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Studying species definitions for mutual nonexclusiveness

THOMAS MCCABE, M.D. M.P.H.
E-mail: tmccab@gci.net

Abstract

In the absence of a single universally accepted species concept, taxonomists rely on working conventions when defining species. One such convention is based on the intuition that no specimen is in more than one existing species: species are disjoint and their definitions should be mutually exclusive. When two species definitions both describe one and the same specimen, the two definitions are not mutually exclusive and do not conform to this assumption. Uncorrected, such nonexclusive species definitions make taxonomic indistinctness.

Here the author, after exploring the notion of mutual nonexclusiveness, presents simple ways to revise or replace a pair of currently accepted species definitions if they are found to be mutually nonexclusive. The author shows some possible consequences of not doing so in two important areas of biologic research—species diversity studies, and heterospecific hybridization experiments. There is a semiformal discussion of nonexclusiveness in an appendix.

Key words: biological taxonomy, conspecific, heterospecific, hybrid, mutual exclusiveness, mutual nonexclusiveness, species circumscription, species diversity, xenotaxy

Introduction

In the absence of a single universally accepted species concept (Agapow *et al*. 2004), taxonomists often recognize species on the basis of barriers to gene flow under natural conditions, and define each species with a unique combination of characters that signify properties observed in individuals thought to be in that species. Taxonomists rely on working conventions when defining species. One such convention is based on the intuition that no organism is in more than one existing species: species are *disjoint* (Kornet 1993; but see Michener 1963, Jardine & Sibson 1968) and *xenotaxic*, that is, species are

> completely distinct, without any overlapping ... the taxonomic system should be univocal, i.e. any given living being should *unambiguously* be ascribed a single place in the system (Dubois 2005: 406, 372) [author's italics].

The disjoint species conjecture is hardly a species concept and does not touch on the origin of existing species; it merely gives some guidance for the practical work of species definition and specimen identification. It means currently accepted species definitions should be *mutually exclusive*—no two of them should describe one and the same specimen.

Two species definitions do not conform to the disjoint species conjecture when they are mutually *nonexclusive*—when there is at least one specimen they both describe. Without correction, this would make the specimen assignable to both currently recognized species. If there is nonexclusiveness among our currently accepted species definitions, the result is taxonomic indistinctness.

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The desirability of mutual exclusiveness for species definitions is implicit in the work of taxonomists; I want to make it explicit. I first survey relevant aspects of current taxonomic practice and explain in general terms what I mean by mutual exclusiveness. Then I present a practical way to check two currently accepted species definitions for nonexclusiveness, and to revise or replace them if they are found to be mutually nonexclusive. I discuss some potential consequences of uncorrected species definition nonexclusiveness for two important areas of biological research—species diversity studies, and heterospecific hybridization experiments. There is a semiformal discussion of nonexclusiveness in an appendix.

Taxonomic practice

First, a brief look at some pertinent aspects of current taxonomic practice (Winston 1999).

Species definition

Suppose one finds a specimen that one cannot assign to a currently recognized species, so that one suspects it is in a yet to be defined species. Then (ideally after finding confirmatory specimens) one may describe these unidentified specimens with a unique combination of characters signifying some of the properties held by these organisms, and publish this combination as a new species definition with a new Latin binominal title (*Lb*, for short). By doing this one is hypothesizing (Frost & Kluge 1994: 262–265) the existence of a previously unrecognized species, entitled *Lb*; and one is claiming this species definition, d*Lb*, describes every specimen in species *Lb*, while describing no specimen not in *Lb*.

Specimen identification

Identification is the assigning or rejecting of a newly observed specimen to or from an already defined species. If an observed organism *fits*—is described by—the currently accepted definition for a given species, one may assign it to that species. To efficiently identify observed organisms, one may use a diagnostic key distilled from a number of currently accepted species definitions. Univocal, unambiguous, mutually exclusive species definitions make keys workable. If an observed organism is not assignable to any currently defined species, it may be in a previously undefined species and one may use it as a source for a new species definition as discussed above.

