THE SPECIES CONCEPT AS AN EMERGENT PROPERTY OF POPULATION BIOLOGY

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Resurgent interest in the genetics of population divergence and speciation coincides with recent critical evaluation of species concepts and proposals for species delimitation. An important result of these parallel trends is a slight but important conceptual shift in focus away from species diagnoses based on prior species concepts or definitions, and toward analyses of the processes acting on lineages of metapopulations that eventually lead to differences recognizable as species taxa. An advantage of this approach is that it identifies quantitative metapopulation differences in continuous variables, rather than discrete entities that do or do not conform to a prior species concept, and species taxa are recognized as an emergent property of population-level processes. The tension between species concepts and diagnosis versus emergent recognition of species taxa is at least as old as Darwin, and is unlikely to be resolved soon in favor of either view, because the products of both approaches (discrete utilitarian taxon names for species, process-based understanding of the origins of differentiated metapopulations) continue to have important applications.

KEY WORDS: unified species concept, metapopulation lineage, speciation, species delimitation

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Starting with the advent of allozyme electrophoresis in the 1960s, and accelerating with the PCR revolution of the 1990s, several generations of population geneticists and phylogeneticists have joined with morphologists, physiologists, and behavioral ecologists in asking “What are species?” and “How can we discriminate them from each other?” The species category in classifications seems to capture an important level of biological organization, and species taxon names are extraordinarily useful in many different applications as proxy labels for strongly similar groups of organisms that differ from other groups. Perhaps as a result of the utility of the species idea and of species names, the multiplication of various species concepts and of methods for species delimitation has attracted considerable attention and generated considerable debate in successive generations of population geneticists and other evolutionary biologists (Hey 2006).

Much of the heat (rather than light) generated by debates over species concepts may have originated in a perceptual problem: de Queiroz (2007) observed that “because species exist at a higher level of organization than the humans observing them [it is] more or less impossible for humans to perceive entire species simply by looking at them, as they do for cells and organisms, which is why biologists have symposia devoted to the topic of species delimitation.” Thus, different perspectives on that higher-level organization focus on different features of its complexity and lead to different emphases on, for example, reproductive isolation, monophyly, mate recognition, or morphological distinctiveness as criteria for distinguishing species from each other. It seems useful if maybe obvious to add that organisms that do not attend symposia also have the same blinkered view of the biological world, which consists of other unicellular or multicellular organisms (not species or other hierarchical groups), some more and others less similar to the viewer, and all potential mates, competitors, or sources of other types of local interactions among individuals that lead to population-level dynamics over time.
Recognizing the primary importance of individual organisms (rather than species) in this mechanistic sense is crucial to an alternative point of view that has often not been heard clearly above the din associated with debates over different species concepts and definitions. From this interesting contrarian point of view, species are artificial taxonomic constructs that we should consider abandoning or at least de-emphasizing because – however useful as proxies or interesting as patterns – they are spandrels (Gould and Lewontin 1979): the recognizable but indirect consequence of processes that act on variety among individual cells or multicellular organisms to produce diversity among populations. Hendry et al. (2000) articulated several important parts of this view for an earlier generation of conservation geneticists, which includes the ideas that:

- Individuals are the crucible in which cooperative or antagonistic interactions among different replicators and different features of the phenotype are integrated through epigenetic and developmental mechanisms and then exposed to selection or other processes as a unitary whole;

- As a result of differences in that integration, individuals are reproductively, phenotypically, and genetically divergent from each other along several (perhaps many) continuous axes of variation;

- The frequency distribution of values for those continuously distributed traits is non-uniform (some combinations of values are common, others have low or zero frequencies);

- Species can (but do not need to) be recognized as sets of populations that are evolving together near the same dynamic mode in this multidimensional landscape of individual variety; and

- The nature and magnitude of the quantitative differences among these dynamic modes will differ among groups of species depending on the stage of the
divergence process (de Queiroz 2007) and the nature of the organisms (e.g., sexual organisms might differ quantitatively in their intrinsic reproductive compatibility or mate recognition, whereas this is not usually a relevant axis of variation for asexual organisms).

More recent developments in this area emphasize these population processes that produce diversity, with less emphasis on either conceptual models of the products or the diagnostic methods for distinguishing the products from each other. Some important landmarks (among many) in this gradual change in emphasis include the modest proposal by Hendry et al. (2000) noted above; the comprehensive book by Coyne & Orr (2004) entitled ‘Speciation’ (notably not entitled ‘Species Concepts’ or ‘Species Delimitation’); Hey’s (2006) lesson on the gradual transition away from species concepts based on single criteria; the synthesis by de Queiroz (2007) of ‘Species concepts and species delimitation’ into a unified concept of species as metapopulation lineages (and their associated demographic characteristics and processes); and the review of ‘The biology of speciation’ by Sobel et al. (2010) that describes a research program for understanding the relative importance of various population-level processes in different parts of the tree of life, at different times, and under different ecological or biogeographical circumstances. Recent issues of this journal include numerous studies of the genetics of speciation, including one entitled ‘The genetics of incipient speciation’ (Etges et al. 2010), that together reflect a resurgent interest in the population genetics of phenotypic diversity without an emphasis either on predefined species concepts or unimodal methods of species delimitation. In general, these treatments of the problem emphasize processes (including genetic drift, natural selection, sexual selection, hybridization, polyploidy, vicariance, extirpation, colonization) that act at the level of individuals and populations and have the effect of producing more or (sometimes maddeningly) less easily identifiable discontinuities in phenotypic and genotypic
frequency distributions that can be labeled species and for which those convenient species names have many important uses.

