sympatrically in the Mexican highlands, these species started to hybridize introgressively some hundreds of years ago to become a single genetic-reproductive-ecological unit over most of their range today (Sibley, 1950).

3 The species category

Categories are the different levels of the Linnaean hierarchy used in biological classification. The species category is the basic level in this hierarchy, in that all other categories are defined at levels relative to it, either directly or secondarily. Most workers have assumed that the species category is the same as the species concept, and hence that the BSC is the species category. This assumption is invalid because the species category must apply to all organisms, including asexual ones, and the biological species concept applies only to sexually reproducing organisms. A broader definition of the species category is needed, concordant with the BSC.

Defining the species category for all organisms is

awkward, but can summarized as: *the fundamental level in the Linnaean hierarchy for describing the diversity of biological organisms that is based on the biological species concept for sexually reproducing organisms or on the equivalent of the ecological unit of biological species for groups of asexual organisms.* This definition omits all mention of monophyly because valid taxa at the level of the species category need not monophyletic under the general sense of that concept. Species taxa include polyploid, aneuploid and apomictic taxa of plants, often evolved from hybridization between two species and which can potentially arise more than once.

4 The species taxon

Species taxa — the taxonomic groups at the level of the species category — are never defined, but are recognized and delimited descriptively to permit identification of individual organisms as members of their species taxon. Given the definition of the species category, the problem facing taxonomists is how to recognize species taxa when describing the total diversity observed in nature. Clearly authors accepting the same species concept (or species category) can differ greatly in recognizing rather broadly or more narrowly delimited species taxa. The criteria used to recognize species taxa, be they for sexually or asexually reproducing organisms, need not be the defining criterion used in the species concept, but may include morphological, behavioral and other phenotypical attributes as well. Starting with the species category, taxonomists proceed to ascertain how to recognize species taxa in nature for both sympatric and allopatric organisms, on the understanding that the limits of the taxa should be approximately equivalent in any one group of organisms, such as birds. Inference about genetic isolation is an important tool in reaching decisions about the specific status of allopatric forms (Mayr, 1996). What must also be kept in mind is that species taxa, just as they do for all other taxa in biological classification, serve as the taxonomic foundation for all other biological disciplines: hence species taxa should be as equivalent as possible.

The argument that the BSC is wrong because it does not apply to all species taxa in all groups of organisms simply has no merit. Contrary to the beliefs of many systematists, the value of the BSC or any other species concept can be decided only by its role within evolutionary theory, not by its role in systematic practice. Recognition of species taxa must, however, be as concordant as possible with the theoretical species concept (Mayr, 1996).

5 The phyletic lineage

The phyletic lineage may be defined as: *the temporal continuum formed by a species taxon reproducing itself generation after generation through time*. It can remain single for long periods of time or it can split into two or more lineages (speciate) from time to time. The characteristics of the members of a phyletic lineage can remain the same over periods of time or can change over time (phyletic evolution). Recognition of actual phyletic lineages is of no concern to neonatologists because of the insignificance of the time period that their samples of Recent organisms represent. Yet recognition of phyletic lineages can be of real concern to paleontologists, especially when dealing with excellent fossil records over significant lengths of time. A cross-section of a phyletic lineage at any point in time is a species taxon. Cross-sections of the same phyletic lineage at different points in time are species taxa. But it is a nonquestion to ask whether these cross-sections are the same or different species taxa because no species boundaries can be established between the different cross-sections. They are simply different cross-sections of the same phyletic lineage, the earlier being ancestral to the later.

Species evolve, but phyletic lineages do not; change take place in the members of a lineage through time, but the lineage remains the same. Species and phyletic lineages are closely related concepts, but they are not the same and must be clearly distinguished from one another. Several species concepts, notably the evolutionary and phylogenetic, fail to distinguish between these two ideas. Phylogenetic, evolutionary, and internodal species concepts actually define a phyletic lineage or segments thereof. Many philosophers of science confuse the species and the phyletic lineage. The species concept, with the idea of species boundaries and differences between species, has meaning only in horizontal comparisons between different phyletic lineages at the same point of time, and not through it (Bock, 1967, 1989). Within evolutionary theory, the species concept and hence species boundaries have absolutely no meaning in vertical comparisons — that is between organisms at different times along the same phyletic lineage. Hence all ideas such as the time of origin of a species, species age, transspecific evolution, and evolution beyond the bounds of a species are equally without meaning within evolutionary theory.

6 Discussion

Over the last two decades, some workers have advocated particularly narrow limits to species taxa, many of them still introgressing with neighboring taxa, under the advocacy of the phylogenetic species concept (PSC). It is argued that such species taxa are more useful because they are strictly monophyletic and are more effective for conservation. These claims ignore the real issue: the nature of the resulting species taxa. It must be noted, first, that the phylogenetic species concept does not necessarily require recognition of narrowly delimited species taxa. Moreover, the consequences of applying narrow recognition criteria to delineate species taxa must be considered carefully.

One consequence is that biologists would have to deal with two quite different types of species taxa, one at or close to the final stages of speciation and the other at the very first stages. Combining of these two types of species taxa in general faunal inventories, inevitable in practice for the fore-

seeable future, would render further analyses difficult at best. The second consequence is that biologists would suddenly find themselves members of several different species taxa of humans, that is, if the narrow limits of species taxa advocated by PSC workers are to be applied consistently across organisms. I, for one, firmly reject this approach, and hence also the narrow criteria for avian species taxa argued under the PSC.

The difficulties in recognizing species taxa, especially among populations that replace one another geographically, is well shown by the North American fox sparrow, *Zonotrichia iliaca* (Zink, 1994). The many subspecies of this polytypic taxon can be combined into four major groups: reddish *iliaca*, grey-headed and slate-colored *schistacea*, grey-headed, browner and thick-billed *megarhyncha*, and sooty *unalaschensis*. These taxa are more similar to one another morphologically than are the other species taxa of *Zonotrichia*, and even more similar to one another than some of the accepted geographic races of the song sparrow (*Zonotrichia melodia*). Zink (1994:106) accepts a phylogenetic species concept which he defines as "*minimally diagnosable clusters of individuals, or basal evolutionary groups, which may or may not be reproductively isolated*." On the basis of this species definition, and in spite of hybridization between members of these major subspecies groups of the fox sparrow, Zink concludes that the four major geographic forms of the fox sparrow should be treated as different species. The result is that the allopatric species taxa of the Fox Sparrow recognized by Zink represent very different evolutionary units from other species taxa of *Zonotrichia* and other genera within the Emberizinae.

The disparity created among recognized species taxa by introduction of the PSC to formulate the species category and hence infer species taxa, whatever its value in conservation, would have disastrous consequences for all subsequent biological studies based on surveys of these species taxa, without any significant advantage over taxa based on the BSC.

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