Species circumscription

Species circumscription pertains to how accurately a species definition demarcates the membership of an existing species.

A species definition *exactly* circumscribes an existing species if it is inclusive and exclusive—if it describes every organism in that species and describes no organism not in it. In *over*circumscription, a currently accepted species definition describes only some of the specimens in a targeted existing species; it is too narrow. In *under*circumscription, the definition describes some specimens not in the targeted existing species; it is too broad. *Splitting* is a subcategory of overcircumscribing: two species definitions respectively describe organisms in two subgroups that together make up one existing species, incorrectly hypothesizing two species where one exists. On the other hand, *lumping* is a subcategory of undercircumscribing: a single species definition describes specimens in two existing species; it incorrectly hypothesizes one species where two exist. Currently accepted species definitions that split or lump existing species lead respectively to overestimating or underestimating the number of existing species (Dayrat 2005).

We cannot observe every organism to check the circumscription of currently accepted species definitions. This is one reason why practicing taxonomists keep these definitions open to revision.

Traditional taxonomic revision

In taxonomic revision, an experienced taxonomist gathers a revision series—a sample that often includes preserved specimens that served as sources for comparable currently accepted species definitions, as well as additionally acquired relevant specimens. The revising taxonomist makes a fresh judgment of the number of existing species represented in the series and compiles any necessary revised definitions for them.

Eliminating an Instance of Nonexclusiveness

Regarding the mutual exclusiveness of currently accepted species definitions, there seems to be no requirement that they be formal contradictions of one another (see for example Heiser *et al*. 1969; Groves 2001: 289–293). Rather, as long as no observed specimen fits a given pair of currently accepted species definitions, the pair may be said to be *operationally mutually exclusive*.

If one discovers an organism that fits two currently accepted species definitions, one has discovered that the two definitions are mutually nonexclusive. One way to remedy this, without merging the two definitions, would be to find a distinguishing property and use the character signifying that property in replacement definitions, so that no observed organism fits more than one of the replacement definitions.

If experienced taxonomists are unable to find operationally mutually exclusive replacement species definitions to remedy a discovered instance of mutual nonexclusiveness, there remains in all cases a remedy of last resort: merge the two discredited species definitions. This default solution eliminates the nonexclusiveness at the price of hypothesizing one species in place of the two originally hypothesized. The necessity of falling back on this remedy would imply that the original pair of definitions had mistakenly split a single existing species.

Practical Applications

There are at least two areas of biosystematic research where nonexclusiveness of currently accepted species definitions takes on special importance: studies in species diversity, and experiments in heterospecific crossing.

Species diversity studies

Counting currently recognized species is one way to estimate species diversity, and would be affected if the currently accepted definitions of some counted species were mutually nonexclusive. This is especially a risk for closely-drawn definitions. In species diversity studies, it is important rule out species definition nonexclusiveness to avoid possible unintended species splitting, with inflation of the number of currently recognized species (Isaac *et al*. 2004).

Heterospecific crossing experiments

Experimental heterospecific crossing is another research area sensitive to nonexclusive species definitions. By a *heterospecific crossing*, I mean a crossing of two parents, each in a separate species, which yields at least one living offspring. In practice, one may allege that an observed crossing is heterospecific when each parent fits a different currently accepted, operationally mutually exclusive species definition. The allegation of parental heterospecificity gains indirect support when the offspring resulting from the cross are reduced in number or infertile (but see Huskins 1929), or have properties thought to be intermediate to those of the two parents (Hubbs 1955: 4; Olby 1966: 28; but see Rieseberg & Ellstrand 1993). Other things suggesting the occurrence of heterospecific crossing are (Rosen 1979: 277): the finding of hybrid zones beyond which the two species are not eroded, mathematical tests of variability in offspring and putative parents, and inference from cladograms.

However, with each allegation of heterospecific crossing, one faces a conundrum: the allegation conflicts with the assumption that existing species are mutually reproductively isolated. One may allege parental heterospecificity of a crossing with greater certainty if one has studied the parental species definitions for nonexclusiveness and either found none, or eliminated any found.