If discretely diagnosed species are not the most important unit of organismal biology and evolution, then “what traits should be used to identify and quantify continuous variation [within and] among groups?” (Hendry et al. 2000). De Queiroz (2007) identified several operational criteria that correspond to competing species concepts (which will be easily recognizable to readers of this journal), and that he considered as lines of evidence for differentiation among members of a metapopulation lineage (and candidate species). The properties include intrinsic reproductive isolation, shared specific mate recognition (including fertilization) mechanisms, ecological niche or adaptive zone, exclusive coalescence of alleles, phenotypic clustering, and genotypic clustering. Focusing on these six operational criteria for recognizable clusters of biological diversity in a metapopulation helps to return the focus of classifications onto the population processes acting on variation in that 6-dimensional (or larger) space. De Queiroz (2007) noted that the process of diversification (whether or not it leads to speciation) may be more interesting along different axes of variation in different groups or for answering different kinds of questions about the origins of variety among individuals and diversity among populations. Applying this approach, and finding the major axes of variation that account for biological diversity in a particular application, corresponds to what has come to be known as integrative taxonomy (e.g., Birky et al. 2010, bdelloid rotifers and other asexual organisms; Carstens & Dewey 2010, bats; Ezard et al. 2010, foraminiferans; Glaw et al. 2010, treefrogs; Tobias et al. 2010, birds). The key improvement in this overall approach is that, rather than starting from a static definition of species and searching for those entities that fulfill the criterion (or scorning those taxa that fail to do so), de Queiroz’ unified concept of the species as a lineage of
metapopulations shifts the focus of study to population-level variation and processes, with quantitatively differentiated species taxa as an emergent property of the whole.

In addition to estimation of differentiated modes in that multidimensional population space (which might be species taxa), such an approach also characterizes the areas of low- or zero-frequency values between those modes. These regions of the multidimensional frequency distribution correspond to combinations of genetic, morphological, reproductive, and behavioral traits that are not observed among (and may have been vacated by, or cannot be expressed by) organisms that form part of nearby modes in the frequency distribution. Conceptually these regions are related to the idea of unoccupied niches in ecology (Hutchinson 1957; Walker and Valentine 1984; Wilson and Turelli 1986). Graphically these troughs or valleys correspond to the unlabeled white space between the named tips of terminal branches in two-dimensional drawings of species phylogenies. Systematics does not seem to have a general term for these antonyms of species.

The ongoing tension between species delimitation based on prior species concepts versus multidimensional analyses of biological variety based on population processes is not new. Darwin himself struggled with this tension between identifying and naming distinctive modes in the multidimensional frequency distribution of biological forms (taxonomic species) versus grappling with the sources and fate of the variety among individuals around each of those modes, because in his view no obviously different mechanism or process distinguished the sources of these two types of variation (see Ereshefsky 2010). Darwin devoted a full eight years of his professional life to honing his taxonomic skills in “discovering, describing, naming, and identifying species and other taxa” of barnacles (Valdecasas et al. 2008). The fruits of that labor were arguably his most significant empirical research: monographic treatments of all fossil and living barnacle species that are authoritative and still frequently cited. He is thought to
have taken on this project mainly to test his ideas about developmental homology as a basis for classification, and also to develop his own Victorian street cred as a taxonomic expert, which he is thought to have considered a necessary qualification for a naturalist about to publish a book on the mechanistic origins of such species diversity (Stott 2003; Richmond 2007). With his taxonomic expertise and credibility established, Darwin’s subsequent empirical work was largely devoted to documenting and understanding variety among individuals as the raw material on which natural selection (or other population processes) might act to produce species diversity, but both areas of expertise were considered important to his intellectual success.

In our own time, advocates (e.g., Padial & de la Riva 2010) for a process-based understanding of biodiversity at the level of populations (possibly at the expense of a focus on species concepts, definitions, and delimitation) have not yet won over the descendants of Mayr (1942) or Hennig (1966) for whom reproductive isolation or monophyly are necessary species criteria. The parallel continuation of these different ways of knowing biological diversity is perhaps a necessary if contentious feature of 21st century evolutionary biology. Species names and classifications based on them are not very likely to be abandoned, however logical it might seem to do so (Hendry et al. 2000), if only because they are critically important for effective communication of knowledge among biologists themselves, and for communicating clear advice and understanding to policy makers and other citizens. At the same time, our understanding of the messy, continuous, and multidimensional (rather than crisp and discrete) nature of individual variety within populations and the diversity among them has simultaneously improved our understanding of the origins of those species.
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LITERATURE CITED


Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the


450.

415-427.

York.


Smith, J. Browne, S. Pocock, M. L. Richmond, and A. Secord, eds. The
correspondence of Charles Darwin, vol. 4. Cambridge University Press,
Cambridge.


Valdecasas, A. G., D. Williams, and Q. D. Wheeler. 2008. ‘Integrative taxonomy’ then

Wilson, D. S., and M. Turelli. 1986. Stable underdominance and the evolutionary