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## Philosophically speaking, how many species concepts are there?

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It's an old question in biology: *what is a species*? Many different answers have been given over the years, and there are indefinitely many "definitions" in the literature. Adding to R. L. Mayden's list of 22 definitions (Mayden, 1997), I counted 26 in play since the Modern Synthesis (2009a), and a new one, which I call the "polyphasic" concept (basically a consilience of many lines of morphological, ecological, genetic, and physiological evidence), has been implicitly extended from bacterial and other microbial contexts to macrobial species, although the terminology has not yet been transplanted (Colwell, 1970; Vandamme *et al.*, 1996). However, on another count there are seven "basic" species concepts: *agamospecies* (asexuals), *biospecies* (reproductively isolated sexual species), *ecospecies* (ecological niche occupiers), *evolutionary species* (evolving lineages), *genetic species* (common gene pool), morphospecies (species defined by their form, or phenotypes), and *taxonomic species* (whatever a taxonomist calls a species).

Notice that some of these seven basic concepts are not concepts of what species are, that is, what makes them species, but instead are concepts based on how we *identify* species: by morphology, or the practices of taxonomists. Others are roughly equivalent. A gene pool is defined as a population of genomes that can be exchanged, and so a genetic species is basically a reproductive species. Evolutionary species are not what species are so much as what happens when some processes (such as ecological adaptation or reproductive isolation) make them species that persist over a long time. One common "concept" of species, the so-called phylogenetic species concept, is likewise a mix either of morphospecies, biospecies or evospecies or all of them (Wilkins, 2009b). The polyphasic concept is also based upon a method for identifying species through many kinds of evidence. Agamospecies are species that *lack* some property: sex. An agamospecies is a not-biospecies species (although some, like G. G. Simpson and Ernst Mayr, simply denied they were species, which is a problem given that sex is a relatively rare property in the universal tree of life; it means most biological taxa do not come in species). So what makes an agamospecies a species? It can't be reproductive isolation, for obvious reasons, so it must be the only thing that we have left on the list: ecological niche adaptation (Wilkins, 2007). It could be chance, but if grouping happens by chance it is unlikely to be maintained by chance. In the absence of sex, therefore, we need ecological niche adaptation to keep the cluster from just randomly evaporating. Of course, few if any species are purely asexual in the sense that they don't ever exchange genes; microbes have several mechanisms to do this even if they lack genders or mating types and fail to reproduce by any other means than division. Some genetic material can be exchanged through viral insertion, through DNA reuptake in the medium after a cell has lysed, or by deliberate insertion of small rings of DNA, plasmids, through pili. "Horizontal" or "lateral" genetic transfer is probably as old as life itself. While this might introduce some genetic variation into a population, it is selection for a local fitness peak that makes the asexual genome not stray too far from the "wild type".

As sex becomes more frequent, rising from near zero recombination per generation up to the maximum of 50% exchanged for obligately sexual organisms, another factor comes into play. Increasingly, the compatibility of genomes, reproductive processes at the cellular, organ, and physiological level become important. In organisms with behavioral signaling (that is, with nervous systems and sensory organs), reproductive behaviours like calls and movements become important. Sex acts to ensure that the organisms that can interbreed tend to be those whose genome and anatomy are consistent enough. I call this "reproductive reach" (2003; 2007): the more closely two organisms are related, the more likely they are within each other's reach as potential mates, and so the species is maintained by reproductive compatibility, and of course *some* ecological adaptation. This is very similar to a definition of "species" by the geneticist Alan Templeton (1989), who said that species were "the most inclusive population of individuals having the potential for genetic and/or demographic exchangeability." [My emphasis.] "Genetic" exchangeability here means the ability to act in the same manner in reproduction – any two members of the species are (more or less) interchangeable. "Demographic" exchangeability means that any two members of the species behave the