Imagine two crossing parents assigned to separate currently recognized species because one parent fits one currently accepted species definition and the other parent fits another currently accepted species definition. Suppose one observes these allegedly heterospecific parents to cross and have an offspring, but the offspring fits both currently accepted parental species definitions. This discovery would reveal the definitions to be mutually nonexclusive. If one discovers such an offspring, say an offspring with one part of itself like one parent, another part like the other parent (Wagner 1962: 98), one may be able to remedy the case by using an additional distinguishing character to devise suitable operationally mutually exclusive replacement definitions as discussed. On the other hand, if the only attainable remedy for the discovered instance of mutual nonexclusiveness is to merge the parental species definitions, then one loses a crucial basis for the allegation that the cross was heterospecific.

Taxonomists use heterospecific crossing experiments to analyze aspects of biosystematics (see for example McDade 1984; Wolstenholme *et al*. 2003; Skarzynski 2004), to study reproductive isolation (Dominguez *et al*. 2005), and to suggest how past heterospecific crossing might affect cladistic analysis (McDade 1990). Conclusions based on such experimental studies depend on the correctness of the allegation that the experimentally crossed parents are indeed heterospecific. The allegation is supported when the relevant parental species definitions are studied for mutual nonexclusiveness, especially with respect to intermediate offspring (Rieseberg 1991: 1233), and none is found. The allegation of parental heterospecificity is not supported if one discovers an instance of nonexclusiveness which can be eliminated only with the default remedy of merging the parental species definitions. If the parental species definitions are not tested for nonexclusiveness, the allegation of parental heterospecificity, and conclusions based on that allegation, are not secure.

Conclusion

To honor the intuition that existing species are disjoint, it is desirable to study species definitions for nonexclusiveness and to eliminate any nonexclusiveness that is discovered. Testing is especially important in species diversity estimates and in heterospecific crossing experiments, where far-reaching conclusions are sometimes based on closely drawn species definitions.

Appendix: Semi-Formal Discussion

The following is a tentative semi-formal analysis of exclusiveness and nonexclusiveness of species definitions.

A.1 Character-Combination

A *signifying biological character* is a word, phrase, image, formula, measurement, and so forth, that signifies a *property*—a structure, function, event, substance, dimension, or other feature (Mahner & Bunge 1997: 9–10) observable in an organism or organisms. For example, the phrase

pectoral fin

is a signifying biological character; it signifies a biological property.

One may use a combination of signifying characters and Boolean logic operators to signify any combination of properties. For example,

pectoral fin AND NOT pelvic fin

signifies a combination of properties in an organism or organisms. Such a character-combination may include temporal terms (Quine 1982: 96, 195–196, 269) signifying developmental properties.

One may describe a sample of organisms with a single character-combination, even when some sample members are variants with respect to characters in the combination. This is possible using the inclusive Boolean OR operator. For example, imagine a sample of fish in which some organisms have thin scales while others have none. The single complex character-combination

scales thin OR scales absent

would describe every organism in this sample with respect to their scales.

One can do more with the character-combination format. One may use the format to represent any currently accepted species definition. Here is an example. The definition for species *Ptilichthys goodei* Bean (Ptilichthyidae), given in Mecklenburg et al (2002: 34–38, 785), may be translated as the following complex character-combination:

> Provenance North Pacific Ocean and Bering Sea AND depth from surface to about 360 m AND single gill opening each side AND NOT bony plates on body AND one eye on each side AND one unnotched dorsal fin of 81–90 isolated anterior spines and 137–157 soft posterior rays AND anal fin more than 25% of standard length AND 185–196 anal fin rays AND 13 pectoral fin rays AND NOT pectoral rays partly free AND NOT pelvic fin AND 3 branchiostegals each side AND 8 gill rakers each side AND 227–240 vertebrae AND color yellow to greenish, with throat region orange AND body elongate with longitudinal streak AND head with dark streaks AND head length 4-7% of standard length AND mouth oblique AND lower jaw projecting with fleshy appendage at tip AND maxilla barely reaching to below eye AND dorsal and anal fins confluent with reduced caudal fin AND caudal fin tapers to a filament AND (scales scattered, very thin OR scales absent) AND gill membranes broadly united, free of isthmus AND standard length to 390 mm.

The character-combination format is generally applicable to species definitions and I will use it in this semiformal discussion. The format works for defining those *polythetic* species in which each organism is hypothesized to have many (but not necessarily all) of a list of properties, so no one character may be said to be diagnostic, or essential, for the species (Sneath & Sokal 1973: 21–22, Van Regenmortel 1997:1–22). Imagine for example, a polythetic species in which every organism is positive for a majority of three signifying characters, *A*, *B*, and *C*, yet no one of these characters is positive in every organism. Nevertheless, one complex character-combination can be found (Beckner 1959: 24, Mellor 1977: 306) that will describe this imagined polythetic species:

(A AND B) OR (A AND C) OR (B AND C).

Each organism in the species will fit this character-combination, since each is imagined to have at least two of the three properties signified by *A*, *B*, and *C*. Even with no one diagnostic property held by every organism in the species, the single character-combination—as a whole—could serve to define this imagined species, if no organism outside this species has more than one of the three properties.

A.2 Circumscription

An existing species is a lineage segment in which each member does or does not fit one or more currently accepted species definitions. On the other hand, each currently accepted species definition is a hypothesis that a targeted species exists, and that all organisms in that species fit the definition. The definition defines a class—the class of all organisms for which the definition is true. One may think of the class defined by a currently accepted species definition as a stand-in for the incompletely ascertainable targeted existing species. The defining taxonomist aims to make the defined class coextensive with the membership of the targeted existing species, exactly circumscribing it. If the class defined by a currently accepted species definition is more extensive than the existing species it targets, it undercircumscribes the species; if it is less extensive than the targeted species, it overcircumscribes it, as illustrated in figure 1.

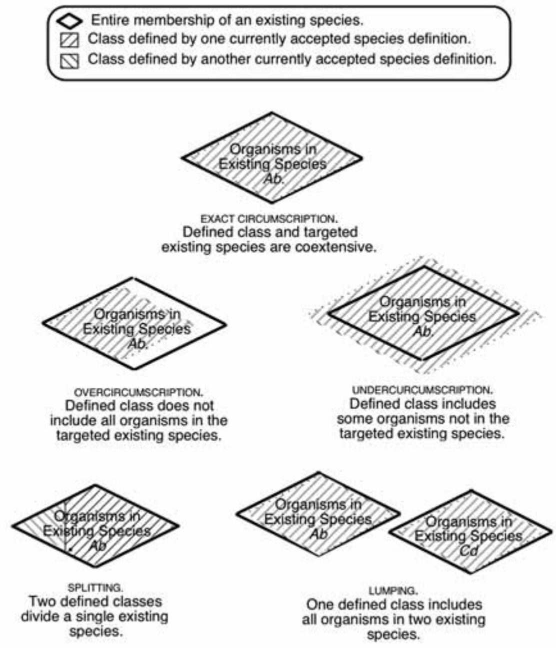

FIGURE 1. Some kinds of species circumscription

A.3 The Problem of Nonexclusiveness

Two character-combinations are mutually exclusive if there is no organism that *fits*—is described by—them both. For example, no single organism can fit the two contradictory descriptions

maximum weight is over 20 grams

versus

NOT maximum weight is over 20 grams.

When two character-combinations are not mutual negations, they may not be mutually exclusive. For example, the two descriptions

color is yellow

and

color is green.

are distinctive (provided colors are clearly defined, Aguiar 2005); but the discovery of a yellow-headed, green-tailed bird fitting both would be an instance revealing them to be mutually nonexclusive.

It may be that one cannot formally assure the mutual exclusiveness of currently accepted species definitions; but one may always remedy a particular discovered instance of mutual nonexclusiveness.

A.4 Some Remedial Methods

Imagine a pair of currently accepted species definitions:

$$\mathrm{d}_1Ab = \mathrm{A}\ \textsc{and}\ (\mathrm{B}\ \textsc{or}\ \mathrm{C})$$

and

$$\mathrm{d}_1Cd = \mathrm{J}\ \textsc{or}\ \mathrm{K}.$$

Characters *A*, *B*, *C*, *J*, and *K* must be unambiguous, as required for all species definitions. Species definition d_1Ab is a hypothesis that every organism in species *Ab* fits d_1Ab, and no organism not in *Ab* fits d_1Ab. Species definition d_1Cd is a hypothesis that every organism in an species *Cd* fits d_1Cd, and no organism not in *Cd* fits d_1Cd. Imagine that so far, no one has found an instance of mutual nonexclusiveness of these two definitions; that is, no observed specimen fits d_1Ab as well as d_1Cd. The two definitions are thus far operationally mutually exclusive.

Suppose now one discovers an organism that fits both species definitions, say an organism having the combination of properties signified by *A AND B AND J*. This finding would reveal d_1Ab and d_1Cd to be mutually nonexclusive.

A.4.1 Remedies that retain the hypothesis that species *Ab* and *Cd* exist

One remedial method depends on finding a common property in each organism thus far assigned to species *Ab* that is not found in any organism thus far assigned to species *Cd*. If one can find such a property, signify it with the character *U*. Then adding *AND U* to the original definition of species *Ab* while adding *AND NOT U* to the original definition of species *Cd* yields replacement definitions

$$\mathrm{d}_2Ab = \mathrm{A}\ \textsc{and}\ (\mathrm{B}\ \textsc{or}\ \mathrm{C})\ \textsc{and}\ \mathrm{U}$$

and

$$\mathrm{d}_2Cd = (\mathrm{J}\ \textsc{or}\ \mathrm{K})\ \textsc{and not}\ \mathrm{U}.$$

These replacements would eliminate the observed instance of nonexclusiveness; the problem organism either has, at some time, the property signified by *U*, or never has it. The organism can fit no more than one of these replacements. In addition, all organisms previously assigned to species *Ab* would fit d_2Ab and not fit d_2Cd, and vice versa for all organisms previously assigned to species *Cd*. Those organisms too would not fit both new definitions.

Another way to preserve the hypothesis of two species would be available if one finds a property of the problem organism that is found at no time in any organism previously assigned either to species *Ab* or to species *Cd*. Signify this property with *Q*. Then one could propose replacements

$$\mathrm{d}_3Ab = \mathrm{A}\ \textsc{and}\ (\mathrm{B}\ \textsc{or}\ \mathrm{C})\ \textsc{and not}\ \mathrm{Q}$$

and

$$\mathrm{d}_3Cd = (\mathrm{J}\ \textsc{or}\ \mathrm{K})\ \textsc{and not}\ \mathrm{Q}.$$

Replacement definitions d_3Ab and d_3Cd would eliminate the observed instance of nonexclusiveness because the problem organism, having the property signified by *Q*, would fit neither definition; it may be in a third existing species. All organisms previously assigned to species *Ab* would fit d_3Ab and not fit d_3Cd, and vice versa for all organisms previously assigned to species *Cd*.

There may be other remedies that would maintain the hypothesis that the two species, *Ab* and *Cd*, both exist.

A.4.2 Default remedy

If one can find no operationally mutually exclusive replacement definitions, it is always possible to eliminate the discovered instance of nonexclusiveness by dropping the original hypothesis of two separate species and merging the two original definitions, d_1Ab and d_1Cd, into a single replacement definition using an OR operator between them. In the imagined example, combining d_1Ab and d_1Cd in this way would give the single merged species definition,

{A AND (B OR C)} OR (J OR K).

The problem organism, having the combination of properties signified by *A AND B AND J*, fits this single replacement definition, as do all organisms that previously fit either d_1Ab or d_1Cd. Presumably, d_1Ab and d_1Cd were splitting what should be hypothesized as a single existing species.

A tacit requirement for any of these imaginary replacement species definitions is that they be kept operationally mutually exclusive with respect to all other currently accepted species definitions.

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